BEHAVIOR OF THE GREATER SANDHILL CRANE

BY

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DEDICATION

I dedicate this paper to my brother, Karl. He was an integral part of the family in which we five siblings developed, in various ways, our interest, concern and respect for living things. His life style reflected his deeply held environmental and ecological convictions in ways which will not soon be forgotten.

ABSTRACT

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I studied captive and wild greater sandhill cranes (Grus canadensis tabida) from the summer of 1973 through the fall of 1974. I observed captive cranes from hatching to one year of age, and wild cranes on nesting territories before and after hatching of young, and in spring and fall flocks. Written observations, motion pictures, and tape recordings of vocalizations were used to document many of their behavior patterns, including maintenance activities, displays (including threat displays and dancing) and vocalizations. I observed captive cranes periodically throughout their first year, and made second-by-second records of their behavior to document changes in their daily activity patterns. I recorded preening, sleeping, drinking, feeding, foraging and resting positions, and determined the percent of time spent in each of these activities, the frequency of bouts and the average length of bouts of these activities for 17 different age intervals. The occurrence of these activities seemed to be affected by various factors, including age, growth of feathers, temperature and weather conditions. In general, bouts of these activities tended to become longer and less frequent with increasing age. I also made observations of captive cranes to document the development of displays and vocalizations.

ACKNOWLEDGEMENTS

I wish to thank Dr. E. Beals, my major professor, for his help and advice in preparation of this thesis, and throughout my graduate school career.

Dr. C. Kepler, Dr. J. Baylis, C. B. Brown and V. Maiorana provided many helpful suggestions and criticisms during the preparation of this thesis.

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Department of Natural Resources personnel at Sandhill Wildlife Demonstration Area and Necedah National Wildlife Refuge, especially J. Updyke, helped me locate wild cranes and allowed me to observe them within the refuges.

Mr. M. Wilcox permitted me to build a blind on his farm to observe cranes at the French Creek Wildlife Area.

Finally, I owe a tremendous debt of gratitude to Dr. George Archibald, Director of the International Crane Foundation. He introduced me to the cranes in 1972, and has been a continual source of help, encouragement and information ever since. Through him, the facilities of the International Crane Foundation have been available to me for the conduction of all my observations on captive cranes.

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I. INTRODUCTION

Much emphasis has been placed on the study of the sandhill crane (Grus canadensis) in the last ten to 15 years. Although many researchers, in the course of studying other aspects of crane biology, have commented upon behavior, there has as yet been no detailed behavioral study. It is the intent of this study to provide a detailed ethogram of Grus canadensis tabida in Wisconsin, as well as information on some aspects of physical and behavioral development.

The sandhill crane has the distinction of being the oldest living bird species, with a fossil record dating back four to nine million years (Walkinshaw, 1973a). The strange calls of this long-necked, long-legged bird echo over a misty marsh as they must have echoed millions of years ago, and in doing so, have stirred the minds and aroused the curiosity of many, including Aldo Leopold, who wrote in Sand County Almanac (1949:96):

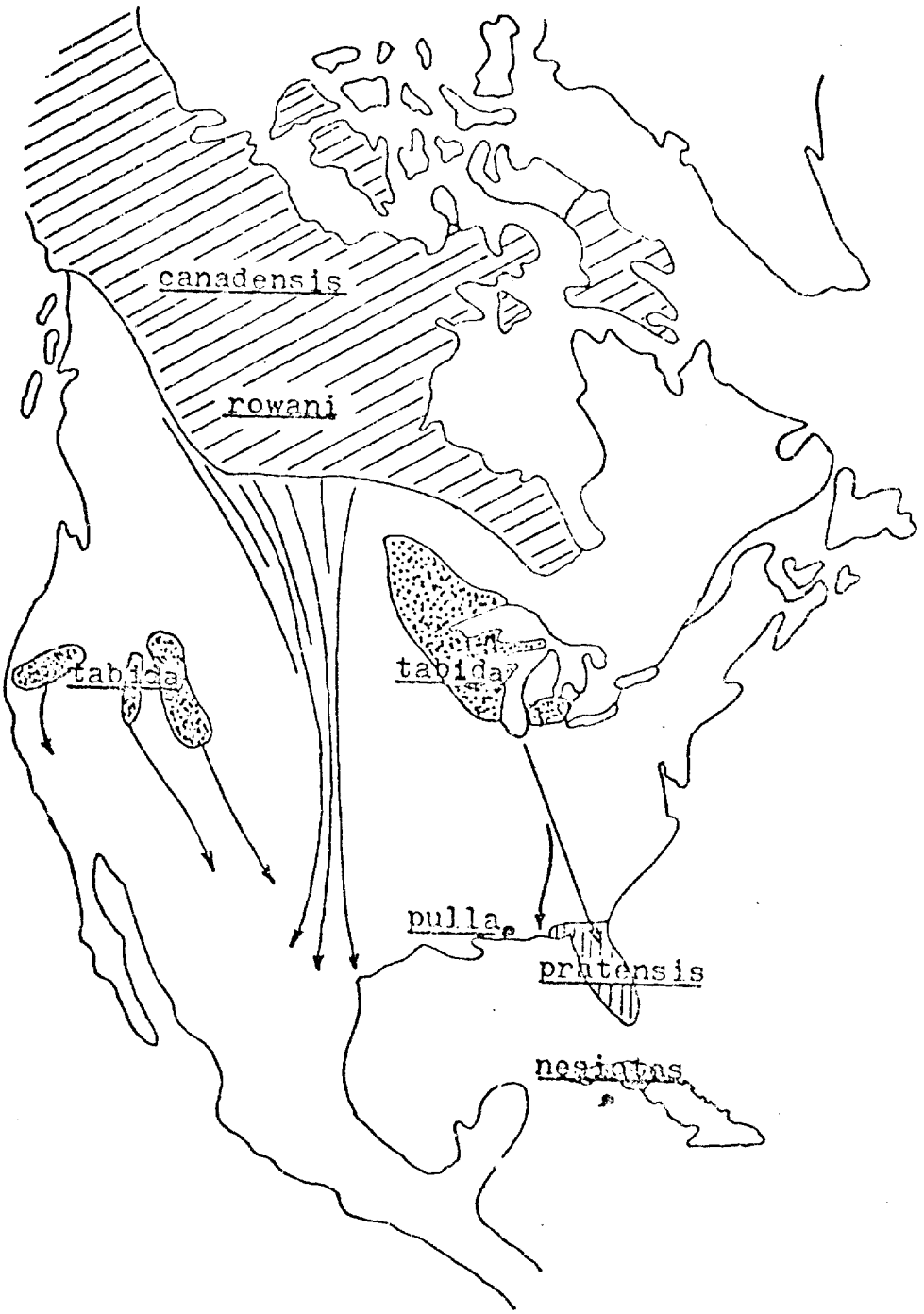
> Out of some far recess of the sky a tinkling of little bells falls soft upon the listening land. Then again silence. Now comes a baying of some sweet-throated hound, soon the clamor of a responding pack. Then a far clear blast of hunting horns, out of the sky into the fog.
>
> High horns, low horns, silence, and finally a pandemonium of trumpets, rattles, croaks, and cries that almost shakes the bog with its nearness, but without yet disclosing whence it comes. At last a glint of sun reveals the approach of a great echelon of birds. On motionless wing they emerge from the lifting mists, sweep a final arc of sky, and settle in clangorous descending spirals to their feeding grounds. A new day has begun on the crane marsh.

The Subspecies of Grus canadensis

Six subspecies of the sandhill crane are recognized (Walkinshaw 1973a). Figure 1 shows approximate migration routes, nesting, and wintering areas of these subspecies. Three are nonmigratory. The

Figure 1

Distribution and migration routes of subspecies of the sandhill crane in North America (from Gluesing, 1974).


canadensis
rowani
tabida
tabida
pulla
pratensis
nesiotes

Florida sandhill crane (G. c. pratensis) is found in Florida and southern Georgia (Walkinshaw 1973a), and its population is estimated to be about 5,000 (Lewis et al. 1975). The Mississippi sandhill crane (G. c. pulla) is found only in Jackson county, Mississippi, and the entire population consists of only 38 to 40 birds (Valentine and Noble 1972). The Cuban sandhill crane (G. c. nesiotes) is found in western Cuba and the Isle of Pines, and is estimated to have a population of about 200 birds (Walkinshaw 1953).

The remaining three subspecies are migratory. The lesser sandhill crane (G. c. canadensis) nests in Siberia, Alaska and Canada. The Canadian sandhill (G. c. rowanii) nests in central Canada. Both of these subspecies winter in the southwestern United States and Mexico (Lewis et al. 1975). Because these two subspecies are impossible to to distinguish in the field, and because of the overlap in their ranges, the population size of each is unknown. Lewis et al. (1975) estimated their minimum combined population to be between 220,000 and 290,000.

The greater sandhill crane (G. c. tabida) occurs in four separate populations, totaling 22,600 to 26,650 (Lewis et al. 1975). The Rocky Mountain population nests from northwestern Colorado and northeastern Utah northward through eastern Idaho, western Wyoming and southwestern Montana, and winters in the middle and lower Rio Grande Valley of New Mexico. The Colorado River Valley population nests in northeastern Nevada and central Idaho and winters in the Imperial and Colorado River Valleys of Arizona. The Central Valley population nests in southeastern Oregon and northeastern California, and winters in the Central Valley of California. The Eastern population nests in central Manitoba, possibly southwestern Ontario, Minnesota, Michigan and Wisconsin, and winters in

Alabama, Georgia and Florida (Lewis et al. 1975). L. H. Walkinshaw (in Lewis et al. 1975) estimates 8,000-10,000 migrate southeastward from the Lake States, while L. Williams (in Lewis et al. 1975) estimates 6,250 greater sandhill cranes winter in Florida. Hence the eastern population probably includes between 6,000 and 10,000 individuals.

History of Cranes in Wisconsin

One of the earliest records of sandhill cranes in Wisconsin dates back to 1804, when a fur trader reported killing a crane in northwest Wisconsin (Hunt 1975). Sandhill cranes were apparently abundant in Wisconsin until about the mid-1800's. Hoy (1885, in Hunt 1975) reported "Sandhill cranes were so common that one could not go any considerable distance on the praries without seeing numbers of these stately birds" (about 1846). At that time there were an estimated three million acres of prairies interspersed with about ten million acres of wetlands (Hunt 1975). There were numerous reports of migrant whooping cranes (Grus americana) in Wisconsin in the early 1800's. Several authors report egg collection or nests in Wisconsin (Carr 1890 and Main 1943 in Hunt 1975), however there is evidence that early residents may have confused the whooping crane with the sandhill crane, and neither eggs nor specimens of whooping cranes taken in Wisconsin have been found. The last sighting of a whooping crane in Wisconsin was made by W. Snyder in April, 1900, at Horicon Marsh (Hunt 1975).

In the late 1800's and early 1900's, there was apparently a great decline in the numbers of sandhill cranes in Wisconsin. This decline has been attributed to hunting, human settlement and marsh drainage (Walkinshaw 1949, Hunt 1975). In 1929 Aldo Leopold reported only five breeding pairs (Hunt 1975). Benika (1936) reported about 25 breeding

pairs. Walkinshaw (1949) estimated the Wisconsin population to be 25 to 50 breeding pairs, and noted that the population had been increasing during the past 10 to 15 years. A 1967 survey of Wisconsin Department of Natural Resources personnel (unpublished, 3 pp.) showed 63 to 128 breeding pairs (Gregg, 1970). In 1973, 250 pairs and 87 young were located in Wisconsin. Gluesing (1974) estimated a total of about 780 adult summer residents. The increase in Wisconsin crane populations has been attributed to abandonment of many early farms in the 1930's and 1940's due to crop failures, drought, and the depression, and to the acquisition of many state wildlife areas, and the restoration of wetland habitat (Gluesing 1974 and Hunt 1975).

Life History of Grus canadensis

Walkinshaw (1949, 1960) suspected that the eastern population of greater sandhill cranes wintered in Florida, because of many observations of large flocks of cranes flying northwest from Florida in early March. Proof came in 1969 when birds banded in Florida appeared on marshes in Michigan and Wisconsin (Walkinshaw, 1973a). Greater sandhill cranes leave Florida during late February and early March, apparently stopping only at Jasper-Pulaski Game Preserve in northern Indiana before arriving at their nesting grounds (Walkinshaw 1960).

Territories. Territories varying in size from 3 to 450 acres are established on marshes of 10 to more than 3,000 acres (Littlefield and Ryder 1968, Walkinshaw 1973, Gluesing 1974). The greatest numbers of cranes nest in central Wisconsin, in Marquette, Green Lake, Columbia, Juneau, Adams, Wood and Portage counties. Cranes nest in river marshes, lake marshes, flooded meadows, sedge marshes, cattail marshes, cranberry reservoirs and bogs. Smaller numbers of cranes are also found in

surrounding counties and in Jefferson county in southeast Wisconsin and Burnett county in northwest Wisconsin (Gluesing 1974). Territories are established very shortly after arrival and are maintained until approximately early August, when the young have fledged and families move to other feeding grounds. Territories must include drinking water, suitable nesting habitat, a food supply and a roosting site (Littlefield and Ryder 1968, Walkinshaw 1973a, 1973b). During the nesting season cranes apparently spend most of their time on their territories, feeding largely on wild plant and animal material (Walkinshaw 1949). The feeding area is usually close to the nesting area (1 km or less away) although sometimes, particularly where crane densities are high and territories are small, territories may be over 3 km away. Even these distant feeding areas seem to be defended by pairs (Walkinshaw 1965a, 1973).

Consistent behavior of pairs on territories and consistent size and coloration of eggs for many consecutive years provide evidence that pairs return to the same nesting territories year after year (Walkinshaw 1950).

Nests. Nest construction may take two days or continue intermittently for two weeks (Walkinshaw 1973a). Both male and female participate in nest building (Walkinshaw 1973b). Nests are generally located in or close to shallow water on the periphery of the marsh and are constructed of the predominant surrounding vegetation (Walkinshaw 1949, 1973b, Littlefield and Ryder 1968, Drewien 1973, Gluesing 1974). They may vary considerably in size and shape. Walkinshaw (1949:81) measured 39 Michigan nests and found the diameters of nests at the base to vary from 42 x 45 cm to 140 x 170 cm and 205 x 93 cm (average, 94 x 82 cm). The average height above water level was 14 cm (extremes, 3 to 31 cm). Surrounding water averaged 17 cm but varied from 0 to 70 cm in depth.

Eggs are laid in early to late April, about a month after arrival. They may be laid much sooner under favorable weather conditions, or much later during a cold spring (Walkinshaw 1950). The normal clutch is two eggs, although this varies from one (occasional) to three (rare) (Walkinshaw 1965b, Drewien 1973, Gluesing 1974).

Incubation. Incubation begins after laying the first egg, and continues for 28 to 32 days (Walkinshaw 1973a, 1973b). Both male and female participate. Walkinshaw (1965a) reports that of approximately 280 hours of daytime observation, eggs were incubated 97.6 percent of the time. Occasionally nests are unattended during the warm part of the day. Littlefield and Ryder (1968) report that in one area where six territories came closely together, males spent a great deal of time displaying near their territorial boundaries. The females were frequently left unrelieved on the nests for long periods of time and had to abandon the nests to feed. These nests suffered heavy predation losses by ravens while the nests were unattended.

Hatching to Fledging. After hatching, chicks remain in the nest 24 to 48 hours, where they are brooded by the parents. They are able swimmers, and often have to swim when leaving the nest (Walkinshaw 1949, 1973). Chicks first eat 24 to 48 hours after hatching, and may be fed bits of their own egg shells by the parent (Walkinshaw 1949, 1973b). They receive almost all their food from their parents, and are fed almost exclusively on animal material, such as insects, worms, grubs, and other invertebrates (Boeker 1961, Walkinshaw 1973a). For about a week after hatching, the chicks are brooded by the parents at night, either at the nest or at another elevated area chosen as a roosting site by the parents.

The family spends its days intermittently foraging, preening and resting. As the chicks grow older they begin to catch insects and other invertebrates, although the parents continue to provide the major part of their food. During the latter part of July, at about 70 days of age, the chicks begin to fly. A week or so later, territories break down and families may fly to nearby farm fields to feed.

Fall Flocks. From mid-August to mid-September, cranes may be seen in increasing numbers at fall staging areas, such as Sandhill Wildlife Demonstration Area (WDA), or Necedah National Wildlife Refuge (NWR). Staging areas contain primary roosts, secondary roosts and feeding areas (Wheeler and Lewis 1972). Cranes spend the night at primary roosts. These areas contain wide shallow expanses of water, suitable for roosting, and are generally surrounded by low vegetation so that cranes have a wide view of the surrounding area. Just after daybreak, cranes leave the primary roost and fly to nearby fields where they may stand, preen, or occasionally forage for 15 min to 2 hours. Wheeler (in Wheeler and Lewis 1972) has designated these areas as secondary roosts. Longer periods of time are spent at the secondary roost on overcast days. From these areas, cranes may fly to hay, corn or grain fields where they spend the day feeding in large flocks. About an hour before sunset they again return to the secondary roost where they preen, rest and dance. Then from just before sunset to 2 hours after sunset, they return to the primary roost for the night. Although large numbers of cranes are present at staging areas from late August to early October, apparently individual birds remain only a few days to several weeks (Walkinshaw 1973a).

Winter and the Following Spring. Families leave Wisconsin intact, and arrive in Florida several days later. The major known stop-over is the Jasper-Pulaski Game Preserve in northern Indiana. Families spend the entire winter together, the chicks still largely dependent upon the parents for food (Walkinshaw 1973, Lewis 1974). In late February or early March, cranes leave Florida, and arrive in Wisconsin a few days later. Jasper-Pulaski Game Preserve is also the major stop-over on the spring migration route (Walkinshaw 1960).

The parents and yearlings apparently separate just before or soon after arriving on Wisconsin territories. Walkinshaw (1949, 1950) and Littlefield and Ryder (1968) report observing adults with yearlings on territories, and adults driving off yearlings.

Non-Breeders. Little is known about non-breeding populations of sandhill cranes. After leaving their parents, yearlings apparently form small flocks with other non-breeders. They spend their days feeding in open fields and marshes, and roost at night in isolated marshes, away from other crane territories (Walkinshaw 1973a). Pairs apparently form in these non-breeding flocks, and at about 3 years of age, newly paired cranes depart from non-breeding flocks to establish territories of their own (Walkinshaw 1973a). In captivity, cranes have bred at 3 and 4 years of age (Walkinshaw 1973a).

Ethogram of G. canadensis tabida

Subjects. I observed both captive and wild sandhill cranes to obtain most of the detailed descriptions of the behavioral patterns in Section II. I made observations primarily on two G. c. tabida chicks in 1973 and one chick in 1974 at the International Crane Foundation, Baraboo, Wis. Two to 14 day old chicks were housed indoors in individual 0.6 x 0.9 m wire mesh pens, under heat lamps. Two to six week old chicks were housed in individual indoor/outdoor pens. Each chick had a 3m x 3m indoor area, connected by a small door to a 3m x 4m concrete outdoor area. Chicks over six weeks old were housed in a 12 m x 18 m hurricane fence-enclosed area, containing a 4m x 4m building which was open to the chick for shelter. The outdoor area contained uncut grasses that reached 0.5 m in height. One of the chicks that I observed extensively was adopted by a Manchurian crane pair at about six weeks of age (Voss 1974). Observations were made from behind a plywood or cardboard barrier, which partially obscured me from the chicks. Their behavior seemed to be unaffected by my presence after an acclimatization period of several minutes.

During the spring and summer of 1974, I observed two pairs of nesting cranes from a blind built approximately 2.5 m above ground level on the edge of a marsh in the French Creek Wildlife Area, near Portage, Wisconsin (Fig. 57). Pair A nested approximately 300 m from my blind and could be closely observed. It was possible to distinguish the male from the female of this pair by individual differences in feather coloration

on the head. This pair did not hatch any eggs. Pair B nested approximately 400 m from my blind, and could not be so easily observed because of taller surrounding vegetation. They hatched one chick which apparently died several days later. A third pair, pair C, whose nest was not visible from my blind, was observed frequently with a single chick. The territories of pairs A and B (Fig. 29) were determined by marking approximate locations and movements of the cranes on a map during each observation period.

During the fall of 1974, families were observed in fall flocks at Sandhill Wildlife Demonstration Area (WDA), and Necedah National Wildlife Refuge (NWR). Observations were made from a blind approximately 20 m from a corn baited area at Necedah NWR, as well as from public observation towers at both areas.

Apparatus and Procedure. Observations of wild cranes were made with 8 x 40 binoculars, and a 15x to 40x spotting scope, and I occasionally used binoculars to observe captive cranes. I recorded as many behaviors as possible on Super-8 movie film using a Vivitar 100 PM movie camera. Most of the figures in Section II were drawn from these films. I also made written descriptions of most behavior repeatedly in field notebooks. I recorded a number of vocalizations, using a Uher 4000 Report-L tape recorder at 7.5 inches per second, and sonographed them with a 6061-13 Sound Spectrograph, Kay Elemetrics Corp., at 7.5 i.p.s. using the wide bandwidth (300 Hz.).

Chicks were occasionally subjected to stress by placing them in the presence of other cranes, a dog, or a hawk, to elicit, or to test for the development of various threat displays.

Age Related Changes in Daily Activity Patterns (Section IV).

I watched one of the captive chicks described above regularly for long periods of time, and made a second-by-second record of its behavior. I analyzed this record to determine trends in (a) the percent of time spent in various activities, (b) the frequency of bouts of a given activity, and (c) the average length of bouts, ± one Standard Error for each given age interval. A detailed description of the methods used and the analysis of data is found on p. 109. Activities analyzed include sleeping postures, resting postures, drinking, feeding and foraging.

III. CATALOGUE OF BEHAVIOR PATTERNS

Masatomi and Kitigawa's (1975) fine paper on G. japonensis is the only published ethogram of any crane species. In addition to my thesis on G. canadensis tabida at least five other persons are currently studying the ethology of other crane species. We are developing a standardized nomenclature for Grus species, but until this project is completed, I feel it is important to avoid unnecessary differences in terminology. I have chosen to follow Masatomi's nomenclature wherever possible, and all names for behaviors have been taken from his work unless otherwise indicated.

Maintenance Activities

Behavior that does not involve interactions between conspecifics or other species is included in this section. This includes resting postures, sleeping, comfort movements, locomotion, food intake and defecation.

Resting Positions

A crane was considered to be resting when in any one of four postures which could be maintained with very little apparent energy expenditure.

In sitting posture (Fig. 21) the crane's legs are completely folded under him, so that the breast and belly are in contact with the ground. The tibiotarsus and tarso-metatarsus are parallel to each other and to the long axis of the body, and the feet are near the breast.

When heel standing (Fig. 2) the tibiotarsus is vertical, and the tarsal joint bears the weight of the bird. The tarsometatarsus is more or less horizontal along the ground, and the toes are flexed slightly so that only the tips of the toes touch the ground. The long axis of the body is about 30 degrees above horizontal.

When in unipedal standing posture (Fig. 3) one leg is vertical from hip to toes, and bears the weight of the bird. The other leg is folded as in sitting posture and is completely buried in the feathers of the breast and belly. The long axis of the body is more or less horizontal.

Bipedal Standing (Fig. 4) is similar to standing on one leg, except that both legs are vertical from hip to toes and both bear the weight of the bird.

In any of these resting postures, the head and neck may be held in various positions, though frequently the neck is curved forward at the base, then upward, so that the upper half of the neck is more or less vertical and the back more or less horizontal. When bipedal standing with head and neck in this position, a crane will henceforth be referred to as standing in a normal upright position (Fig. 4).

Figure 2

Heel standing posture.

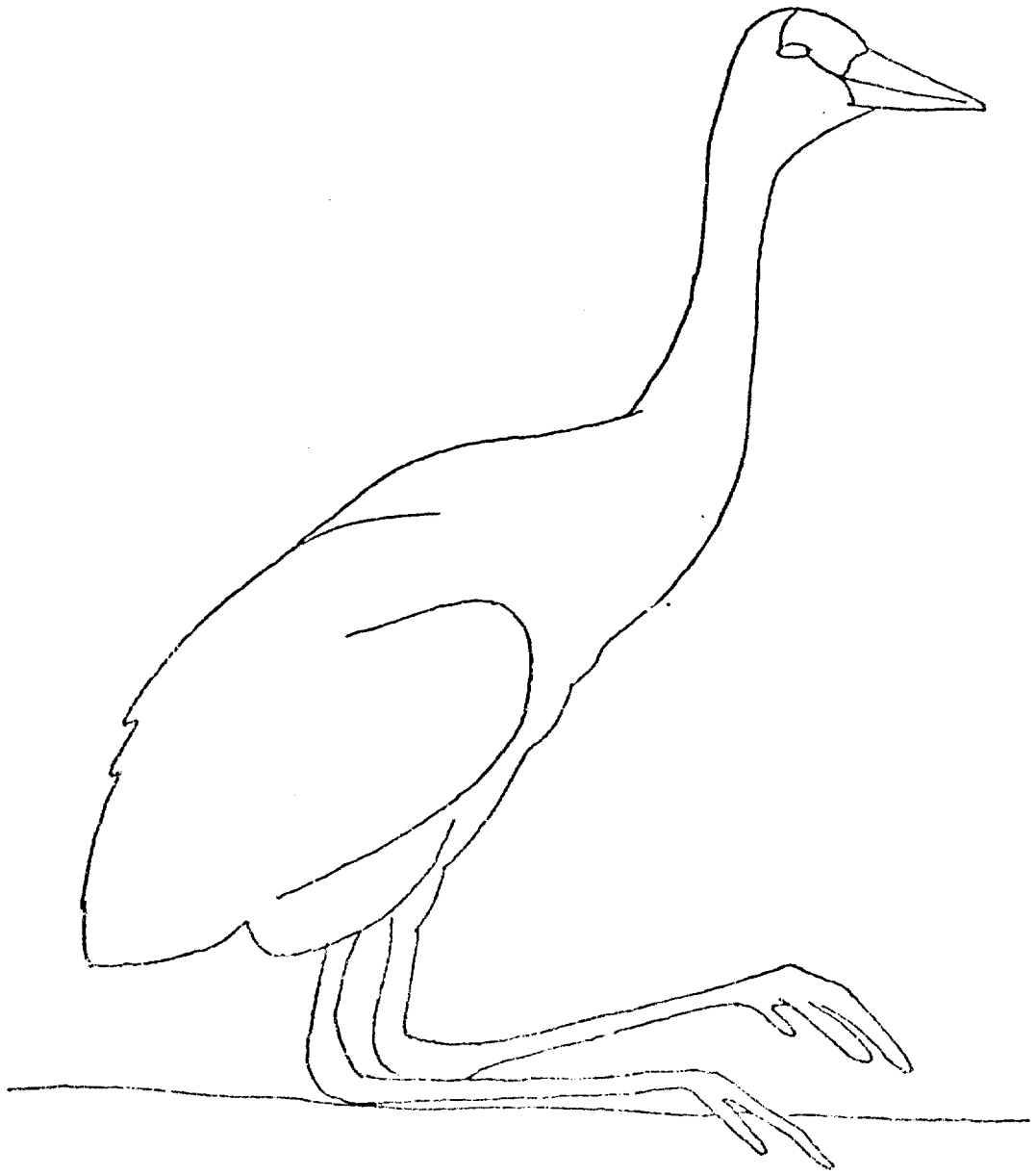


Figure 3

Unipedal standing and back sleeping posture.

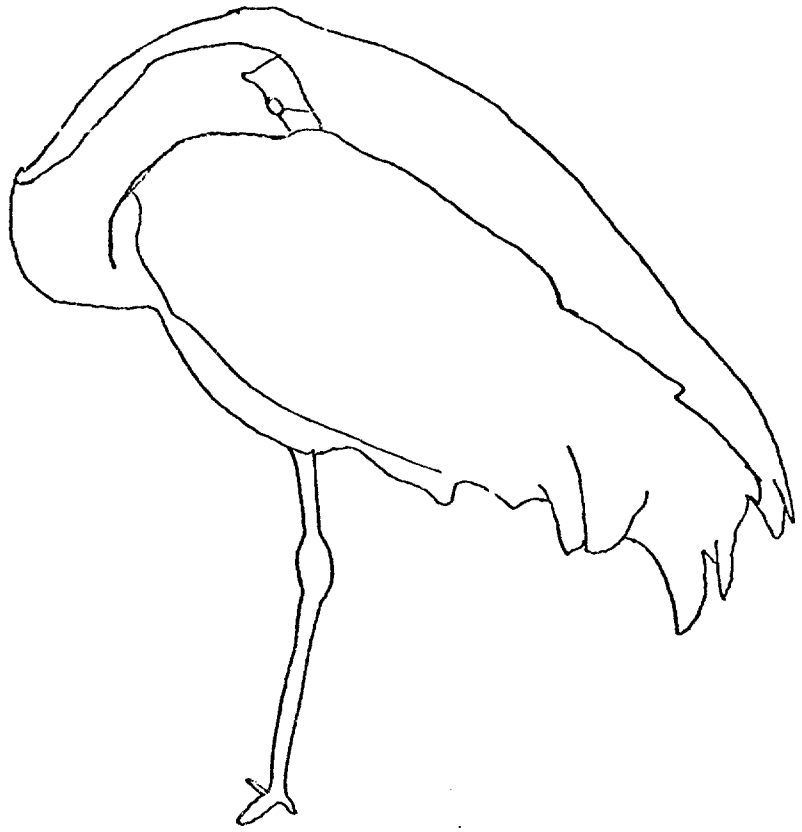
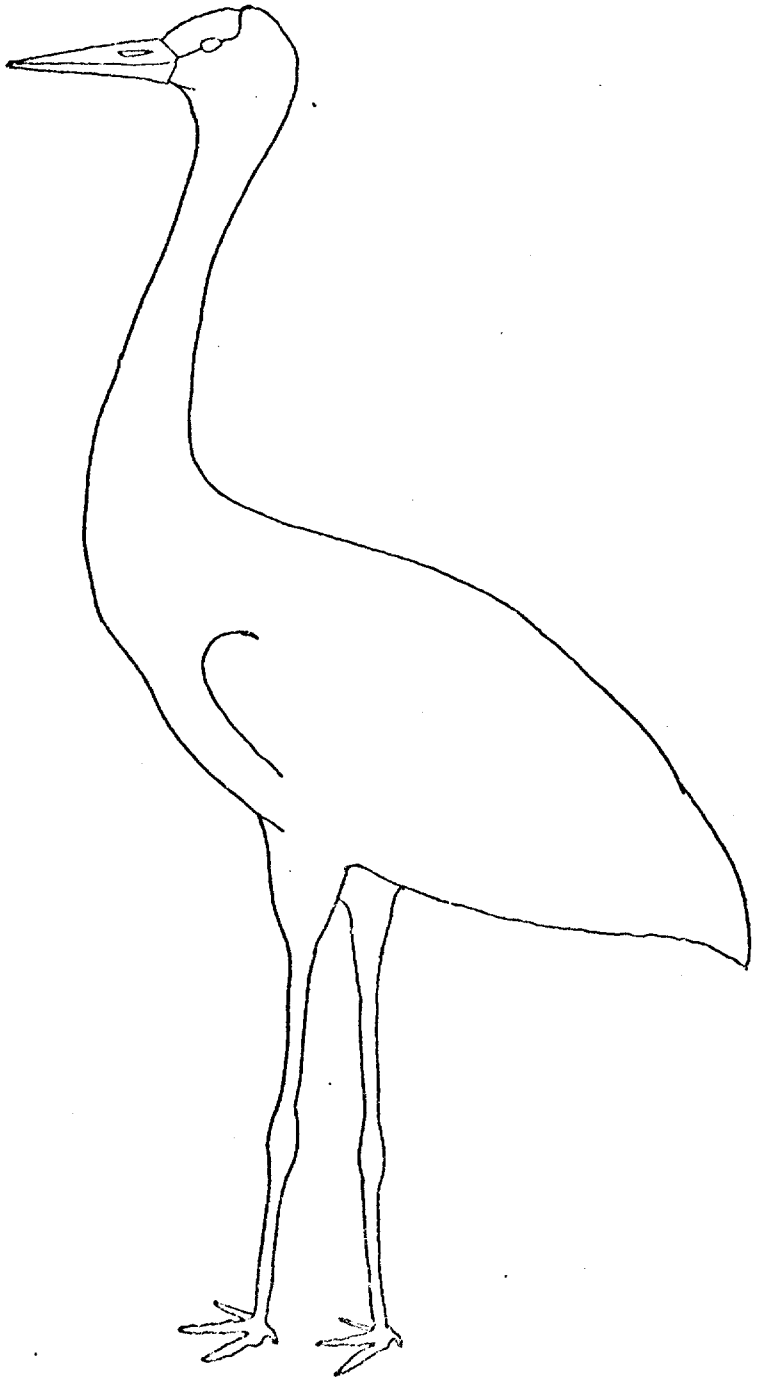


Figure 4

Bipedal standing in normal upright position.



The neck may also be retracted further so that the base of the neck forms a "U" shape; the head is just above the level of the back, and the bill is angled slightly downward. Masatomi (p. 843) refers to this as neck shortening resting (Fig. 5). Cranes also rest in the back sleeping position (Fig. 3), but the eyes remain open (sleep-like resting: Masatomi, p. 843).

Sleeping

A crane was considered to be sleeping when its eyes were closed. The feathered eyelid is greyish-white, lighter than the surrounding facial feathers, and a closed eye could be distinguished from an open eye at a distance with binoculars or spotting scope. When it was not possible to actually see the closed eye, the crane was assumed to be sleeping if it remained motionless in a sleep posture. Sleeping cranes generally assumed one of three different sleeping postures.

Head out. Chicks less than 2.5 weeks old slept exclusively in head out position (Fig. 6). While sitting, the crane's neck was either rested on the ground directly forward in front of the crane, head tipped to one side so that the beak and one side of the face rested on the ground, or, more commonly, the neck was curved around the body to either the left or right, and the head rested on the ground below the wing.

Chicks older than 2.5 weeks slept in either bill down sleeping or back sleeping position. Bill down sleeping (Fig. 7) can be assumed while sitting, in hock posture, or standing on one or two legs. The crane's neck is held vertical, though not extended upward. Occasionally the beak is held horizontally, though usually it is pointed vertically downward, and almost touching the neck. Masatomi (p. 845) refers to this as simply down sleeping.

Figure 5

Neck shortening resting.

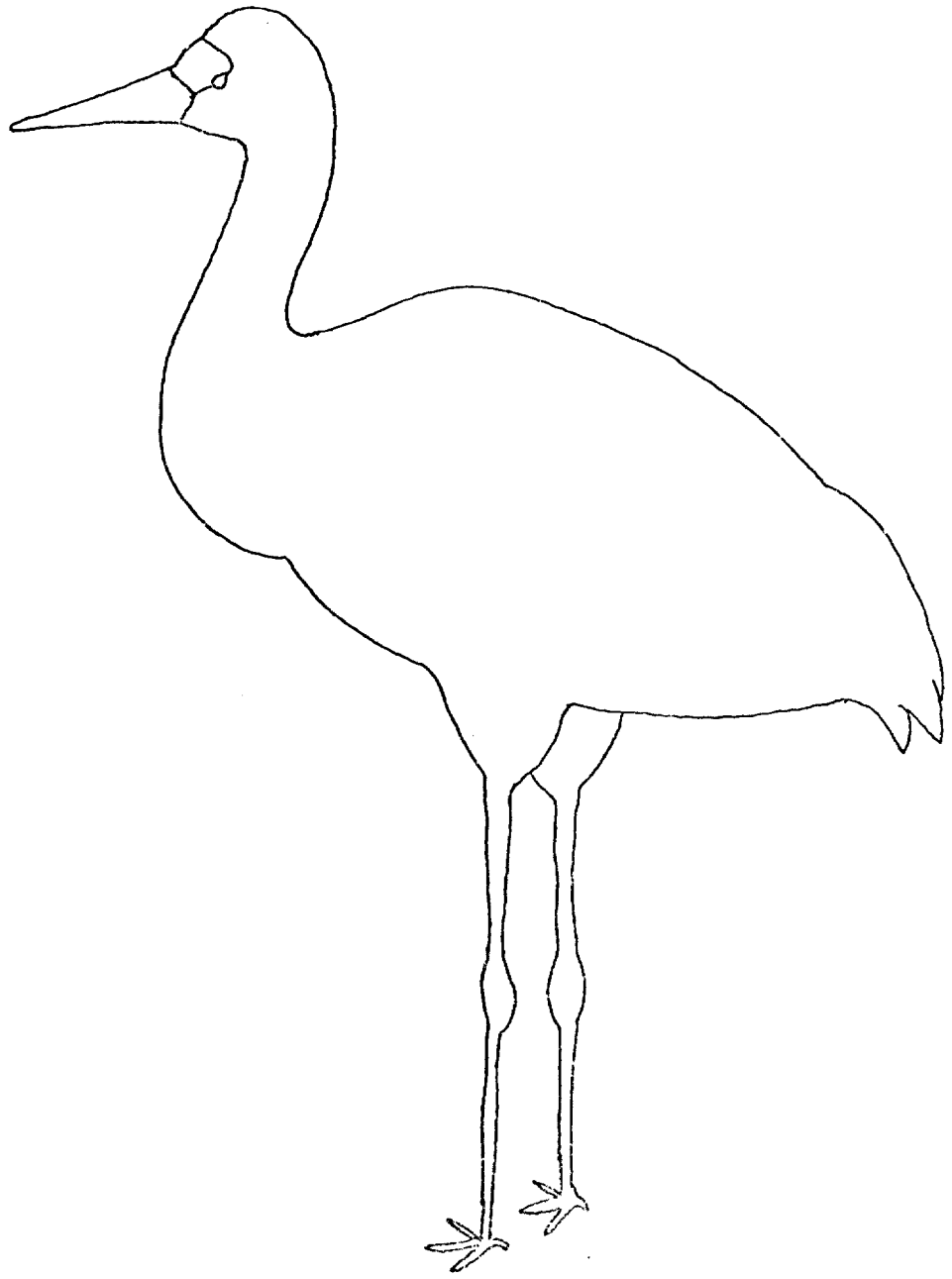


Figure 6

Sleeping in head out position.

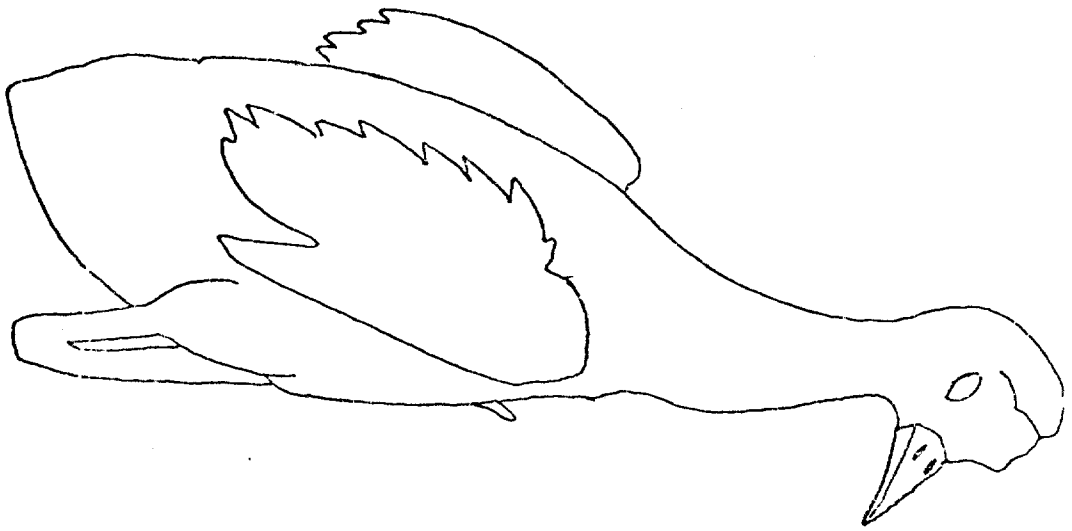
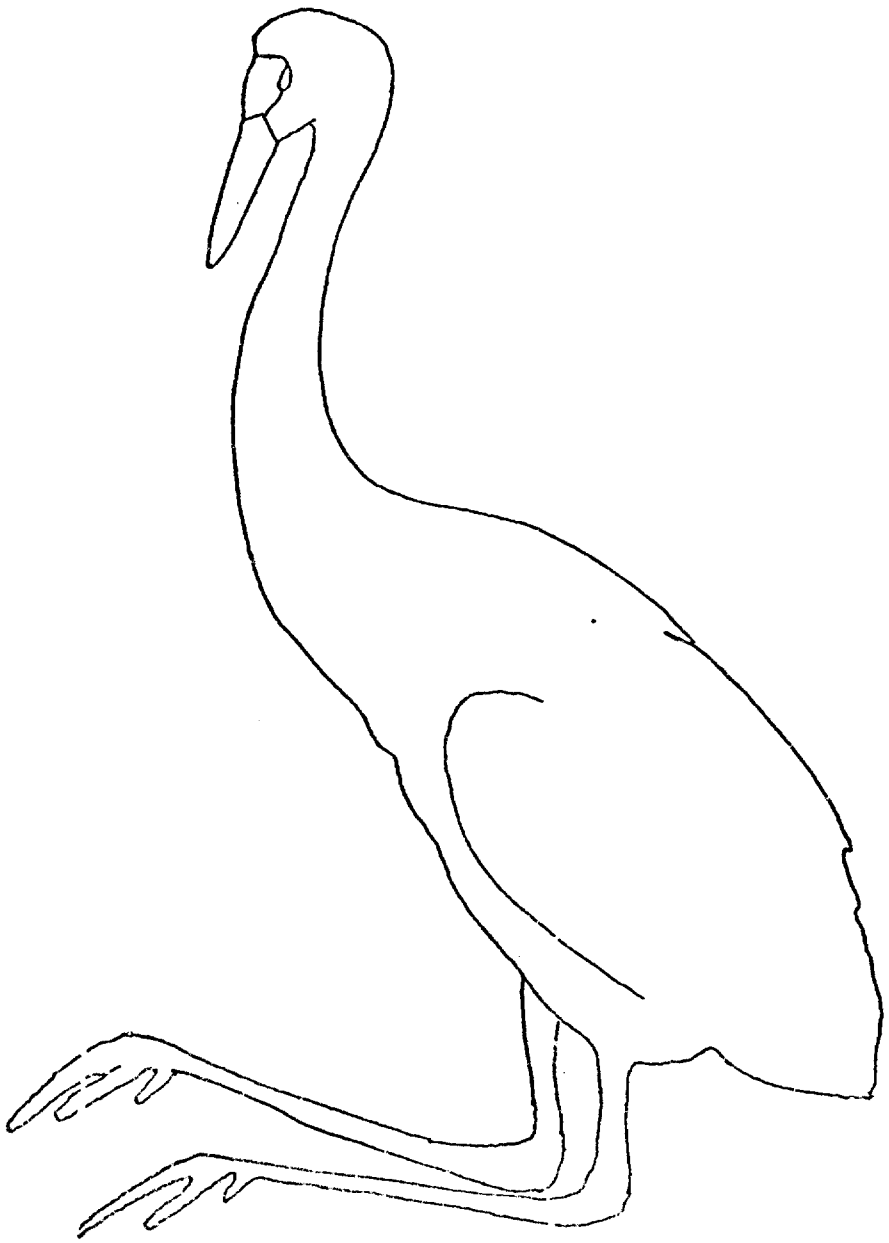


Figure 7

Sleeping, bill down position.



Back sleeping position (Fig. 3) can be assumed while the crane is sitting or standing. Either right hand or left hand positions can be assumed. If the neck is curved to the left, the throat and base of the beak rest on the upper back, and the beak is buried in the scapular and tertial feathers on the left side. In cold weather, the whole left side of the head and much of the crown may be covered by scapular feathers.

Comfort Movements

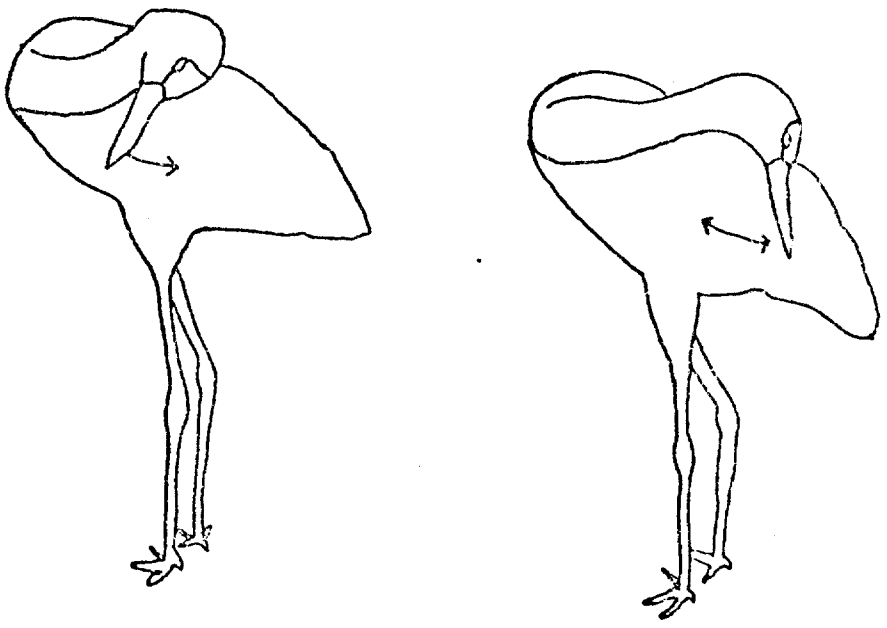
Comfort movements include activities which function in care of the body surfaces, stretches and shakes (McKinney 1965).

Preening involves a rather wide variety of activities since different preening movements are used for different body regions and different feather types. Bouts of preening lasted from several seconds to several minutes. Typically, cranes preen one body region, such as breast, belly or wing covers, for 0.5 to 20 seconds, then preen another body region, etc. When preening remiges or rectrices, a crane will dig and nibble at the base of the feather with the tip of its beak, then taking the base of the feather between its upper and lower mandibles, pull it from base to tip through its beak. Wing coverts and body contour feathers were preened similarly, though more time was spent digging and nibbling at the bases of the feathers and skin, and individual feathers were only occasionally pulled through the beak.

Head rubbing (Fig. 8) is a preening motion that appeared to serve a number of different functions. To rub the head on the left side, the neck is bent to the left so that the left side of the head and beak are in contact with the feathers on the surface of the back and folded wing, beak pointing downward. Then the head and beak are moved vigorously and rapidly back and forth over the surface of the feathers, describing an

Figure 8

Head rubbing.



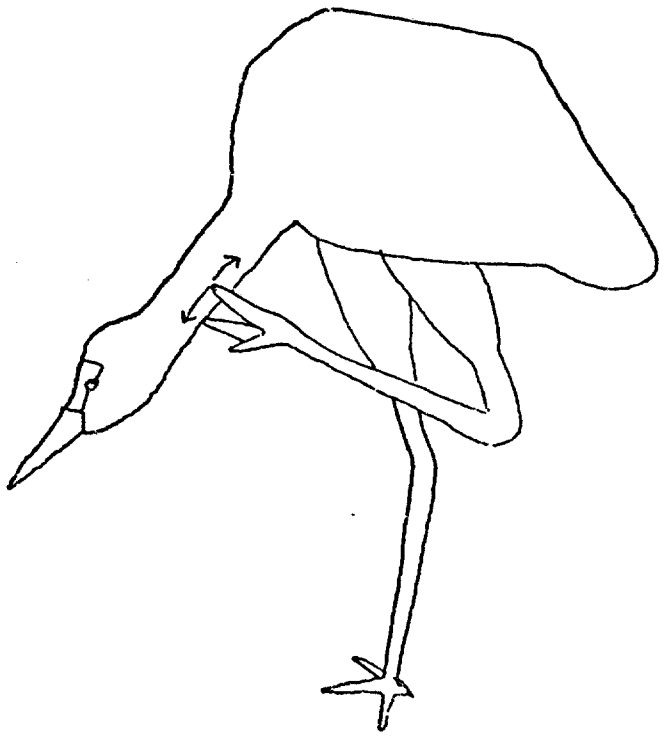
arc of about 90 degrees, with the pivot point approximately at the base of the skull. This movement may be used over surface feathers of the back, breast, belly, sides of wings, base of neck and base of legs. Cranes often head rub after nibbling at and rubbing the sides of the beak and head on the oil gland, apparently to spread oil to the rest of the feathers of the body. Masatomi (p. 847) refers to these motions associated with the spreading of oil as oiling. A very quick head rubbing movement also seems to function in removing insects from around the eyes and bare skin areas of the head. Masatomi refers to head rubbing as ordinary head rubbing, but I believe this is an unnecessarily cumbersome term.

Head scratching and neck scratching (Fig. 9). A crane may use the tip and medial side of its middle toe to scratch its neck, head or jaw. The crane extends its neck downward and forward, the exact position depending upon what area needs scratching. At the same time, the tarsal joint is flexed and the tarsometatarsus raised until the toe contacts the head or neck. Scratching occurs at a rate of about 2 scratches per sec, and usually lasts less than 10 secs. The toe may contact the neck or head for a length of 3 to 10 cm while the toe is moving downward. Most of the movement of the toe results from flexion and extension of the tarsal joint, and the toe may contact the head or neck for only a part of the arc it travels through. Occasionally young cranes were observed going through head scratching motions without actually contacting the head or neck. This seemed to be largely due to the inability of the young crane to balance well on one foot.

Feather painting is an unusual and little understood behavior engaged in by two species of cranes, the sandhill and the European crane,

Figure 9

Neck scratching.



Grus grus, (Archibald, pers. comm.). The crane begins by digging vigorously with its beak where there is an area of mud, or mud and grass. The mud collected may be a discreet pellet of mud and grass held in the tip of the beak, a dangling piece of mud-covered vegetation, or mud simply stuck to the surface of the beak. The crane then preens vigorously, mostly by head rubbing or wiping its feathers with the muddy grass, but occasionally by digging vigorously with the tip of its beak, and drawing flight feathers through its beak. During a single bout of feather painting, a crane will alternately dig in the mud and preen many times. This feather painting results in a brown staining of all body feathers below the upper one-third of the neck. Since the crane cannot reach the upper part of its neck with the beak, it remains the normal gray coloration.

Feather painting was first observed at 15 weeks of age. A captive chick was observed "begging" and receiving pellets of muddy grass from its adoptive Manchurian crane (Grus japanonsis) parent in the same manner that it begged food. Feather painting was also observed several times by cranes on nesting territories.

Kennard (1918) analyzed stained feathers of various species of waterfowl and found that the staining was due to ferric oxide. Analysis of the stained feathers of sandhill cranes showed that they too were stained by ferric oxide (Taverner 1929). Several authors have noted that this staining probably results from the cranes' habit of preening their feathers with muddy beaks (Walkinshaw 1949, Johnson and Stewert 1974). However, no authors seem to recognize that this brown feather stain is not merely incidental to preening with muddy bills, but results from a unique feather painting behavior. Interestingly, Lovett Williams (in Wheeler

and Lewis notes that cranes marked with green patagial tags will cover the marker with red clay.

The stained feathers of adult cranes are virtually identical in color to the natural brown plumage of immatures (Taverner 1929). The significance of this fact, and of feather painting itself, is unknown. Drewien (1975) postulates that the brown stain aids in cryptic coloration, blending with the colors of residual marsh vegetation. Inconspicuousness probably reduces the chance of detection of incubating adults on nests. He also suggests that cryptic coloration may be advantageous during the molt of flight feathers, which leaves cranes flightless in mid- to late summer. At this time of the year, though, Wisconsin marshes are predominantly green rather than brown.

Bathing

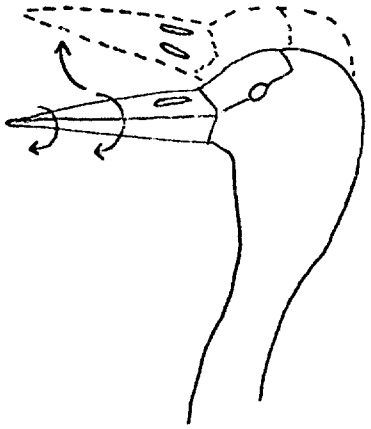
Captive and wild cranes were observed bathing approximately five times in captivity and twice in the wild. The crane crouches down so that its breast and belly are in the water, then flaps its wings either alternately or simultaneously. The wings are raised up and down off the body from the shoulder, while the rest of the wing remains loosely folded. The bird may also move up and down so that the breast bobs in and out of the water. This bathing behavior is stereotypic enough that it could be recognized in a 15 day old chick attempting to bathe in a small dish of water. Bathing bouts may last several seconds or several minutes, and are usually followed by standing and preening.

Shaking

Head flick (Fig. 10). This movement lasts approximately 0.5 sec and may occur only once or three to four times in succession. When the crane is standing in a normal upright position, the head and bill are

Figure 10

Head flick.



flicked diagonally upward and to one side, and at the same time the head and bill are rotated slightly (10 to 20 degrees) about the long axis of the bill. This movement may also occur while the head and neck are in other positions, such as down, while foraging. The head flick seems to function primarily in dislodging insects from the head. This behavior is not described by Masatomi, but is described by McKinney (1965) for Anatidae.

Tail wagging. Tail wagging may occur during various activities such as preening, foraging or resting. The axis of the body and the tail are more or less parallel, or the tail axis may be lowered up to approximately 10 degrees below the axis of the body. The tail, feathers not fanned, is shaken from side to side three to five times at a rate of about three shakes per sec. I made no detailed record of the circumstances under which tail wagging occurred, hence I am uncertain about the function of this behavior.

Body-wing shaking. Initially the crane stands with its body horizontal, its neck vertical, and its back horizontal. Often this movement is directly preceded by fluffing so that the feathers of the body, neck and head are raised. The neck is extended forward and up to 30 degrees above horizontal, and the body is slightly above horizontal. The crane then very rapidly shakes its body, rotating about the long axis of the body and neck. The wings, loosely folded, may be flapped, although they are not raised more than a few cm from the body, and the flapping is not ritualized, as described for irrelevant body-wing shaking threat. Body-wing shaking ceases very abruptly as the crane raises its head, assumes a normal upright standing position, and lowers its body feathers to a nor-

mal position. The function of body-wing shaking is not entirely clear, although it may serve to help settle the feathers properly on the body.

Stretches

Cranes perform three stretches in which major muscle groups are used. These stretches often occur while a crane is preening or foraging, and often two or three stretches occur within a few minutes. Several typical sequences are: preening, lateral wing stretch, wing raising stretch, preening; foraging, lateral wing stretch, tail wagging, body-wing shaking, foraging.

When wing raising (Fig. 11) the crane stands with body horizontal, neck up and forward at about 45° above horizontal, back horizontal. The wings are raised at the shoulders, so that the elbows are high in the air (Fig. 11a). The bird lowers its head and neck and bends its body forward, its legs flexing at the tarsal joint (Fig. 11b). At the deepest point in this forward bending, the neck is outstretched forward, with the head horizontal but slightly lower than the body, which is angled from 5 to 10 degrees below the horizontal. The wings are arched high above the back with elbows high and wrists low (Fig. 11c). The bird may hold this position for several seconds, then raise its head and refold its wings (Fig. 11d). The wings remain flexed at the wrist and elbow throughout the wing raising stretch.

Lateral wing stretch. During a lateral wing stretch (Fig. 12) the crane stands with its body about 20 degrees above horizontal, its neck more or less vertical and extended, and its beak horizontal. Then it fully extends its wings straight out laterally from its body. This position is held 3 to 5 sec, then the wings are refolded, and the body is

Figure 11

Wing raising.

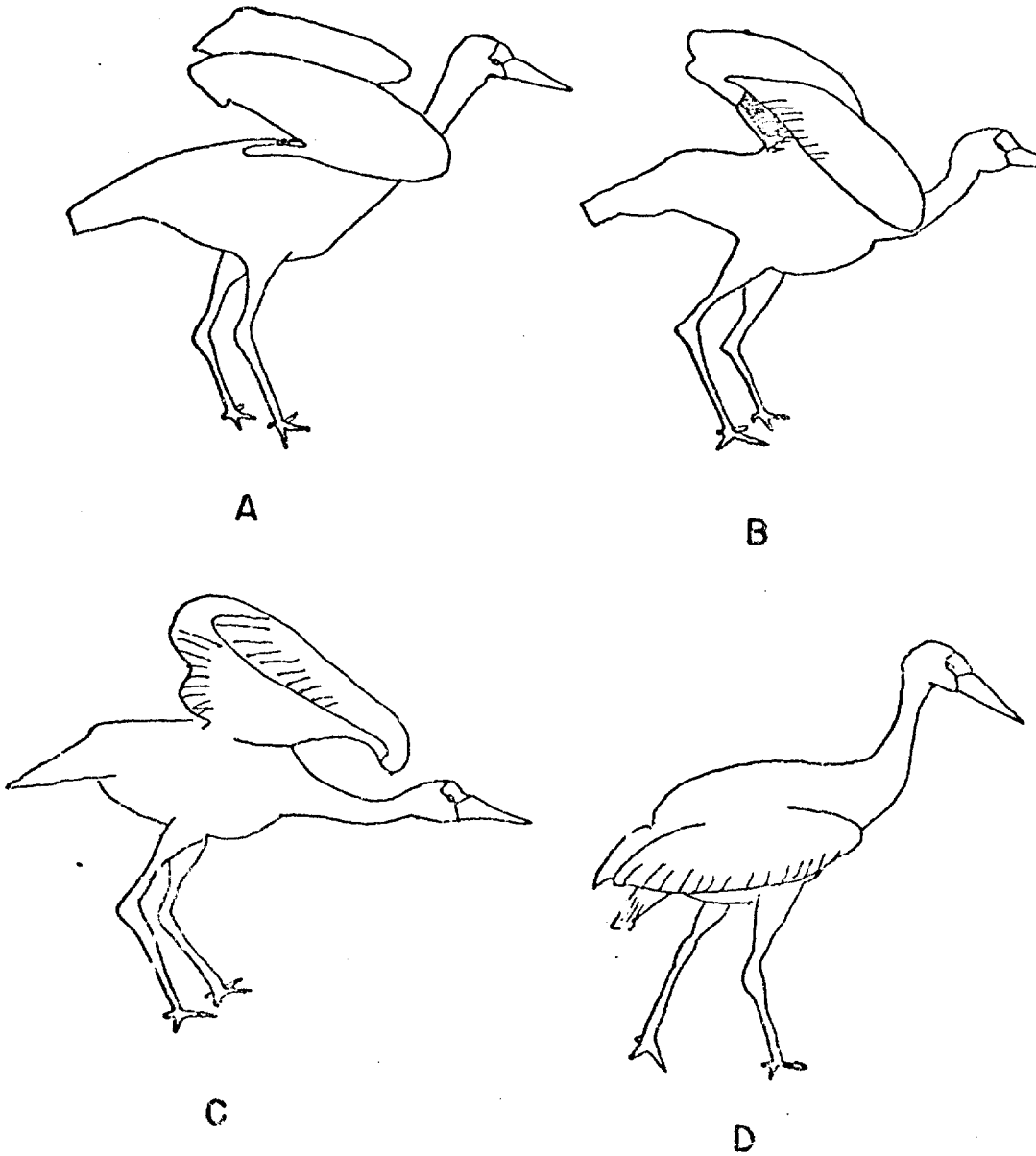
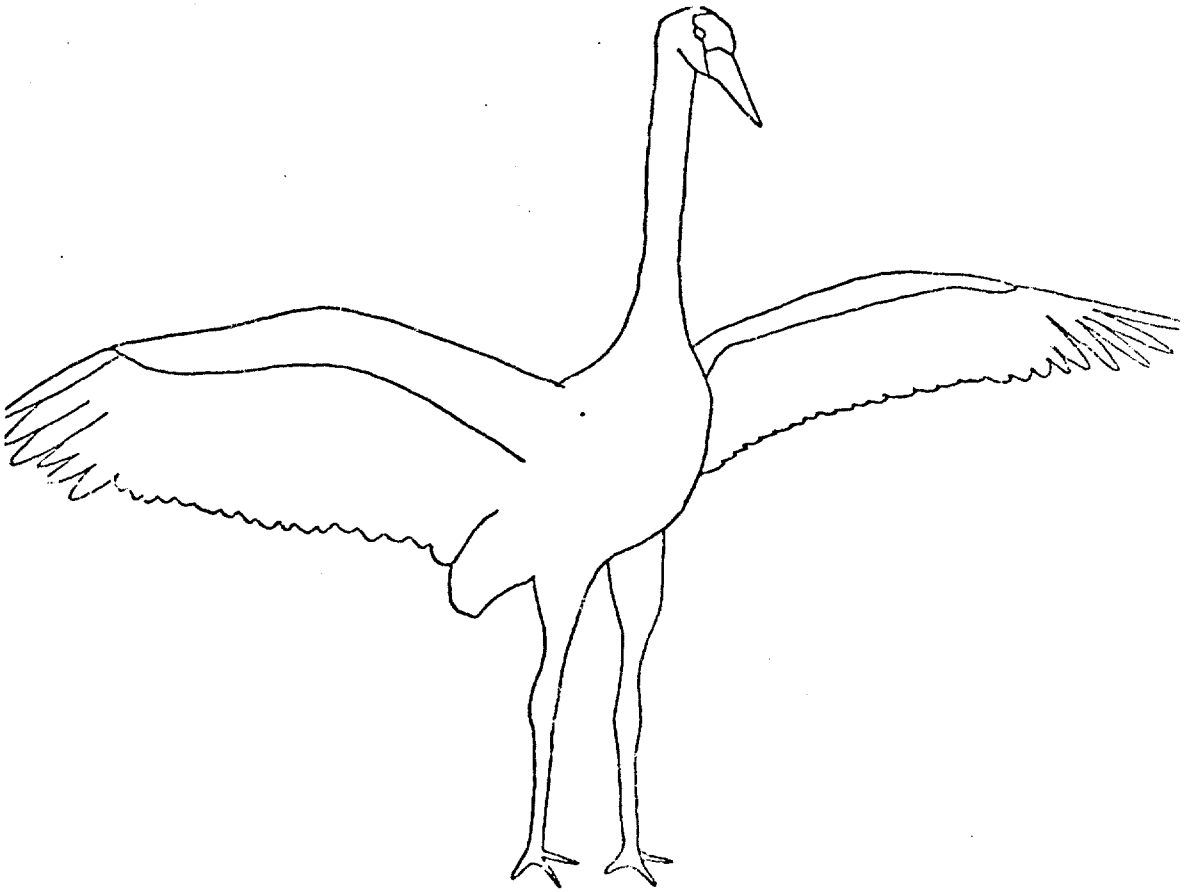


Figure 12

Lateral wing stretch.



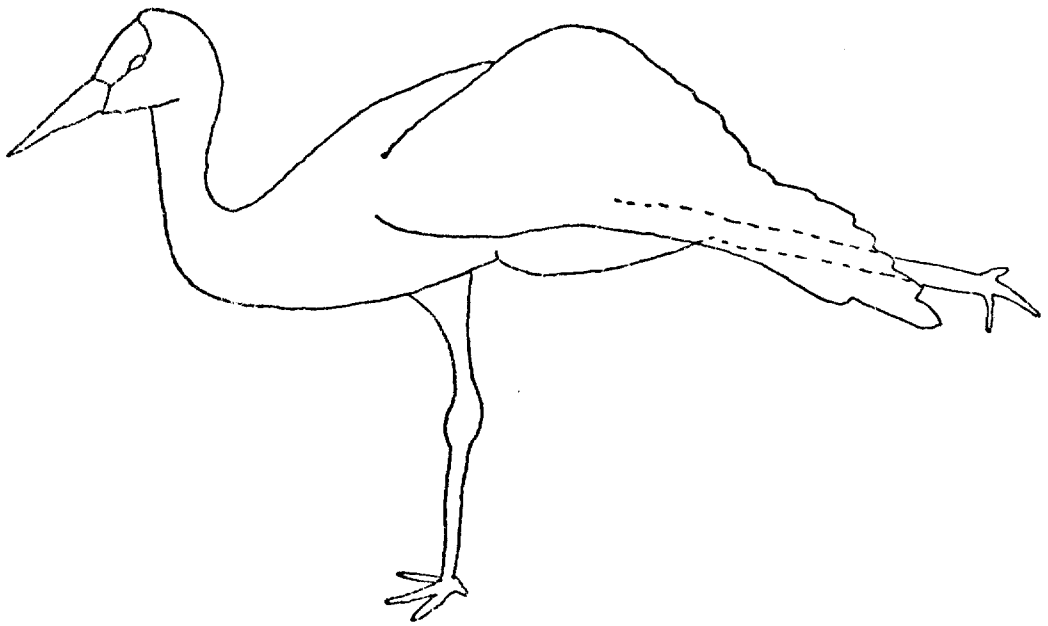
lowered to a horizontal position. This stretch is not described by Masatomi.

A leg-wing stretch (Fig. 13) begins with the crane standing, neck vertical but not extended. The crane then stands on one foot, and stretches the other straightened leg backward at about 45 degrees above vertical with the toes extended and spread outward. As the leg reaches this position, the wing on the same side of the body is unfolded and stretched outward, backward and downward until it is parallel to the leg and almost touching it. This position is held for about 1 sec, then the straightened toes are brought together so that they are parallel with the leg. After about 1 more sec, the toes are curled, the tarsal joint bent, and the leg drawn forward. The toes are again spread, and the foot placed on the ground. The wing is refolded simultaneously with the bending of the tarsal joint. Masatomi (p. 848) refers to this same stretch as simply leg stretching; however, leg-wing stretching is more descriptive, since the stretching of the leg and the wing always occurred together.

The jaw stretch often occurs during periods of relative inactivity, such as resting, preening, or between bouts of sleeping. The crane usually stands with its body horizontal, its neck more or less vertical but not extended, and its back approximately horizontal. The mandibles are opened 20 to 30 degrees for 1 to 3 sec, then closed again. No other movement accompanies the jaw stretch. Masatomi (p. 850) refers to this stretch as yawning, however McKinney (1965) uses the term jaw stretch, and notes that "yawning" does not occur in birds as it does in mammals, there being no marked inhalation in birds. Jaw stretch is a more de-

Figure 13

Leg-wing stretch.



scriptive term, and avoids implying an incorrect function for this behavior.

Wing Flapping (Fig. 14)

The crane stands with its body about 60 degrees above horizontal, its neck vertical, but not extended, and its head and beak horizontal. Wings are almost fully extended and flapped vigorously back and forth, each wing moving in a more or less horizontal arc of about 120 degrees. A single bout of wing flapping usually consists of one to seven wing beats, and may last 1 to 5 sec.

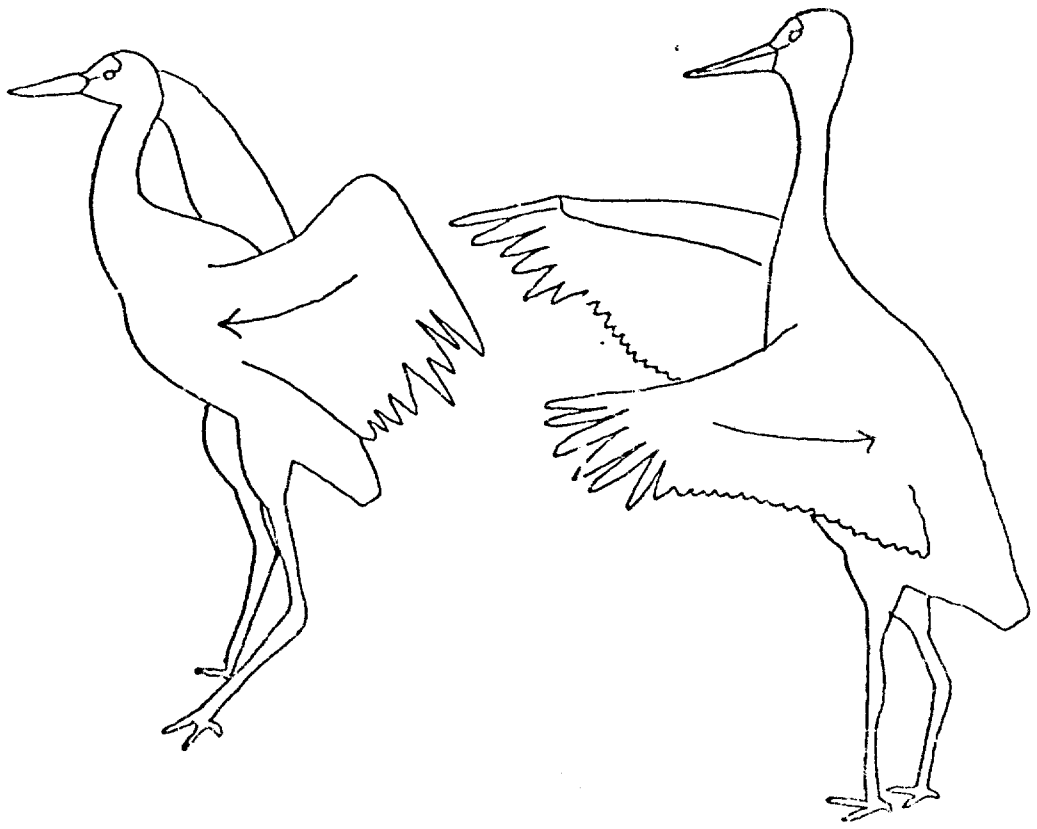
Fluffing

The crane stands and appears relaxed, in that its movements do not appear to be tense, and although its neck is usually vertical, it is not extended. Its body is more or less horizontal. The feathers of the body including the back, breast, abdomen, rump, neck and head are erected more or less perpendicular to the skin, held erect for several seconds, then lowered. A bout of fluffing from the beginning of feather erection until the feathers are lowered to the normal position lasts 5 to 10 secs. Often, rather than lowering the body feathers, fluffing is immediately followed by body-wing shaking and the feathers are lowered after this.

Fluffing frequently occurs between bouts of preening or sleeping, or while the crane is standing. On cold days I observed cranes standing and resting with feathers fluffed, apparently to reduce body heat loss.

Figure 14

Wing flapping.



Locomotion

Walking and Running

Cranes move about on the ground by both walking and running. A crane is considered to be walking when one foot is always in contact with the ground, and steps are taken at a rate of about 0.5 to 1.5 steps per second. When running, a crane leaps from one foot to the other, so that for a short interval of each step, neither foot is on the ground. Running cranes take about three steps per sec. The gait is often bouncy, giving the impression that the crane is "trotting." Running often occurs when a crane is chasing some mobile prey, or chasing another crane. When running very fast, a crane will often also flap its fully extended wings, apparently to gain added speed, and for balance.

Swimming

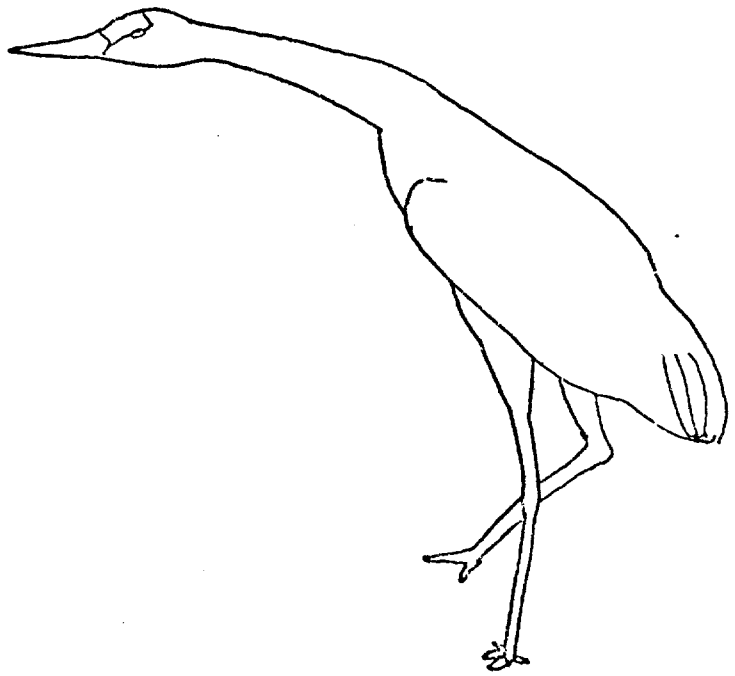
Masatomi reports swimming as a very rare behavior in adults, although frequently young chicks must swim when leaving the nest. I observed a crane swim only once. An approximately six week old chick simply walked into a deep water area in the marsh, until the water was too deep to stand, and began swimming. This occurred while the chick was foraging with its parents, and the chick swam from one side of this deep water area to the other, then continued foraging.

Flying

Pre-flight posture (Fig. 15). Except when a crane is startled suddenly into flight, flying is preceded by pre-flight posture. This is an intention movement, held for a few seconds to a minute before a crane takes flight. The crane faces into the wind, with its body about 10 degrees above horizontal, its neck fully extended and almost horizontal,

Figure 15

Pre-flight posture.



and beak pointed forward and horizontal. The feathers of the body are sleeked, and wrists held prominently, slightly away from the body. The crane maintains this position while standing or walking slowly into the wind, and may give a flight intention call, a brief, high frequency, unbroken call (Archibald 1975). The crane then takes flight by springing from bent legs into the air, and flapping its wings.

Pre-flight posture was also observed frequently in wild birds, both in families soon after the chicks could fly, and in flocks. When disturbed, whole flocks of cranes will stand in pre-flight posture for several seconds before flying. I observed fall flocks from a blind near an area baited with corn at Necedah NWR. Here it was possible to hear one or several cranes give low alarm calls which resulted in the whole flock immediately becoming silent, then assuming pre-flight posture and finally all taking flight nearly simultaneously. Masatomi (p. 851) uses the term intentional posture instead of pre-flight posture. I believe the latter term is clearer and less confusing.

Pre-flight posture is followed by dashing. The body is more or less horizontal, the neck either horizontal or curved upward, and the wings fully extended and taking deep powerful wing strokes as the crane runs forward approximately 2 to 5 m. Dashing is followed by taking off. With the neck and body 30 to 45 degrees above horizontal, and with deep wing strokes and a final push-off of one or both feet, the crane is airborne. Alternatively, the crane may crouch low, neck curved forward then upward, then leap into the air. This is not preceded by either pre-flight posture or dashing.

Masatomi also describes flapping flight, soaring, gliding and landing. I did not observe these activities in enough detail to describe

them, but it seems likely that there is little difference among Grus species.

Food Intake

Feeding

Feeding was defined only for captive cranes, since they were provided food in feeders. A crane was considered to be feeding when picking at and swallowing food pellets provided in a feeder.

Foraging

Foraging, of necessity, was defined somewhat differently for captive and wild cranes. Captive cranes were considered to be foraging whenever pecking and probing at objects other than food pellets, such as grass, soil, fencing, building foundations and woodchips.

Wild cranes were considered to be foraging anytime they were engaged in activity that appeared to result in the ingestion of food.

Searching. When searching for animal food, such as flying or crawling invertebrates, a crane would walk slowly, 0.5 to 1 step per second, through the vegetation, its head turning sharply from side to side and moving up and down in search of food.

Chasing. When a food object was sighted, the crane would step quickly towards it, sometimes running 3 m or more, and jab at it with its beak.

Three times, once in captivity and twice in the wild, I watched cranes catch a small rodent. All three times, cranes appeared to use auditory rather than, or in addition to, visual clues. When this was observed in captivity, the rodent could be heard, but not seen tunneling through thick grass, although it is possible that slight movement of the

grass could be seen by the crane. The crane followed the rodent closely on its irregular path through the grass, and when the rodent stopped, the crane stood, appearing very tense or intent, jerking its head from side to side, apparently listening to and trying to localize the slight noises I could hear being made by the mouse. The crane then jabbed into the grass two or three times with its beak and finally caught the mouse. Wild cranes behaved in a very similar manner. The crane would run irregularly for 10 to 20 m, apparently chasing something, then stand, jerking its head from side to side, attempting to locate its prey. On one occasion, the crane's mate and single young joined him in standing and head jerking, apparently also trying to locate the prey.

Digging. Wild cranes often dig in muddy areas for both plant roots and tubers, and underground invertebrates. A crane will stand, vigorously jabbing vertically downward into the mud for the full length of its beak, for 5 secs to over a minute, then with a sideways motion of the beak, pivoting at the base of the head, flick mud out of the hole 1 to 5 times. Alternatively, the crane will remove mud from the hole by raising its mud-filled beak, still pointed vertically downward, and deposit mud about 15 cm away from the hole. Cranes were observed digging and swallowing round objects, about 4 cm in diameter, probably tubers. Plant material was not identified, although Guthery (1972) reports that cranes wintering in southern Texas fed on tubers of nut grasses (*Cyperus* spp.), Arrowhead (*Sagittaria* spp.) and water-lily (*Nymphaea elegans*) and bulbs of wood sorrel (*Oxalis drummondii*) and pleat leaf (*Zustylis purpurea*).

Guthery (1972) notes that "Spiderworts, insect larvae, beetles and pupae were unearthed by scratching." Presumably scratching was done in

some manner with the feet. I never observed this method of foraging in either captive or wild cranes. Archibald (pers. comm.) does not know of any crane species that use this method of foraging.

Masatomi (p. 853) uses foraging instead of searching. I think this is too specific a use of the word, since digging is also a type of foraging. He uses sticking instead of digging. I believe the latter is a more descriptive term. He includes chasing under the term eating-moving-animal.

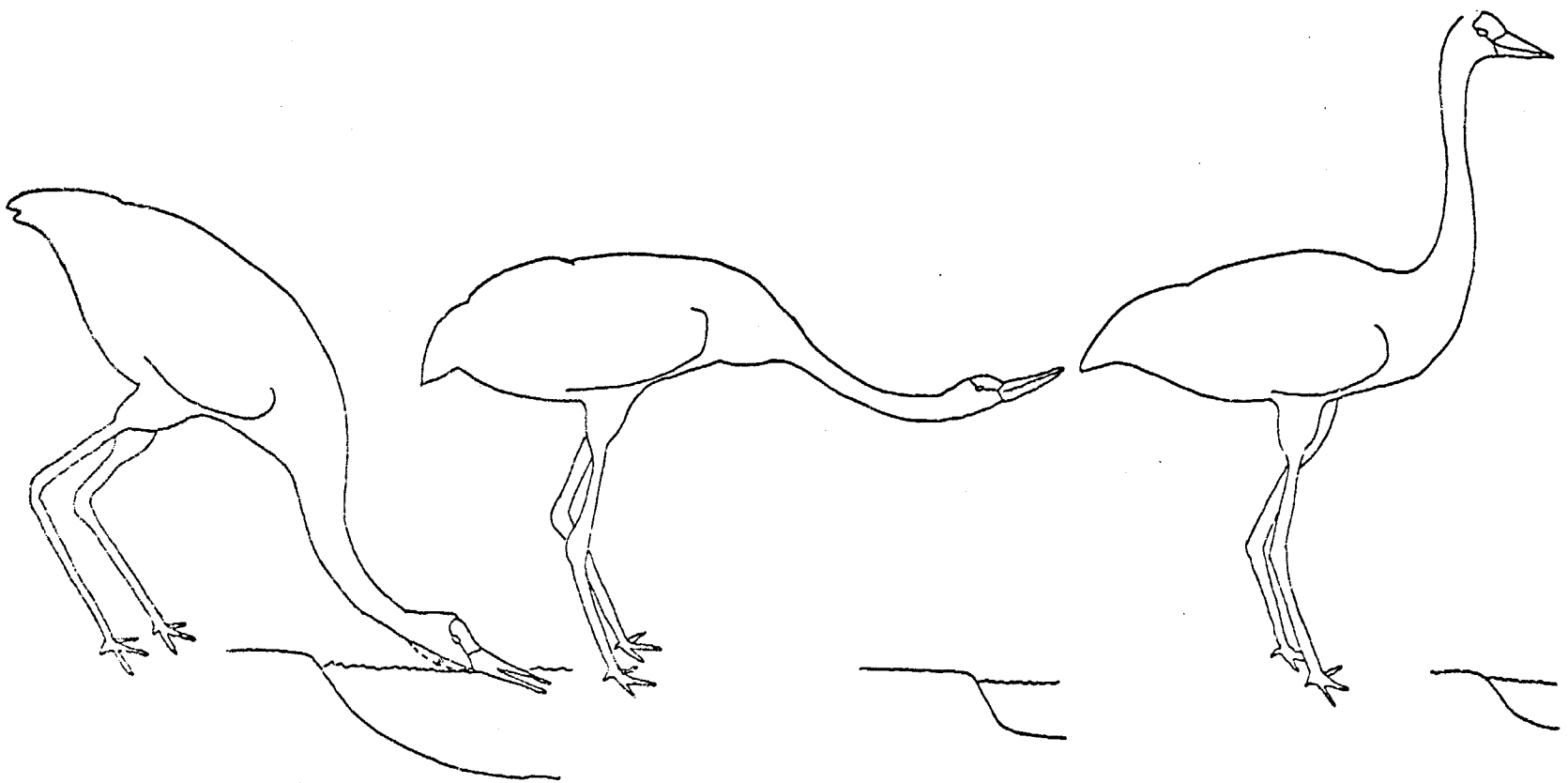
After catching an animal food item, the crane either swallowed it immediately, or picked it up and dropped it several times, apparently breaking or softening it before swallowing it. When eating grains (or food pellets, in captivity), a grain is grasped in the tip of the bill, then tossed upward with a vertical flick of the bill, caught in the back of the mouth, and swallowed.

Drinking (Fig. 16)

When drinking, a crane stands with its neck vertically downward, and the beak almost horizontal, the lower mandible just under the surface of the water. The legs are bent at the tarsal joint, and the body is tilted downward about 30 degrees. The crane opens and closes its beak about 5 times in 2 sec, with visible inward and outward movement of the neck, at the base of the beak (Fig. 16a). Then the beak is tilted upward to slightly above horizontal, and the head and neck are raised to a normal upright posture as the legs are straightened (Fig. 16b, c). The water appears to be swallowed once the head and neck are above the level of the body. This drinking procedure takes about 5 sec, and may be repeated 4 to 7 times in a single drinking sequence.

Figure 16

Drinking.


A
B
C

Defecation

Defecation occurs while a crane is standing, with very little associated movement. The whole posterior end of the bird is raised slightly, as defecation only very briefly interrupts other activities, such as foraging or preening. If walking, the crane pauses just as defecation occurs. In captive birds, defecation occured 0.2 to 1.2 times per hour, but if alarmed or disturbed, cranes may defecate several times within a few minutes.

Cranes will occasionally defecate when wing raising (Fig. 11). When this happens, defecation occurs when the crane is in the most forward tilted position of the wing raising stretch.

Interindividual or Social Behavior

All behaviors that result from the presence of conspecifics are discussed in this section. Included are agonistic, reproductive and parental behavior. Agonistic behavior includes both dominant and submissive behavior most frequently seen during aggressive interactions. Reproductive behavior includes dancing displays, pre-copulatory and copulatory behavior, nest building, incubation and the behavior of pairs on their territories. Since reproductive displays frequently contain components of agonistic displays, they are often not easily distinguished. Hence the demarcation between these two categories is often not clear-cut.

The behavior of families with chicks of varying ages is discussed in the section entitled Parental Behavior. Vocalizations are also described and a discussion of interactions with other species is also included here.

Agonistic Behavior

Although many authors mention that sandhill cranes strongly defend their territories, there are almost no detailed descriptions of their behavior, and no mention of threat displays used by Sandhill cranes in spring and fall flocks. Because of the paucity of sandhill literature in this area, Masatomi's excellent paper on the behavior of G. japonensis is again referred to frequently. Published records of the agonistic behavior of sandhill cranes are summarized below.

Miller and Broughton (1971) observed a pair of sandhill cranes chase a caribou cow from their territory: "Landing between us and the cow, the crane began calling loudly and charged at her." They also noted that while they were on the cranes' territory, ". . . both cranes continued walking back and forth, vocalizing nearly continuously, occasionally flapping their wings briskly, and making short charges in our direction." Littlefield and Ryder (1968) observed that ". . . conflict between territorial birds and single individuals was frequent. Bodily contact was observed on several occasions, usually between neighboring pairs." When driving off the presumed offspring of the previous year, "The single bird always flew or ran from the area when approached by an individual performing a threat display and no bodily contact was observed." However they do not describe the above mentioned threat displays.

Drewien (1973) reports that on two occasions he observed pairs harassing and successfully driving dogs from the vicinity of their hidden young.

Caslick (1955) described the behavior of a crane pair when he approached their nest:

> When I was approximately fifty meters away, the bird arose slowly from the nest and walked silently towards me. When it was some twenty meters from the nest, it sounded an alarm call which was answered immediately by the mate which was feeding nearby, and it too then walked rapidly towards me. While they advanced, both birds called, quivered their half-stretched wings, splashed water by stamping their feet, and picked large beakfulls of rushes which they shook violently and then discarded.

Harvey et al. (1968) describe an apparent spread-wing display by a crane attempting to prey upon the eggs of a Blue Goose (Chen caerulescens):

> Before it (the crane) could break an egg however, an adult Blue Goose landed beside the nest, and stood over the eggs with its head held low in a threat position. The crane jumped back a meter. The goose then extended its wings with the wrists high and the tips of the primaries touching the ground, thus presenting the typical high intensity threat display of the Blue Goose. The crane responded with a similar display, and was immediately attacked.

Most of the threat displays described in this thesis were observed repeatedly both in captive and wild cranes. They have been classified as threat displays because of the circumstances under which they occurred and the ensuing behavior of other cranes in the vicinity of the displaying bird. Threat displays almost always involved either two clearly aggressive birds, both displaying, or one threat displaying crane and one or more clearly submissive birds. When two cranes initiate threat displays, one usually assumes a submissive posture in less than a minute. If both continue displaying, an actual fight may occur. Occasionally, both cranes cease displaying within a few seconds, without an apparent clear resolution to the conflict.

Threat displays were observed frequently on nesting territories, and in fall flocks. There was a very high frequency of threat displays among cranes at a corn baiting area, probably because of an abnormally high density of cranes here. When cranes in flocks gave threat dis-

plays, it was usually easy to determine what crane was the object of the display by its proximity to the displaying crane, and by its response to the displaying crane.

On nesting territories, the object of a crane's threat displays was not always readily apparent. However, by observing the displaying crane, it was often possible to eventually locate a strange crane within or near the territory of the displaying crane.

Threat Displays

Red Crown Expansion (Figs. 17a, b). Thirteen of the fifteen crane species have bare red or pink skin in the head or neck area. Seven of these have bare skin limited to the forehead and crown. This area can be expanded or contracted to cover varying amounts of head surface area. Adult sandhill cranes have red papillose skin, covered with short black bristles, extending from the culmen back over the forehead and crown (Fig. 17).

The bare red skin can be pulled back to cover the entire crown area almost to the base of the skull. At the same time, the tissue beneath the bare skin becomes engorged, and swells above the surrounding head area. This effect may be enhanced by sleeking of the surrounding feathers of the head and neck (Fig. 17b). Expansion of the red area occurs under many stressful situations. It is a part of all threat displays, but also accompanies other behaviors that contain agressive components, such as dancing, unison calling, and copulation. It is markedly absent in a submissive bird when in the presence of a clearly dominant conspecific.

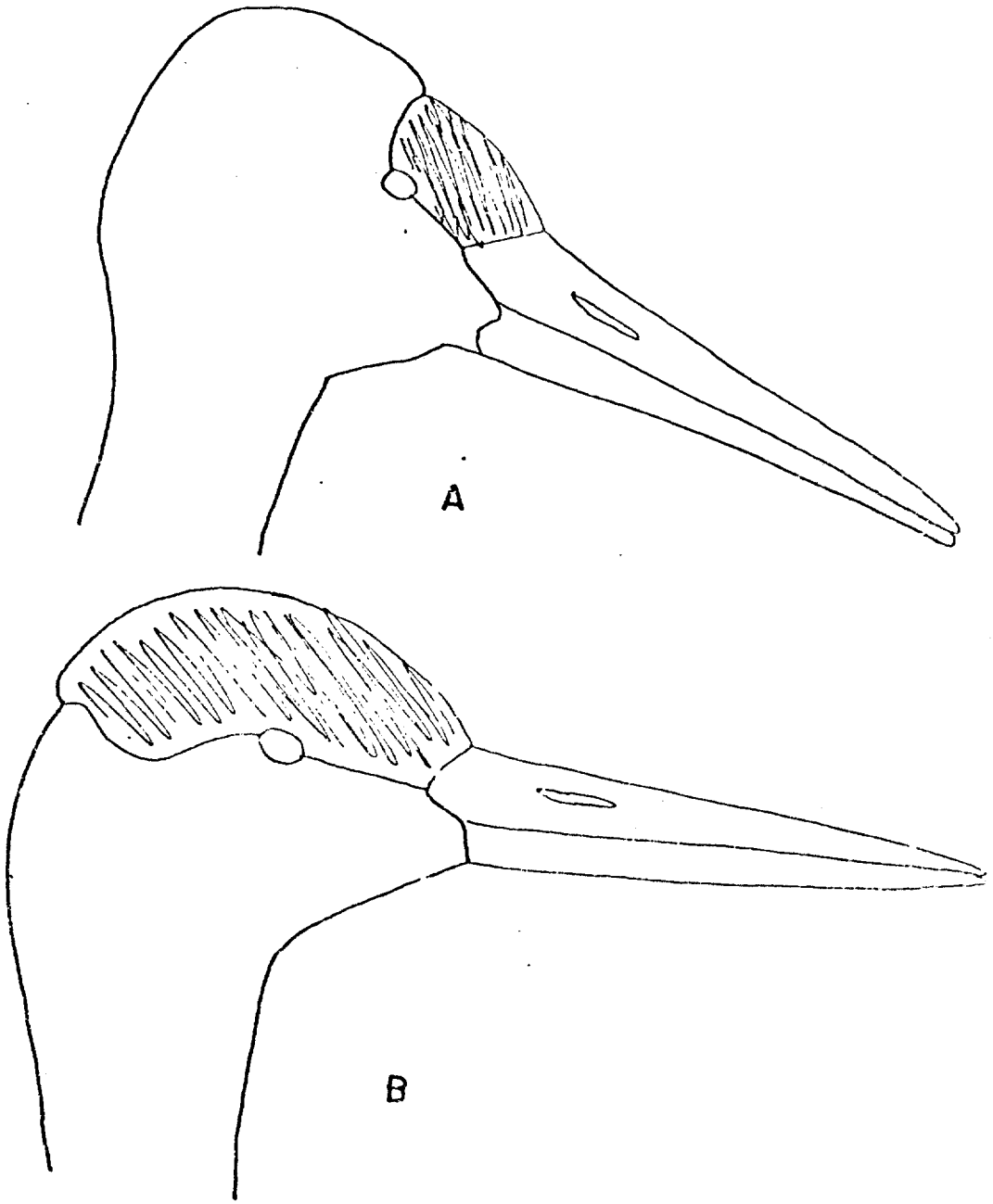
Prior to the post-juvenal molt, the crown of young sandhills is covered with tawny feathers. These feathers are lost during and after

Figure 17

Red crown expansion.

a) Crown not engorged.

b) Crown greatly engorged.



the post-juvenal molt, and the skin on the crown gradually becomes pinkish, then red. The age of development of adult red head coloration varies widely in both captive and wild cranes (Lewis 1974:176). However, the expansion of the crown area was observed in 16 week old chicks before any development of red head coloration.

Adornment display (Figs. 18a, b). The adornment display varies depending upon the aggressiveness elicited by the stimulus. When giving a low intensity adornment display (Masatomi: forward adornment, p. 856) the crane stands with its body horizontal or slightly above horizontal, and its neck either vertical or curved forward then upward. The beak is horizontal, or pointing slightly downward, and the red crown is expanded. The tertial feathers, which are long enough to completely cover the tail, are raised so that they form a vertical fan. Under a high intensity stimulus (Fig. 18b) the crane will bend forward so that its body is tilted downward at an angle of up to 30 degrees, its neck is curved downward then forward, and its beak is pointed straight downward. The red crown is expanded, and both the tertials and the posterior portion of the folded wings are raised. This is similar to Masatomi's lowered adornment for G. japonensis, however he does not describe the downward-tilted body observed in sandhills. This display may last several seconds to several minutes, and is often given first in a sequence of displays.

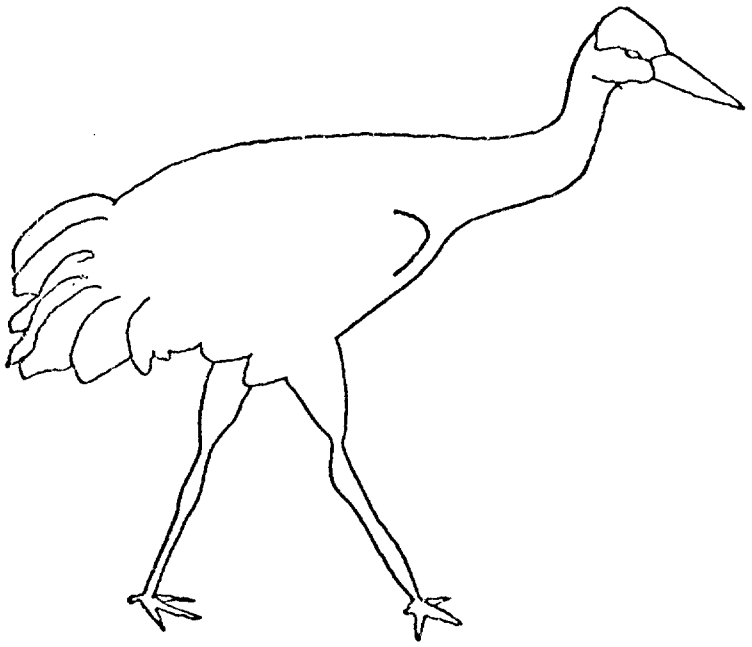
Adornment walk. The adornment display may be incorporated into a very ritualized walking display. The body is held in the same posture as in either the high or low intensity adornment display. The bird then walks at a rate of about 1 step per sec, either walking toward the crane being displayed to, or semi-circling around it. When semi-circling, the

Figure 13

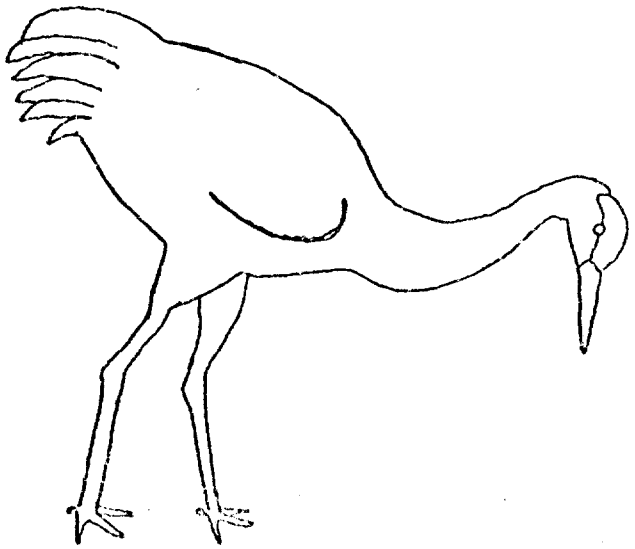
Adornment display.

a) Forward (low intensity) adornment.

b) Lowered (high intensity) adornment.



A



B

expanded red crown is tilted toward the other crane, so that a maximum amount of red is visible to it.

Low bowing display (Fig. 19 a-c). The low bowing display occurs under a variety of circumstances, and can vary in form depending upon the circumstances. It is often given just after landing (Fig. 19a) (especially when landing in or near a flock of cranes), when chasing another crane, and almost always following copulation. The low bowing display may be given while running. walking, or standing still. If running, the wings are often flapped vigorously, apparently to help in gaining speed; alternatively, the wings may remain folded. In any case, the body is between 5 and 20 degrees above horizontal, the neck and head pointed straight downwards, and the feathers at the base of the neck and upper back are conspicuously raised (Fig. 19b). The red crown is expanded. Whether walking, running or standing, this position may be held 5 to 10 secs, then the crane abruptly stands upright (Fig. 19c). Frequently, a few jabs at vegetation (ritualized foraging) will precede standing upright. This display was first observed in captive chicks at 11 weeks of age.

Masatomi (p. 858) also describes a high bowing display in G. japonensis in which the body and neck are angled upward about 45 degrees above horizontal, and the bill is pointed vertically down, or towards the breast. This display was not observed in sandhills.

Stamping. The crane quickly lifts and lowers its feet alternately so that each foot "stamps" about 3 to 5 times per sec. This display is rare in sandhills, and I have not observed it, although Archibald (pers. comm.) has described it. Masatomi does not describe this display in

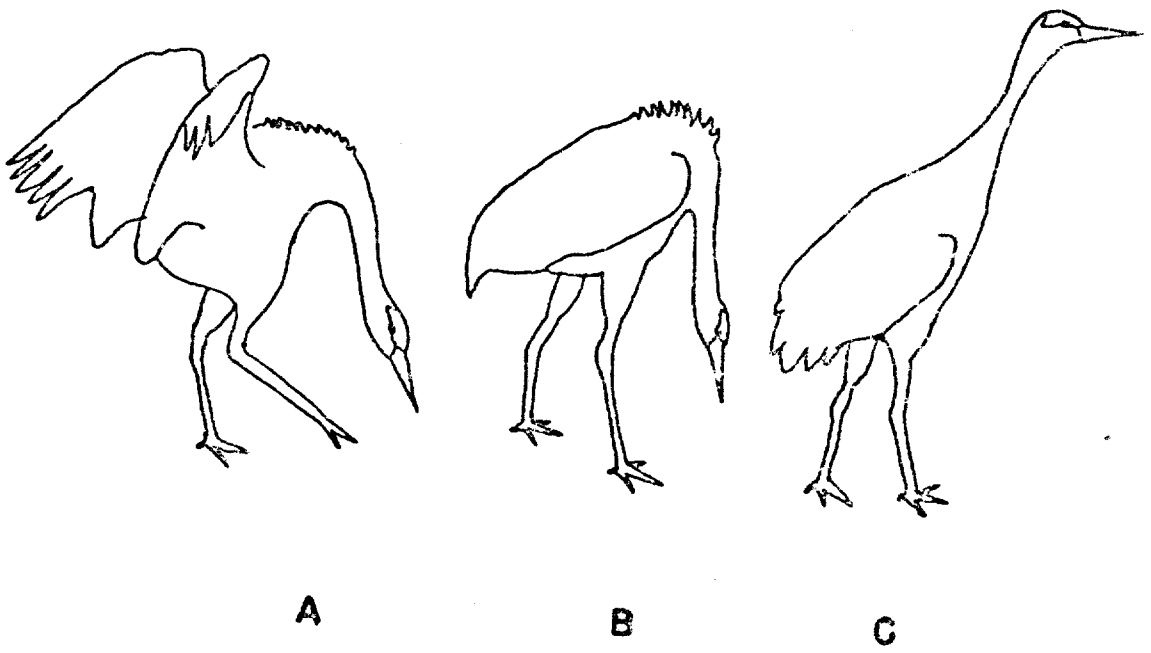
Figure 19

Low bowing display.

a) Posture when low bowing immediately follows landing.

b) Typical low bowing posture.

c) Posture following low bowing display.



G. japonensis, but mentions it while describing arching (p. 857), a display not given by sandhill cranes.

Irrelevant Threat Displays

Masatomi (p. 858) groups a number of threat displays under the title Irrelevant Postures. These displays seem to have evolved from maintenance or other activities without signal function, and are now given "out of context," and in highly ritualized form.

Irrelevant foraging display. The crane stands, with its body angled 10 to 20 degrees below horizontal, and its head lowered so that the tip of the bill is near the ground. The red crown is expanded, and the tertials may be raised. The crane may pick up and drop bits of vegetation, yank or jab vigorously at the vegetation with its bill, or simply stand, bill down, without actually touching the vegetation. The display may last several sec to several min, the longer bouts involving vigorous jabbing and yanking at the vegetation. Masatomi refers to this display as irrelevant ground sticking, however I prefer irrelevant foraging since it does not always involve jabbing at the ground.

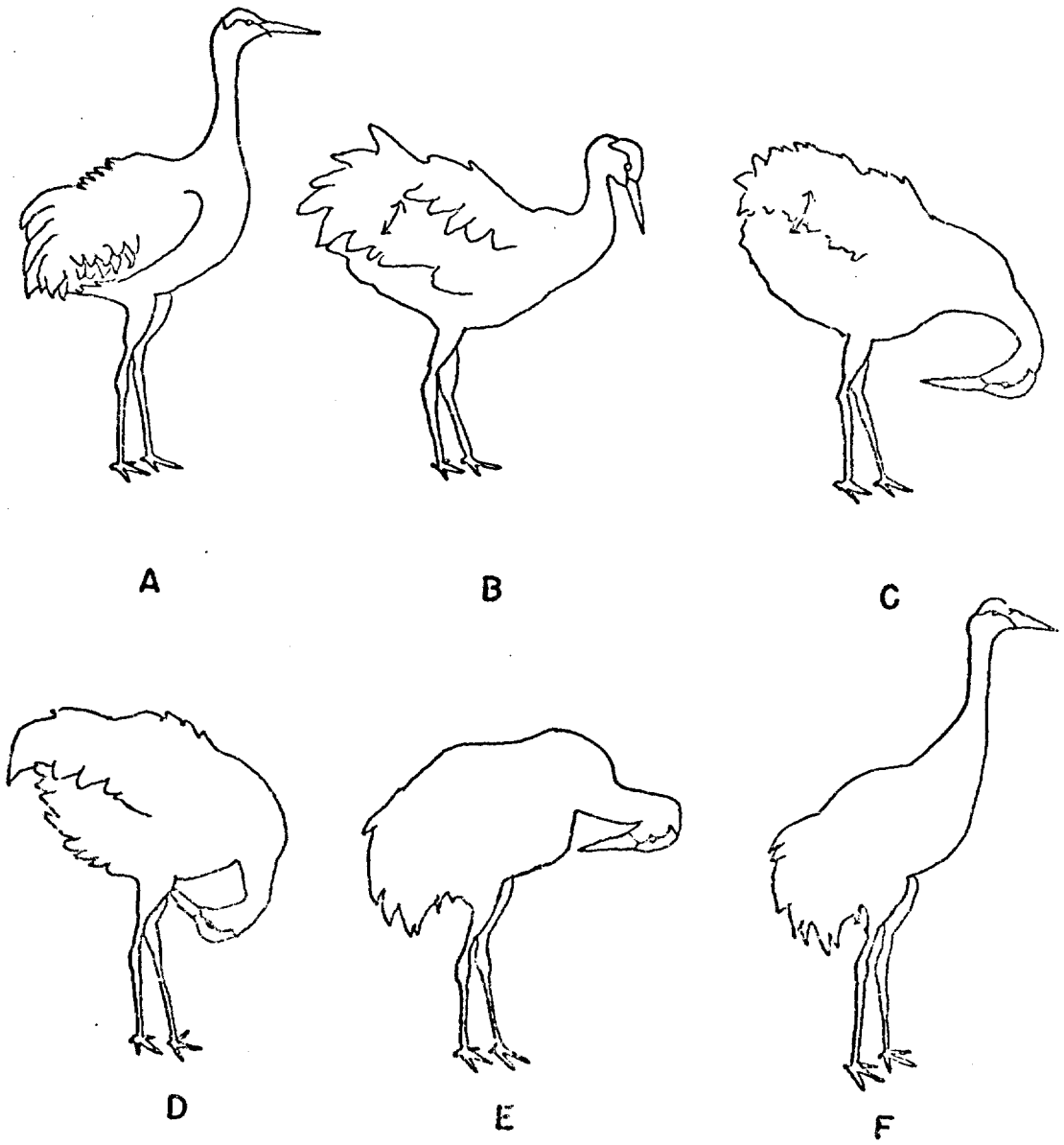
Irrelevant body-wing shaking display (Fig. 20a, b). The crane stands upright with its body horizontal and its neck vertical, the red crown expanded (Fig. 20a). The display begins with erection of the feathers on the neck, back, breast, abdomen and wing surfaces. The crane raises a loosely folded wing slightly off the body at the shoulder, then lowers it to slightly below the normal folded position. Opposite wings are flapped alternately. At first, each wing flaps about once per sec, but the rate quickly increases so that after 3 to 4 secs, it is not possible to count individual wing flaps, and the total impression is of the bird

Figure 20

Body-wing shaking display.

a-b) Simple body-wing shaking display.

a-f) Body-wing shaking-leg preening



shaking or "ruffling" rapidly from side to side. During this display, the neck may be outstretched forward, or retracted with beak pointing downward (Fig. 20b). After 0.5 to 10 secs, the crane stops body-wing shaking, lowers the feathers of the body, and returns to an upright standing position with its body horizontal and neck vertical, the red crown still expanded.

This body-wing shaking display is also incorporated into a number of display sequences. After irrelevant body-wing shaking, the crane may go directly into irrelevant leg, breast or abdomen preening, or foraging. When irrelevant preening is incorporated into the display as shaking begins, the neck is retracted so that the head is just above the back (Fig. 20b), then swung in one continuous movement forward and downward and under the breast, so that the tip of the beak touches the feathers of the upper leg or the abdomen in ritualized preening (Fig. 20c, d). As the beak touches the feathers, shaking stops, and the crane lowers the erected feathers of the body. The crane may immediately raise its head and neck to a vertical position (Fig. 20e, f), or the ritualized preening may transpose to real preening, when the crane actually nibbles and pulls at its feathers. After several seconds, the crane may lift its head and stand upright, or preening may continue on other parts of the body, such as back, wings or neck. Knoeder (1964) clearly describes body-wing shaking-abdomen preening display given by captive reared cranes:

> Typically, the male will approach the observer with wing coverts noticeably elevated, tail arched, neck slightly arched, and with rather slow, deliberate, stiff movements. The contour feathers are depressed. The crane approaches usually to within 3-4 feet and turns sideways in a ritualistic fashion, presenting a lateral view to the observer. Immediately, the wings are rapidly

> shifted up and down 6-10 times, held close to the sides and completely folded: simultaneously, the neck is curved and extended in a single sweeping motion into an arc until the bill is placed into the abdominal feathers; while half-way through this arc, a low pitched, throaty-rumble of a call is given, which is terminated by the time the point of the bill reaches the abdomen. This note is low in volume, and cannot normally be heard more than 10 feet away. This display always terminates in perfunctory preening of the feathers of the lower breast, which lasts for several seconds. The bird then regains normal stance, and quite commonly stalks away.

He observed this display in captive males only, however I have observed all displays given by both males and females. He tentatively suspected that "It is some type of threat or intimidation activity."

Masatomi (p. 860) describes irrelevant leg-preening and irrelevant back-preening as separate displays. However these preening displays never occur independently in sandhill cranes. Irrelevant back or shoulder preening follows irrelevant body-wing shaking only very rarely in sandhills, but is a much more common display in G. japonensis.

In the body-wing shaking-foraging display, as shaking begins, the crane lowers its outstretched neck forward and downward, pendulum like, until the tip of its beak touches, or nearly touches, the ground just in front of its feet. This position may be held for up to 5 secs, then the feathers of the body are lowered, and the crane very quickly raises his head and neck. Occasionally this display transposes to actual foraging, in which case the crane may not raise its head at the end of this display.

A body-wing shaking-unison sequence given by a male was also observed once. He began by shaking and bending forward slightly as if to begin a body-wing shaking-leg preening display (Fig. 20b), but then raised his head high, neck vertical, and gave the male half of the unison

call (Fig. 35). He continued shaking for the first 2 to 3 secs of the unison call, and then ceased shaking and held the wings folded but slightly above the body.

The body-wing shaking display first appeared in crane chicks at 14 weeks of age. It is similar to the adult display, except that wing flapping is not as ritualized, and the wings can be flapped simultaneously, alternately, or both, during a single display. The head is often lowered during flapping as if to follow body-wing shaking with a preening or foraging display, but the beak never actually reaches the feathers or the ground. This shaking was recognized as a display rather than maintenance activity in chicks by the abrupt return to an upright posture following body-wing shaking, and by the context under which it was given. This display occurred under stress conditions, such as in the presence of a sibling or a dog.

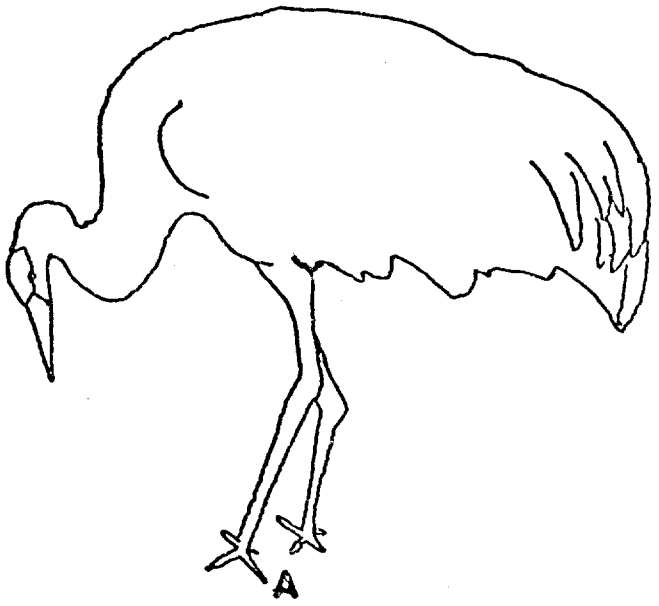
Body-wing shaking displays were frequently observed in wild cranes, especially in fall flocks. Cranes which had just landed at the edge of a flock frequently gave this display within a few minutes of landing.

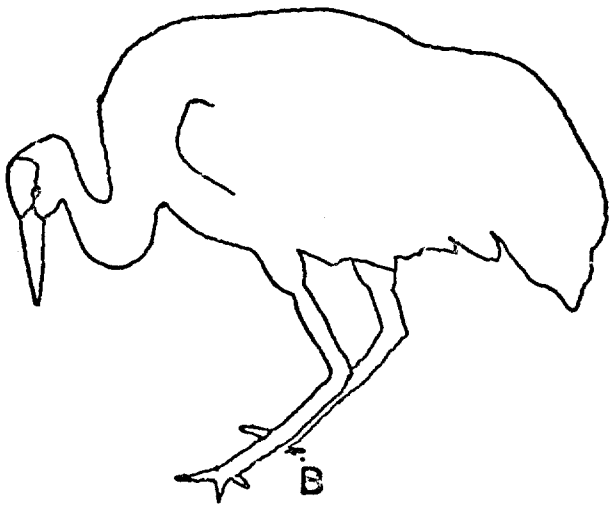
Irrelevant crouch display (Fig. 21a, b, c). This behavior pattern was first observed in captivity in 11 week old chicks. It occurs in the presence of conspecifics, and was never observed in the presence of possible predators such as dogs or hawks.

The crane stands, body horizontal, neck retracted and curved downward, beak pointing downward, red crown expanded (Fig. 21a). He then bends his tarsal joints, lowers himself to hock posture (Fig. 21b), then immediately to sitting posture (Fig. 21c). The base of the neck touches the ground, but the rest of the neck is more or less vertical, with beak pointing downwards. The wings remain loosely folded, and may be held

Figure 21

Irrelevant crouch display.


A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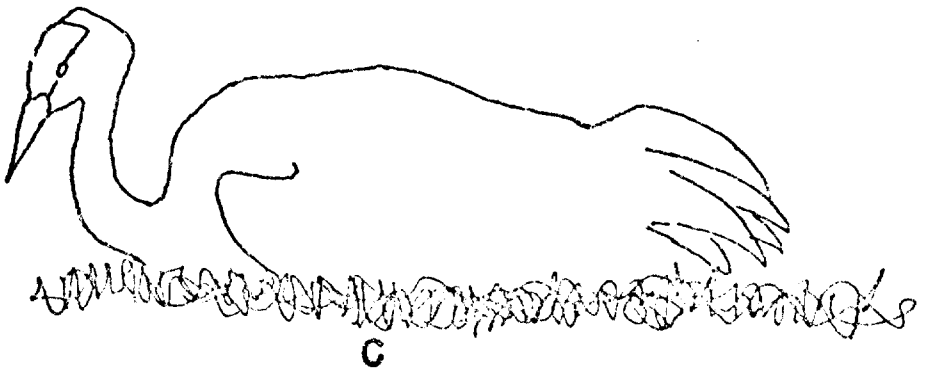

C

slightly away from the body at the wrists. The tertial feathers are raised. The crane may hold this position 0.5 to 30 secs, and then stand up. Threat displays may then cease, or the crouch may be followed by continued red crown expansion, and other threat displays, such as adornment or body-wing shaking.

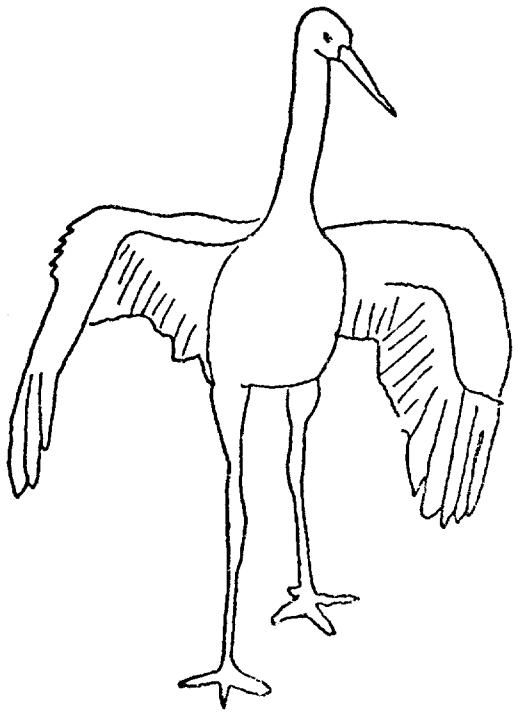
A crouch display was observed once given by a wild bird. Two pairs approached each other, all giving adornment displays, then one crane ran at the other pair while low bowing. They retreated immediately in neck retracted submissive posture and the charging crane performed a partial crouch threat (his tibiotarsal joints did not actually touch the ground before he stood upright). In this instance, the crouch display was directed towards two clearly submissive cranes. Archibald (pers. comm.) believes this display is derived from incubation posture.

Spread Wing Display (Fig. 22)

This display was first observed in captive six week old chicks, and seen most frequently in chicks less than six months old. It was seldom seen in adults, although Harvey et al. (1968) described this display, directed by an adult crane towards a Blue Goose. The crane stands with its body above horizontal, its neck vertical or slightly forward, back pointing downward. The feathers of the head, neck and body are sleeked, and the crown area is expanded, even in chicks which have not yet developed red crowns. The wings are held horizontally outward from the body, either fully extended, or drooping at the wrists. The crane may either stand or walk about, facing the stressful object. Spread wing posture may be maintained for several seconds to several minutes, and was elicited in captive cranes by clearly dominant conspecifics, dogs, and a captive red-tailed hawk.

Figure 22

Spread wing display.



I did not observe this display in wild cranes.

Masatomi (p. 860) describes a similar posture as upright pecking. However pecking was never involved in this display in sandhills.

Attack (Fig. 23 a-e)

Occasionally one crane will attack another with or without preliminary threat displays. Attacks were observed several times in captive cranes. Wild cranes in fall flocks were observed fighting twice, both times in an area where there was a high density of cranes. I never observed actual fighting on nesting territories, although Littlefield and Ryder (1968) report observing bodily contact on several occasions.

Chasing (Fig. 23a). Attacks include chasing, where the attacker runs toward the attacked crane, neck outstretched at about 50 degrees above horizontal (Fig. 26a). Masatomi (p. 861) reports a similar chasing posture, except that the neck is forward and somewhat retracted, and the head is only slightly above the level of the back.

Kicking (Fig. 23 b-e). Chasing is often followed by kicking. As the crane approaches the attacked crane, it flaps its wings and jumps 1 to 2 m into the air, so that its body is vertical and legs thrust forward (Fig. 23b). It kicks forward and downward at the other crane (Fig. 23c, d). One or both cranes may jump and kick like this until one or the other retreats.

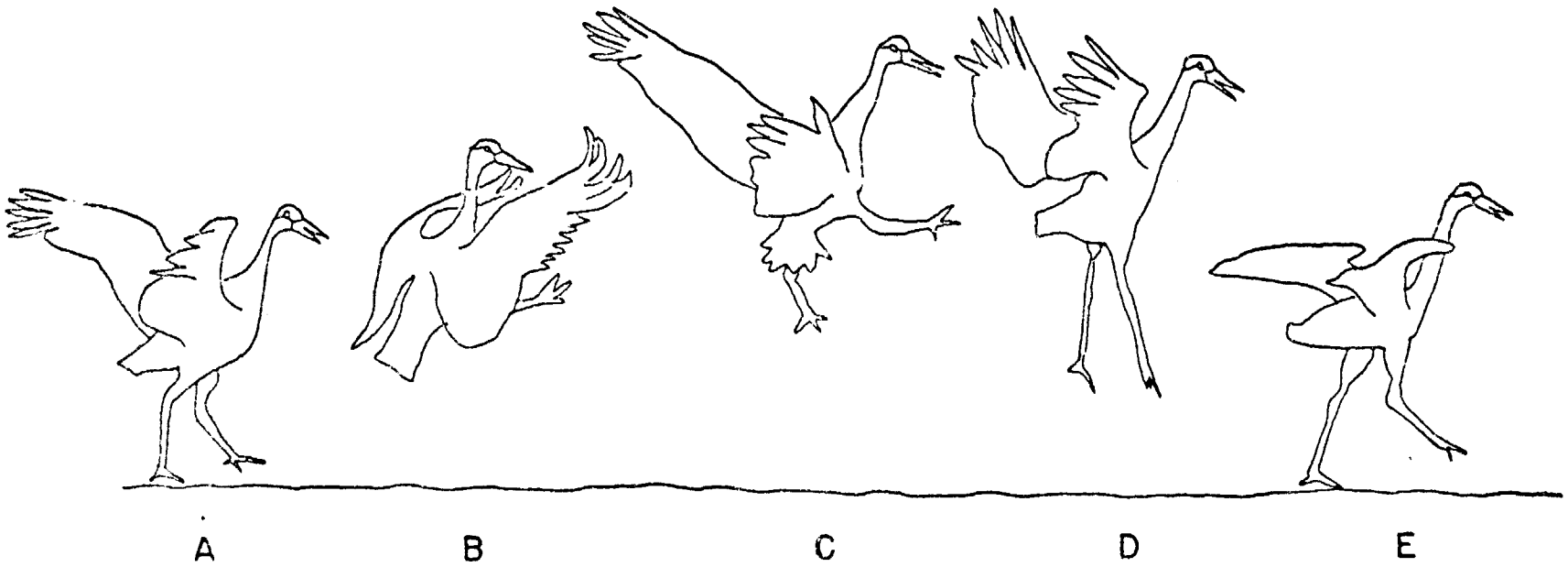
Upright pecking. Two cranes may stand facing each other approximately 1 m apart, each with its body and neck angled up at 40 to 50 degrees above horizontal. The wings may be partially or fully opened. The crane may then peck at the other's head, neck, or back. Upright pecking

Figure 23

Attack.

a) Chasing.

b-e) Kicking.


A
B
C
D
E

is also often followed by kicking. This posture is very similar to the spread wing posture (Fig. 22), but occurs only when two cranes are in very close proximity, and is usually a part of actual fighting.

Interchick Aggression

Sandhill crane chicks exhibit unusual aggressiveness towards each other from a few hours after hatching until approximately 50 days of age (Boeker 1961, Walkinshaw 1973a). The stronger chick, which may be either the first or second hatched, will occasionally drive its sibling from the nest (Walkinshaw 1973). Some observers believe that this may contribute significantly to chick mortality at this age (Harvey, et al. 1968). The parents apparently separate the chicks by as much as 200 m during the day, one parent staying with and feeding each chick (Boeker 1961, Harvey et al. 1968, Drewien, 1973). The family comes together only at night, when one parent may brood both chicks, thus preventing fighting. At about 50 days of age, this aggression apparently subsides, and families may be observed foraging together (Walkinshaw 1965).

This interchick aggression has also been observed in captive reared chicks until about 50 days of age (Boeker 1963, Archibald, pers. comm.). Quale (1975, in press) found that in captivity chicks are more aggressive when hungry or when in their territory, and are more aggressive towards chicks smaller than themselves than towards chicks larger than themselves. Drewien (1973) found that in each of three broods captured in 1970, one young weighed considerably less than its sibling, suggesting that the larger chick may preempt food provided by the parents.

Ambivalent Behavior

Alert posture (Fig. 24). The crane stands or walks, neck extended vertically upward, and its movements appear tense rather than relaxed. The feathers of the body are held much closer to the body than they are normally, so that the neck appears thinner than normal, and the wrists stand out prominently rather than contributing to the normal smooth contours of the crane's body. Alert posture was observed ten times in captive cranes, and eight times could be directly attributed to the approach of dogs or strange humans, or the flight of a hawk or crows overhead. Two times the immediate cause of this behavior was not known, although cranes in adjacent pens also gave guard and alarm calls, and appeared tense. Twice alert posture was followed by preflight posture, then flight. Masatomi (p. 863) believes this behavior results from two opposing urges: to stay and to flee.

Submissive Behavior

This section includes the behavior of the submissive crane in agonistic encounters. The red crown is always contracted.

Neck retracted submissive posture (Fig. 25a, b). The crane stands with body horizontal and neck retracted so that its head is near the base of the neck. The bill is more or less horizontal, or pointing slightly downward and the red crown is contracted. The wings are loosely folded, and the body feathers are slightly elevated, so that the crane appears slightly fluffy (Fig. 25a). Chicks may raise their back and tertial feathers much higher than adults, and hence appear much fluffier. When walking in neck retracted submissive posture, the crane is very relaxed and loose jointed, with no sign of stiffness in its gait.

Figure 24

Alert posture.

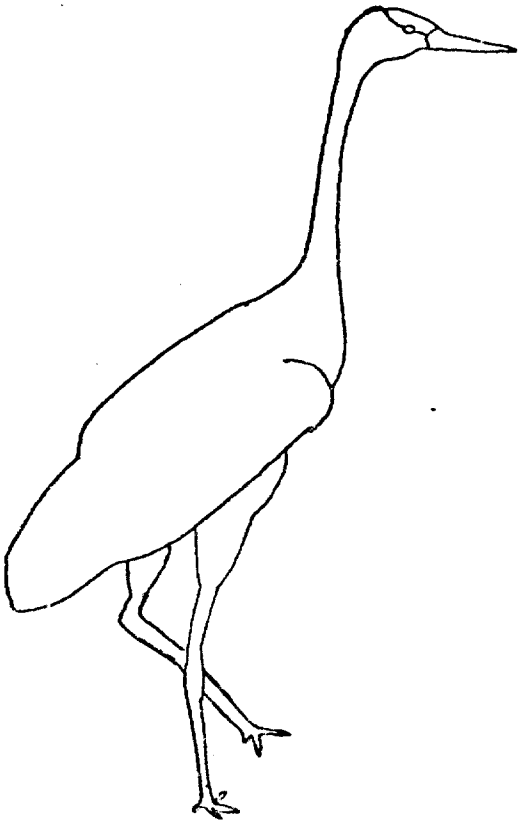
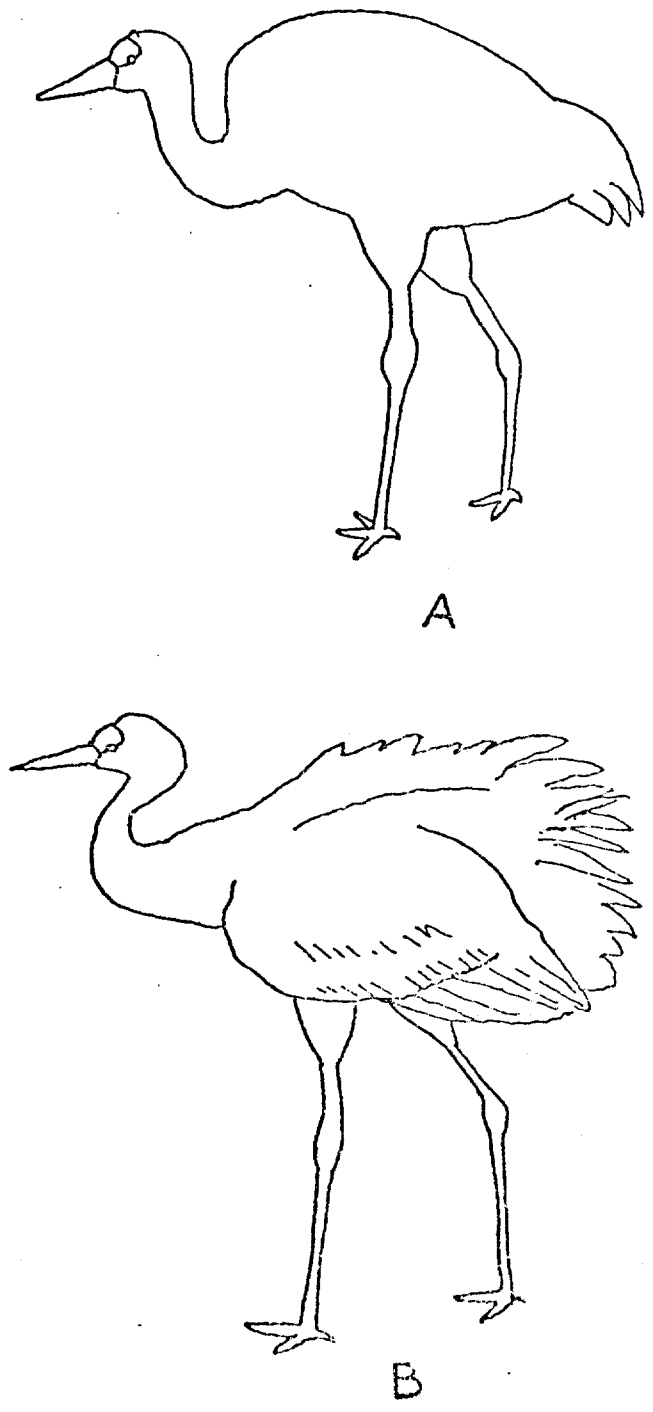


Figure 25

Neck retracted submissive posture.

a) Adult.

b) Immature.



This posture was first observed in chicks at about six weeks of age. Chicks often assume this posture when near their parents, particularly when food begging. This position is almost always assumed by the submissive bird, whether immature or adult, in any threat encounter. When families interact, chicks of both families, whether dominant or submissive, usually remain in neck retracted submissive posture. In feeding flocks, where some individuals are constantly displaying, other individuals are almost constantly in neck retracted submissive posture while foraging.

Fleeing. A submissive crane may flee from an aggressive crane. The crane runs with the body 0 to 30 degrees above horizontal. The neck is usually retracted into an "s"-shaped curve, but may be extended forward at about 45 degrees above horizontal. The wings may be closed, or flapped to provide added speed. A crane may flee for 1 to 10 m or more. Fleeing may be followed by flight, or by neck retracted submissive posture if the pursuing crane ceases chasing.

Wing spreading posture (Fig. 28a, female). Chicks in captivity began assuming the female copulatory wing spreading posture at about six weeks of age. This posture was assumed only when a chick was approached by a human with which he was very familiar, or a clearly dominant sibling. The context under which this posture was assumed seems to indicate that it may have been used as a submissive posture by the chick. This posture was not observed in wild chicks. Masatomi does not describe this submissive posture for G. japonensis.

Reproductive Behavior

Dancing

The dancing behavior of cranes has long been recognized as a part of courtship ritual (Visher 1910, Storber 1940). However, it is almost certainly a multifunctional behavior. Walkinshaw (1949) notes that "they apparently perform regardless of the number of birds present and regardless of age, sex, season, place or time of day."

Dancing may begin when chicks are less than two days old (Walkinshaw 1949, Grange 1955, Rand 1956). Archibald (pers. comm.) believes that dancing in young chicks occurs as a part of motor development. He also observes that in captivity, unpaired two and three year old cranes seem to dance more than any other age group, and that dancing probably serves to thwart aggression and facilitate formation of pairs.

Several observers report that although dancing occurs year around, it occurs more frequently in the spring on the roosting ground, just before nesting (Walkinshaw 1949, 1973, Rand 1956). Archibald (pers. comm.) believes that dancing sexually synchronizes both members of a pair prior to copulation and egg laying, and that the frequency of dancing sharply decreases after nesting begins. He also reports that older pairs seem to dance less than young pairs, apparently because of their already greater sexual synchrony and a reduced need to thwart aggression.

Dancing also seems to serve as a release for nervous energy, or to be a displacement behavior. Archibald (pers. comm.) reports that at feeding stations in Japan, Manchurian cranes (Grus japonensis) will retreat at the approach of humans bringing food, but that many cranes dance as the human leaves. Walkinshaw (1949) reports that when he inspects nests, the cranes will often dance as he retreats.

I observed dancing regularly in captive chicks from the age of two days on, in wild birds in fall and spring flocks and in nesting birds, both in pairs and individually. I observed dancing five times in spring and fall flocks, both on roosting areas and on feeding grounds. Individuals and pairs danced most frequently, although once a larger group danced. In this group, there was little or no actual coordinated group dancing. Different individuals danced every few minutes so that over a period of about 15 min, dancing was occurring about half the time. Walkinshaw (1949) wrote that dancing was done by individuals and groups scattered throughout a flock, and that various members of the flock, first one then another, then many, would dance at a time. He also reported that while dancing, "the flock was sometimes entirely noiseless (and sometimes) it raised a great din of voices."

In pre-nesting pairs I observed dancing three times. Twice it followed copulation or pre-copulatory behavior, and once a crane danced after flying approximately 600 m from one part of its territory to another. The non-incubating member of a nesting pair was observed dancing six times, each time right after a bout of foraging.

Dancing behavior can be divided into several component parts, which may occur separately, or together in various combinations. In chicks too young to fly, dancing consisted exclusively of wing flapping, leaping, or bouncing, and occasionally running. The chick flaps its extended wings 2 to 3 times per sec while bouncing or leaping up and down 2 times per sec. In very young chicks, the tips of the toes remain in contact with the ground, and dances last only 3 to 4 secs. By about 40 days of age, chicks can leap several inches into the air, and dances last about 10 secs. When wing flapping is accompanied by running rather than

leaping the chick leaps into the air from one foot, extends the other leg forward, and lands on it. Thus the crane moves forward in a series of leaps. In chicks, only three to four leaps were usually given in sequence. In adult cranes, these leaps are extended, and many are given in sequence, so that the crane appears to run while dancing.

Dances of older cranes may be broken up into several component parts. Stooping, pre-leaping and leaping were first observed at 14 weeks. While stooping (Fig. 26a, c) the crane bends forward so that the body is about 30 degrees below horizontal, the legs slightly bent at the tarsal joints. The neck is retracted so that the head is close to the body, beak pointing downward. The wings are held either fully extended (Fig. 26a) above the back, or raised high above the back while remaining folded at the wrists (Fig. 26c). The crane then quickly raises its body and extends its neck upward, straightening its legs, until its body is up to 20 degrees above horizontal (pre-leaping, Fig. 26b), then again quickly retracts its neck and stoops forward (Fig. 26c). The crane may stoop 1 to 2 times per sec. Masatomi (p. 867) refers to many repeated stoops as pumping (Fig. 26 a-c).

Alternatively, actual leaping may follow pre-leaping. When this happens, the crane leaps upward in much the same posture as pre-leaping, but with enough forcefulness to raise the body 1 to 3 m above the ground. The wings may also be flapped during leaping.

Picking up (Fig. 27a) is very similar in form to stooping except that as the crane stoops deeply, it extends its neck forward and downward and grasps a bit of vegetation in its bill. The crane then quickly raises its body and extends its neck upward (Fig. 27b) and finally flings its bill upward, pivoting at the base of the head, releasing the vegeta-

Figure 26

Dancing: pumping

a,c) Stooping

b) Pre-leaping

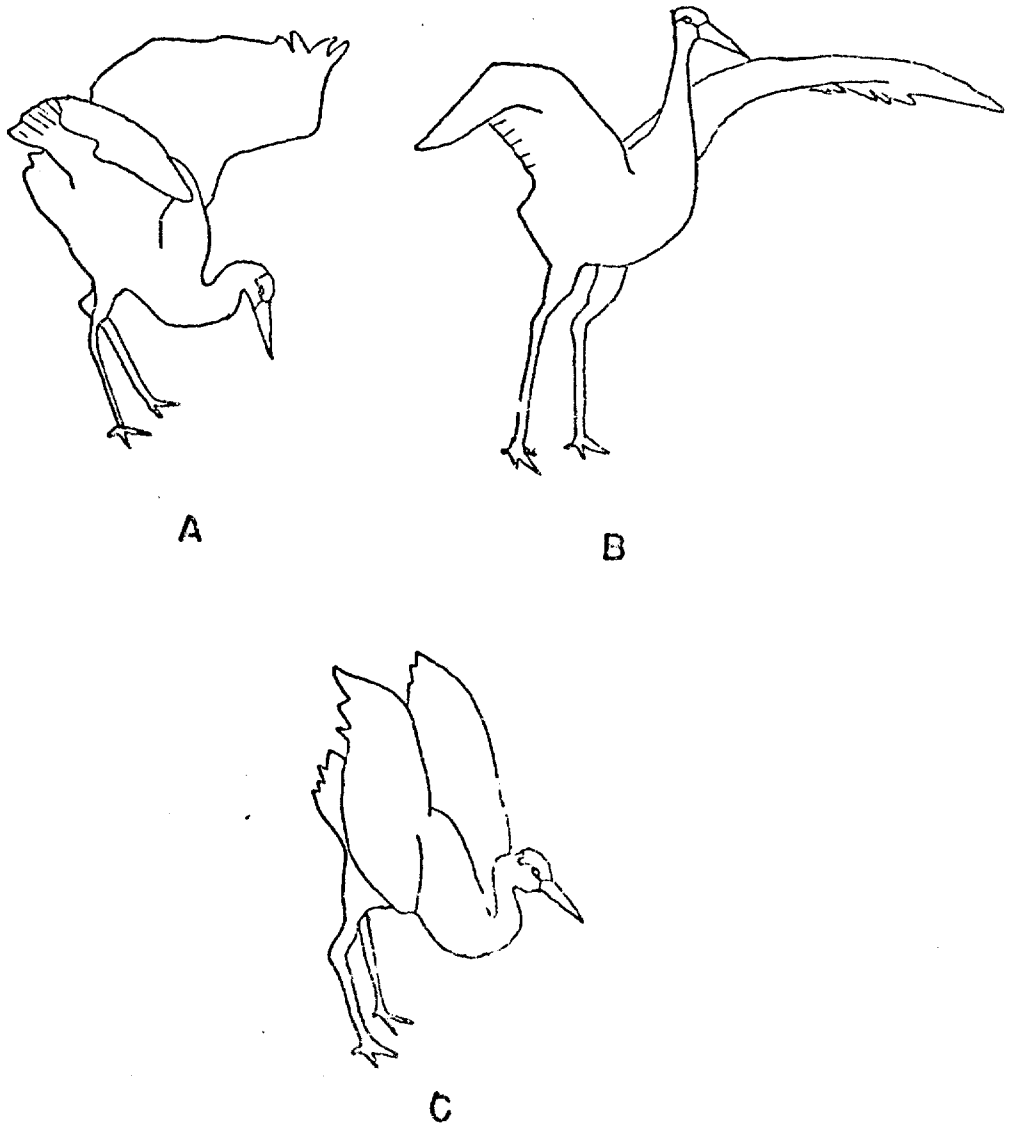


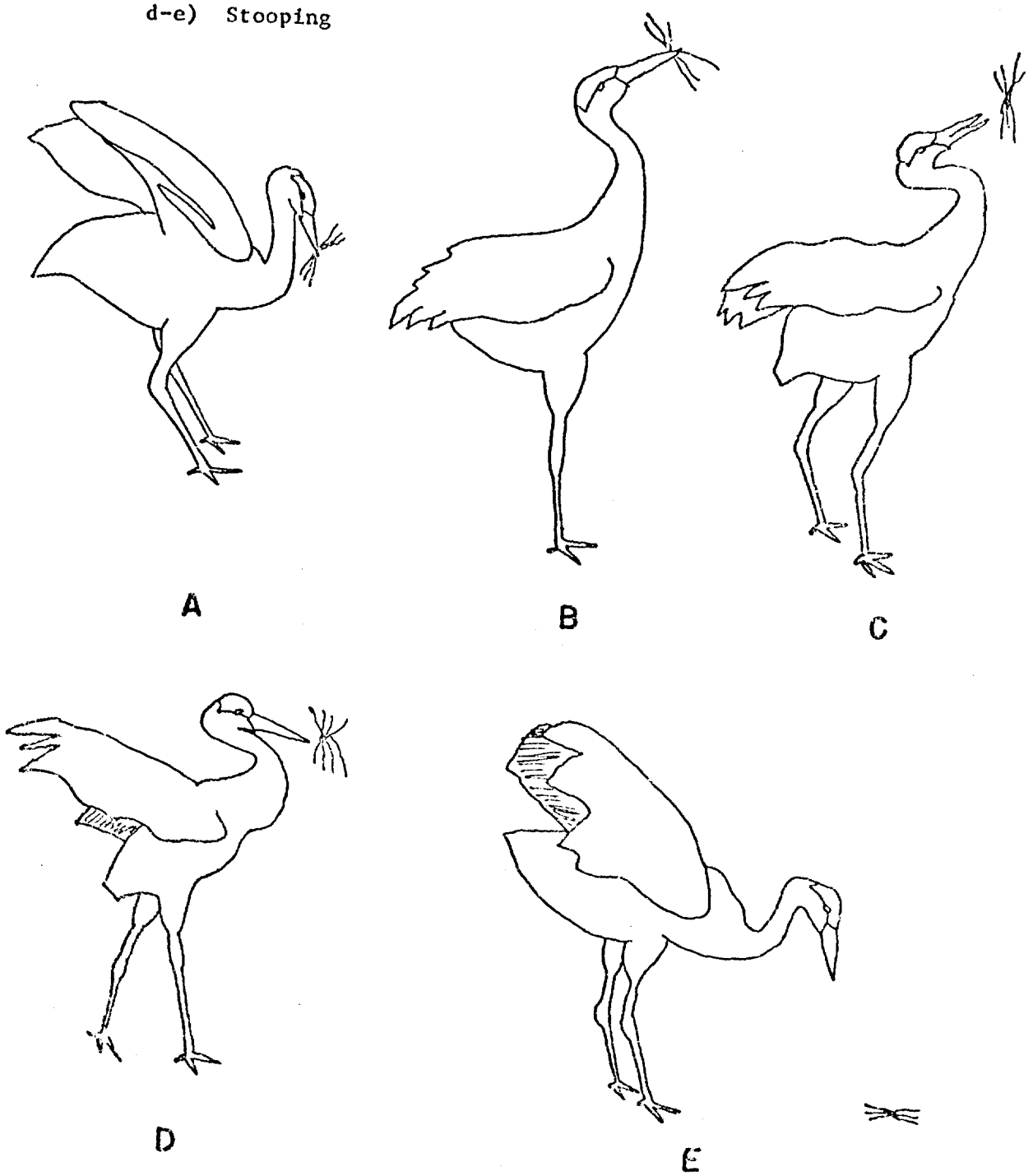
Figure 27

Dancing:

a) Picking up.

b-c) Throwing.

d-e) Stooping



tion (throwing, Fig. 27c). The neck is then quickly retracted, the head near the base of the neck, and the bird stoops forward (Fig. 27d, e). Picking up and throwing were first observed at 17 weeks. They are often interspersed with stooping and pre-leaping.

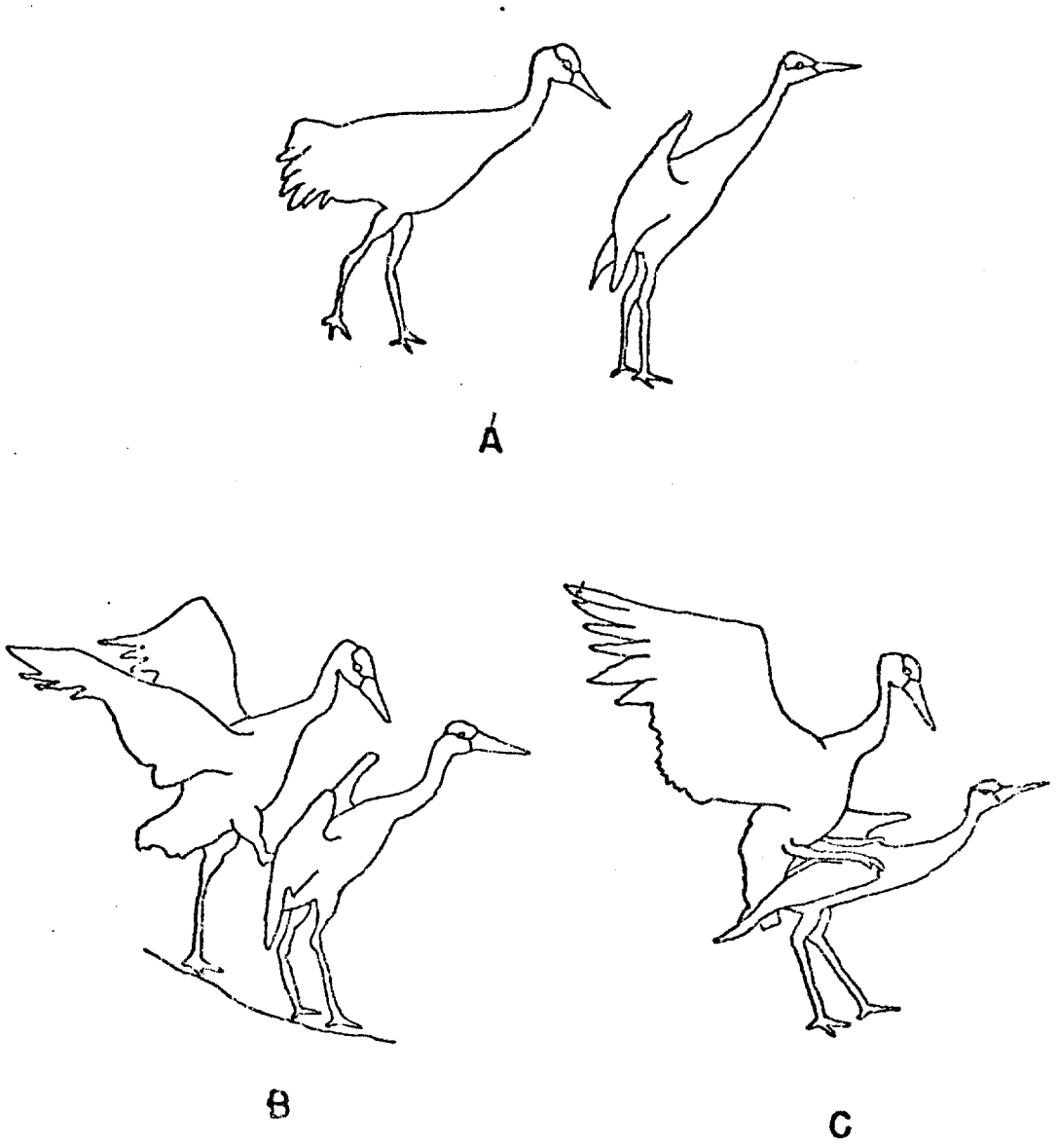
The red crown of sandhills is always expanded during dancing.

Pre-Copulatory and Copulatory Behavior

The red crowns of both the male and female are expanded throughout the pre-copulatory and copulatory sequence. Pre-copulatory behavior may be initiated by either the male or the female, but most frequently, both begin displaying almost simultaneously. Typically, the male is behind the female at the beginning of the display, anywhere from 0.5 to 50 m away. He walks toward the female at a rate of about 1 step per sec, with tertials raised, as in the adornment display. His neck is stretched vertically upward at about 80 degrees above horizontal, and his beak is pointing upward at about 60 degrees above horizontal (bill raising, Masatomi, p. 868). Simultaneously, he gives the pre-copulatory call, a series of short, purr-like calls, gradually swelling in volume. The female holds her head and neck in the same position as the male, and either stands, back to the male, or initially walks slowly away. When the male approaches within 3 m, the female holds her wings straight out horizontally from her body, but drooped at the wrists (wing spreading, Fig. 28a). As the male approaches to within 0.5 m, he pivots his head until his beak is pointing slightly downwards (Fig. 28a). When 5 m away, he beats his wings once or twice, and hops up onto her back, hooking his toes over her forewing, his tarsal joints resting on her rump (mounting, Fig. 28b, c). Simultaneously, the female bends forward so that her body is almost horizontal. Her neck is curved upward, but not extended, so that her head is

Figure 28

Copulation.



above her breast (being mounted, Fig. 20c). The male remains on the female's back about 3 to 5 sec, flapping his wings to maintain balance. Copulation is very brief and difficult to observe. The male dismounts either by stepping off backward while beating his wings, or by hopping off over her head. The female immediately folds her wings as he dismounts.

Copulation is followed by a post-copulatory display sequence which usually lasts about 20 secs, although the number of displays and length of the sequence may vary. Typically, the birds stand side-by-side, necks stretched vertically upward, red crown expanded. Simultaneously, the cranes give a low bowing display, while taking one to two steps forward (Fig. 19), then stand, necks vertical, beaks horizontal, red crown expanded for 5 to 10 secs, then give a body-wing shaking or body-wing shaking-leg preening display (Fig. 20). This may be followed by foraging, preening or dancing.

Pre-copulatory sequences were often observed aborted before the male actually mounted the female. In these instances, the male would stop approaching before he reached the female, or walk past her instead of mounting. As soon as the normal pre-copulatory sequence was interrupted, the female would fold her wings. The pair then often began a post-copulatory display sequence similar to that observed after complete copulation.

Nest Building

Cranes build their nests in an extremely ritualized manner. Most nest building occurs prior to egg-laying and incubation, but cranes continually add new material to the nest throughout the incubation period, particularly when a crane has just relieved its mate on the nest. To add

material to the nest, the crane, either sitting or standing over the nest, will reach forward with its beak, grasp a piece of grass, reed or twig, then, with beak pointing downward, the crane bends its neck either to the left or the right, and drops the vegetation at its side. This movement is repeated in exactly the same way each time, regardless of where the crane is in relation to its nest. Hence if the crane is 1 to 2 m away from the actual nest, the vegetation is placed at its side, but not on the nest. During active nest building, the same piece of vegetation may be picked up and moved several times. Hence, as the crane moves closer to the nest, the vegetation becomes concentrated at the nest site. This nest-building movement is so ritualized that it is carried to completion even if the crane drops the vegetation midway.

Young cranes were first observed carrying out nest building movements in November at 25 weeks of age. Although there was no actual nest site, the ritualized placement of twigs was unmistakable.

Masatomi reports that G. japonensis will carry nest material some distance to the nest. This was never observed in sandhills.

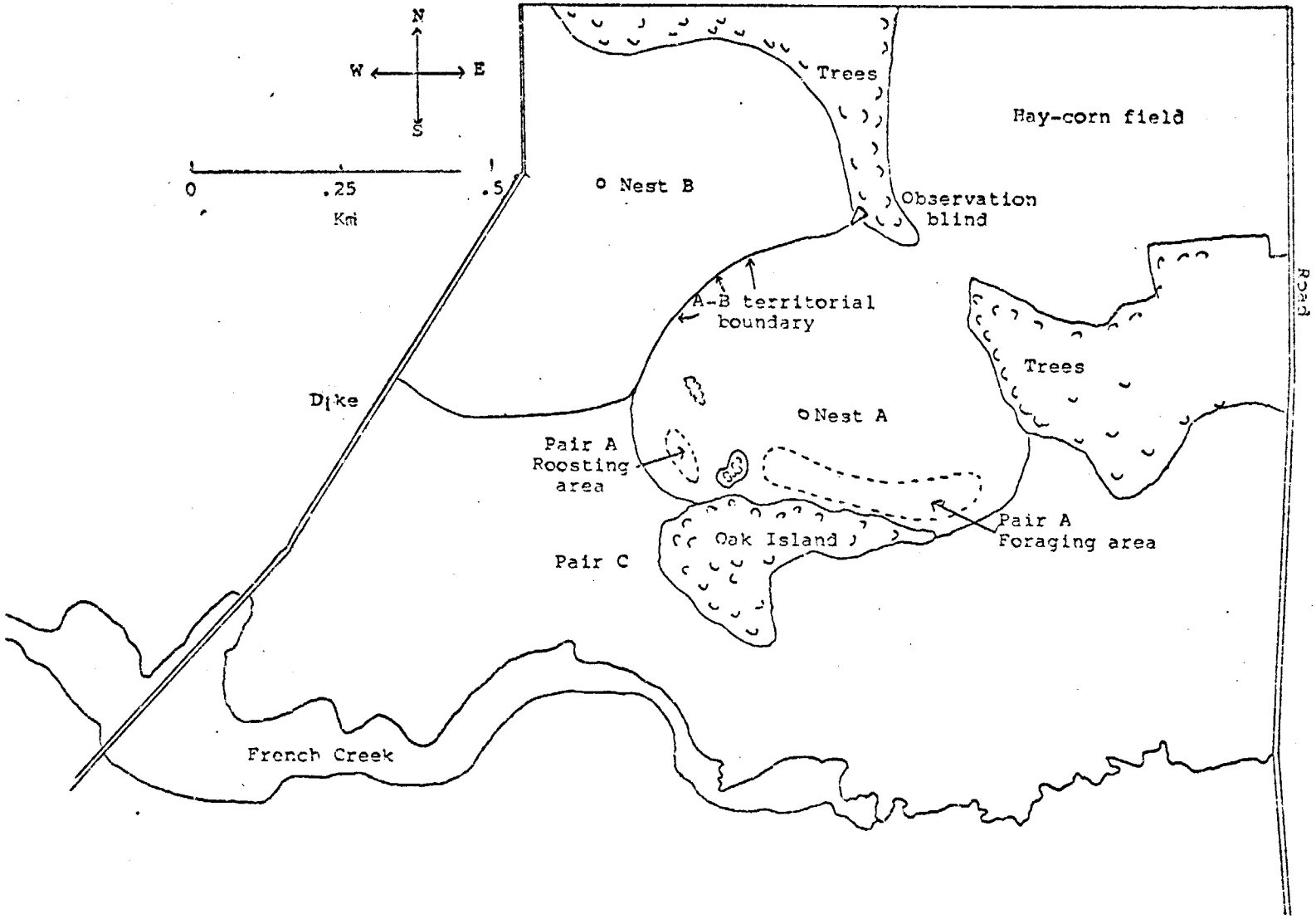
Behavior of Nesting Crane Pairs

Duration of Incubation

Pair A (Fig. 29) was first observed on 28 April. Copulation occurred but there was no evidence of nest building activity. Six days later, a nest had been built, and incubation had begun. They incubated until 15 to 19 June, at least 42 days, and possibly as long as 50 days. On about the fortieth day of incubation, the nest was left unattended at night. Although two days later they incubated during the day, four days after that they ceased incubation. Several days after they had ceased incubat-

Figure 29

Territories of crane pairs observed at French Crreek Wildlife Area, Portage, Wisconsin.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Trees
Hay-corn field
Nest B
Observation blind
A-B territorial boundary
Road
Trees
Dike
Nest A
Pair A Roosting area
Pair A Foraging area
Oak Island
Pair C
French Creek

ing, I observed two unhatched eggs in the nest.

The normal incubation period for G. canadensis is 28 to 32 days (Walkinshaw 1973a, 1973b), however Walkinshaw (1965b) reported that "in cases where both eggs were infertile, cranes often incubated them long beyond the normal period, once until 1 July."

Behavior on the Nest

During the 42 days of observed incubation, one member of pair A was always on the nest until about four days before they ceased incubating. While incubating, the crane spent most of its time sitting, either in back sleeping position, or with its neck vertical. Walkinshaw (1959) reports that the incubating bird will also flatten its head and neck to the ground at the approach of an intruder, and will remain in this position unless the intruder approaches too closely. I observed this once when a farmer's tractor came to the edge of the marsh, about 300 m from the crane's nest. The crane occasionally closed its eyes and apparently slept for several seconds to several minutes at a time, and preening was also done occasionally by the incubating bird.

Activity during incubation seemed to follow a repeating pattern. After 0.5 to three or more hours of sitting motionless on the nest, the incubating crane often spent periods of 1 to 30 min of increased activity at the nest. The crane would stand, neck vertically downward, apparently turning the eggs (shifting, Masatomi, p. 872) and working with the nest material (nest mending, Masatomi, p. 873) for several sec to 5 min, sit again for several min, then again stand and work with the eggs and nest material. After a period of intermittent standing, the crane again resumed a period of almost motionless sitting. These cycles of motionless sitting followed by periods of activity varied in length from 40 min to

over three hours. Of the 52 hours that the male was observed at the nest, the female spent 14 percent of her time in non-incubating activities.

The average length of an incubation bout was hard to determine, since so few were observed from beginning to end (Table I). Of the bouts observed, including incomplete bouts, the male averaged 180 min and the female 60 min per bout. Since many bouts were incomplete, the actual average length of bouts was probably much longer. Of approximately 70 hours of daytime incubation, the male incubated 76 percent and the female 24 percent of the time.

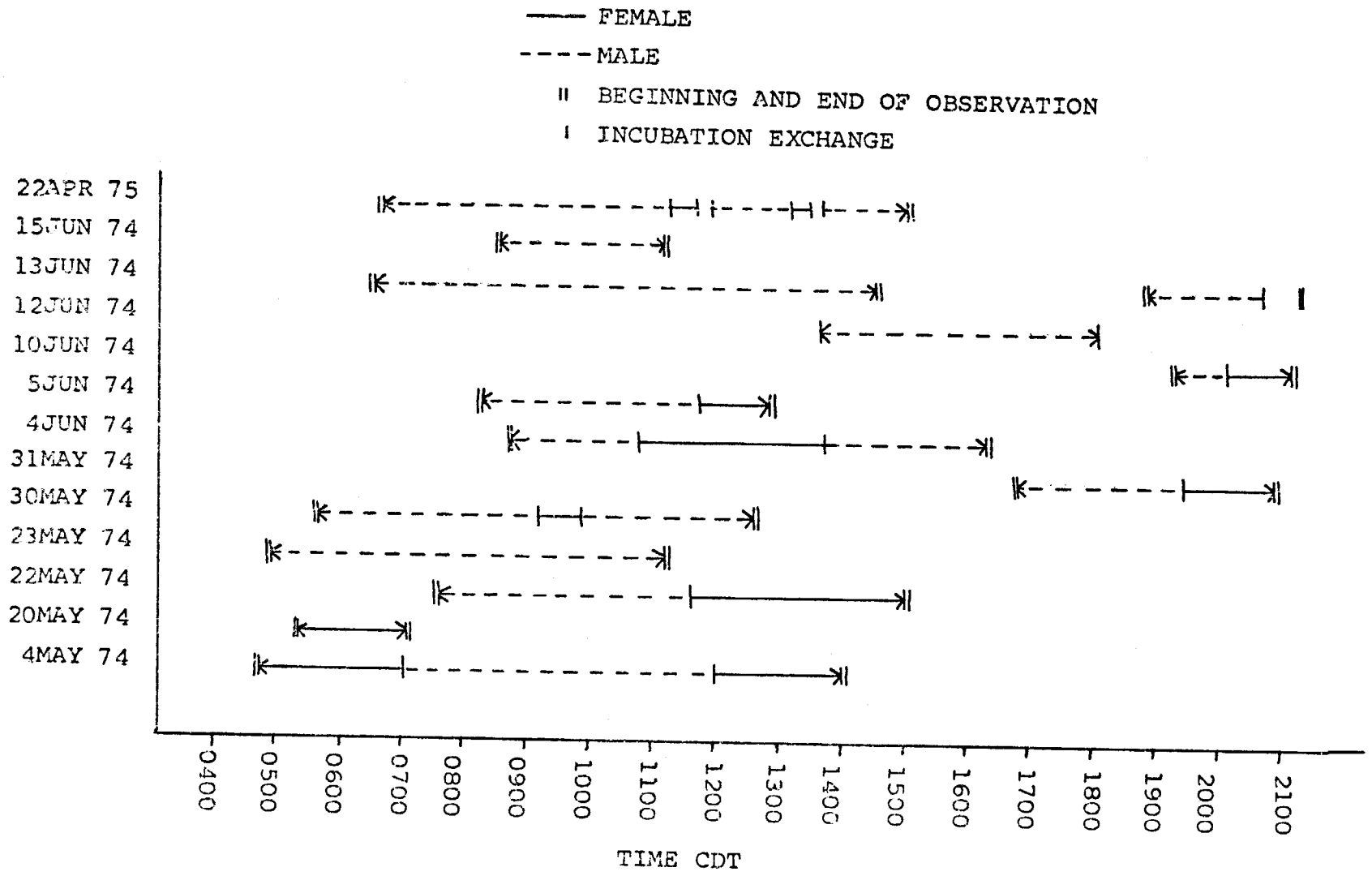
Walkinshaw (1965a) reports that during approximately 280 hours of daytime observation, males incubated 52 percent and females 48 percent of the time. Forty-one bouts of incubation by the male lasted an average of 215 min, and 33 bouts by the female lasted an average of 194 min. Based on the observations of birds going to the nest at night or leaving it in the morning, however, he believes that the female incubated at night 64 percent of the time.

Incubation Exchange

Incubation exchanges were observed 12 times. The behavior of both birds was quite variable. Nine of the 12 exchanges were accompanied by unison calls, usually just as the foraging bird reached the nesting bird. The foraging bird approached the nest by walking for ten of the 12 exchanges, and twice flew to the nest. Nicholson (1926) reported that: "Cranes upon entering and leaving the nest, unless flushed, walk some little distance before taking flight, and upon returning, alight (some distance from the nest) and walk to the nest. Every nest has two to five pathways leading from the nest." Three times, the incubating bird stood up just before the foraging bird approached the nest, and one of these

Table I

Incubation Bouts of Pair A


FEMALE
MALE
BEGINNING AND END OF OBSERVATION
INCUBATION EXCHANGE
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15JUN 74
13JUN 74
12JUN 74
10JUN 74
5JUN 74
4JUN 74
31MAY 74
30MAY 74
23MAY 74
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times, the incubating male called while standing. This standing and calling by the incubating bird apparently initiated the return of the foraging bird to the nest. When the foraging bird began walking toward the nest, it usually walked steadily at one to 1.5 steps per second, directly toward the nest. Less frequently, it would meander through the marsh, foraging as it slowly approached the nest. The incubation exchange time interval was defined as beginning when the foraging crane was within 10 m of the nest and it became evident that one bird was about to replace the other at the nest, and ending when the new incubating bird took its place on the nest. The incubation exchange interval varied from 2 to 10 min, but was less than 4 min for eight of the 12 incubation exchanges. Four times, the newly relieved crane engaged in nest building activity just after nest exchange, for 1 to 16 min.

Behavior of the Non-Incubating Crane

The non-incubating bird spent virtually all of its time foraging, preening, standing, or walking (Table II). Although no food material was actually identified, it was evident that tubers made up a significant portion of the crane's diet. They spent a good deal of time in certain parts of their territory digging up tubers 3 to 4 cm in diameter, which could be seen moving down their necks as they swallowed them. They also spent much time meandering through their territory, catching insects and other invertebrates which happened to be within their reach, occasionally chasing an insect for up to 10 m to catch it. It was generally impossible to see food taken in this manner, though occasionally I observed the crane taking large insects such as dragonflies and moths or butterflies. Cranes were frequently attacked by red-winged blackbirds and black terns. These birds would dive and peck at cranes, sometimes even landing on the

TABLE II

Activities of Non-Incubating Crane

During Nesting

Percent of Non-Incubating Time

	Male	Female
Foraging	59	58
Preening	13	20
Standing	27	20
Walking	9	9
	108	102

crane's back to peck at it. Although I never observed cranes preying on any other bird species, it seems quite probable that cranes may take young of other species if available. Lesser sandhill cranes frequently prey upon the eggs and young of the blue goose (Chen caerulescens) and the willow ptarmigan (Lagopus lagopus) (Harvey et al. 1968). Cranes also prey upon small rodents and reptiles.

The non-incubating crane spent 10 to 20 percent of its time preening (Table II). Wild cranes preened in the same manner that captive cranes did. I observed feather painting twice, once for 3 min, and once for almost an hour. During this extended period of feather painting, the crane alternately dug vigorously in the mud with its beak, and preened. Distance and tall grass prevented detailed observation. However, after 5 to 30 sec of vigorous digging, the crane would raise its head, wipe its beak back and forth over the surface of its body feathers, dig the tip of its beak into its body feathers, and pull flight feathers through its beak. In 24 min there were 31 bouts of alternate digging, then feather painting.

The non-incubating crane spent 20 to 30 percent of its time standing with no other activity. This occurred almost any time of day, though cranes seemed to be most active in the morning, and hence less likely to simply stand then. Although vegetation and distance made it difficult to observe whether a crane was sleeping or not, sleeping was occasionally observed, and undoubtedly at least some of the time, the crane was actually sleeping while standing.

Foraging, preening and standing took up almost all of the time of the non-incubating crane. Walking, which took up 4 to 9 percent of the time, occurred when a crane was approaching or leaving the nest, and

when approaching another crane near the territorial boundary. A crane was recorded as walking when moving at a rate of at least 0.5 steps per sec, with no evidence of foraging or other activity.

Vocalizations During Incubation

Vocalizations were infrequent during the nesting period. During approximately 70 hours of observation, pairs A and B vocalized 45 times (Table III). Two major events stimulating vocalization were incubation exchange, and the visual or auditory presence of other cranes near a pair's territory. Thirty-five of the vocalizations could be associated with one or both of these two events (Table III). Of these 35 vocalizations, 31 could be partly or wholly associated with the presence of other cranes. Cranes flying over a pair's territory, cranes calling in the distance, or members of two pairs (A and B, or A and C) near the common border of their territories all stimulated vocalizations. If the female was incubating when another crane approached the territory, the male often responded by flying or walking toward the intruder, and giving the male half of the unison call. Twice the female simultaneously gave the female half of the unison call from the nest. Nine times the male was incubating when another crane approached pair A's territory. Every time, the female, red crown expanded, walked silently to the nest, and the pair unisoned at the nest. Six times, the female replaced the male at the nest, and the male walked or flew in the direction of the intruder. Three times, the male continued incubating, and the female left the nest after several min. Only once did the female vocalize by herself. This was at dawn when many other cranes were calling simultaneously. I was unable to associate ten vocalizations with the occurrance

TABLE III

Circumstances of Vocalizations in Nesting Crane Pairs

	Male-Female Unison	Male-Female Guard	Male Male ½ Unison	Male Guard	Female Guard	Total
Other Cranes	6	1	18		1	25
Nest Exchange	4					4
Other Cranes and Nest Exchange	6					6
Unknown	6		2	2		10

of any other specific events. It is quite possible that at least some of these vocalizations were caused by the presence of other cranes that I did not see or hear.

Interactions of Pairs at Their Boundaries

Interactions of pairs near their boundaries were rare during nesting, and often so subtle that it was difficult to tell whether an interaction or display was occurring, or whether it was simply chance that brought a bird near its territorial boundary. During nesting, females were never observed displaying near territorial boundaries. The male of pair A was observed displaying near a territorial boundary six times. Five times the interactions occurred between male A and male B, once between male A and one of pair C. The most intense interaction observed occurred when pair A had been incubating less than six days. Initially, female A, who had been foraging, stood with her neck vertical and red crown expanded, facing the male of pair B, about 700 m away. She stood motionless for 3 min, red crown expanded, then walked directly to the nest. Pair A unison called, then she replaced the male on the nest. Both male and female carried on intermittent nest mending activity for about 20 min, then male A flew near and landed about 200 m from male B, and began foraging. Male B immediately began walking stiffly and rapidly (1.5 steps per sec) toward male A, red crown highly expanded. For about 40 min both birds intermittently foraged and walked obliquely towards each other, and approximately parallel to their common boundary, red crowns constantly expanded. Each gave the male half of the unison call once during this time. The distance between the two birds was never less than 100 m. After approximately 40 min they gradually foraged farther

and farther apart until they had returned to more central regions of their territories. All boundary displays were characterized by a male flying or walking, either directly or indirectly, to an area near his territorial boundary. He would alternately walk, stand and forage, red crown expanded, near the boundary for 10 to 40 min, then walk or fly to a more central region of his territory. Each time he gave the male half of the unison call once. Sometimes both males give similar displays and sometimes the other male does not appear to respond to the displaying male, although he is always clearly visible to the displaying male. When approach and retreat from the territorial boundary are made indirectly by walking and foraging, the whole display may be very subtle.

Parental Behavior

Behavior of Pairs With Chicks

Families With Very Young Chicks on Nesting Territories. Pair B at French Creek Wildlife Area hatched one young, and cared for this chick for at least three days. However, the chick apparently died between four and ten days of age. The presence of the chick was first detected by striking changes in the foraging behavior of the adult cranes. The adults spent almost no time digging for roots or tubers, but were almost constantly catching small invertebrates, such as moths and worms. After catching each food item, the crane would return to the same location, lower the food item in its beak into the marsh grass, then after a few seconds, raise its empty beak (low feeding, Masatomi, p. 873). Occasionally the parent would pick up and drop the food item several times over a period of 10 to 60 sec before leaving the apparent location of the chick. This happened particularly if the food item was large. During periods of active feeding, the chick received food from one or the other

parent approximately once every 2 min. Although this chick was never actually visible, the behavior of pair B was virtually identical to parental feeding behavior observed in captivity (Voss 1974).

This distinctive foraging behavior was observed almost continuously for two days. During this time, the parents ranged over only a small portion of their territory, around an elevated area, about 3 m in diameter, where they appeared to brood the chick for part of the day and the evening. Then for several days the parents' behavior became ambiguous. They were seen to carry food as if feeding a chick, but only infrequently. Finally they ceased carrying food and ranged farther and farther from the brooding area. There was no other evidence of the presence of a chick, and I assume that the chick died.

Families With Older Chicks on Nesting Territories. Crane families with chicks approximately five to 15 weeks old were observed at Sandhill WDA and Necedah NWR during June, July and August, 1974. Two families were frequently observed, each with one chick. Families spent almost all of their time foraging and preening together. Chicks were almost never more than 10 m from one of their parents. Most foraging involved chasing and catching insects or other invertebrates. Parents frequently fed their chicks, but chicks also did a great deal of foraging on their own. They spent much time catching insects on or around the parents' heads and bodies. While adult cranes occasionally dug for food, chicks never did, although they frequently stood at their parent's side, and received food from the parent's beak as it was dug up. The chick would stand, head down, beak almost touching the parent's beak as he dug. When the parent retrieved a food item from the hole, he would either drop it on the ground next to the hole (indirect feeding, Masatomi, p. 874), or the

chick would take it directly from the parent's beak (direct feeding). Parents apparently give a "feeding call" when they have a food item for the chick. Several times a chick was observed at least 20 m from the parent, engaged in preening or foraging, when the parent raised its head, with a bit of food in its beak. The chick, previously not apparently attentive to the adult's activities, immediately trotted at a rate of about 3 steps per second to the parent, and received the food from the parent. Since the chick, on at least several occasions, did not seem to be aware of any visual cues from the parent, it seems likely that auditory cues were used. A captive sandhill chick adopted by a Manchurian crane (Grus japonensis) responded regularly to a distinctive "feeding call" given by the Manchurian male. The captive chick also gave a "food begging" call when receiving food from the Manchurian crane male.

Before chicks are capable of flight, they apparently avoid predators by hiding. This was observed during an unsuccessful attempt to band an approximately eight week old chick. When two men approached to within 100 m of the family, the adults flew, and the chick disappeared in the vegetation. About 10 min after the men left, the chick reappeared about where he had disappeared, and the parents, who had apparently walked back through the marsh, reappeared with the chick.

Although the exact ages of the wild chicks were not known, they were first observed flying on 22 July. The were probably about the same age as captive chicks which began flying on 21 July at 10 weeks of age. Twice chicks were observed to initiate family flight. The chick stood in preflight posture (Fig. 15) 10 to 15 sec before the parents did, and

flew slightly before them. On other occasions, all three stood in pre-flight posture together, and took off simultaneously.

Family Behavior in Fall Flocks. In September and October, families were observed in fall flocks at Necedah NWR, and Sandhill WDA. Chicks observed were probably 18 to 25 weeks old. Cranes in these areas spent a great deal of time digging for food, probably both plant and animal matter. Chicks were still fed frequently by their parents, but were also beginning to dig for food themselves. A chick would still stand next to its digging parent, head down near its parent's head, beak pointed to the parent's hole. The parent still dropped food next to the hole for the chick, and let the chick take food directly from its beak. The chick also would occasionally reach into the parent's hole with its beak to retrieve a food item. Later in the fall, chicks were seen digging their own holes, near their parents. Chick vocalizations were still at the high frequency of immature birds, and they could frequently be heard giving the food begging call as they received food from their parents.

Quite frequently chicks did not join in parent displays, vocalizations, or other interactions with other cranes. However, six times, chicks were observed to take part in these interactions. Adults frequently give a body-wing shaking display when near other cranes. Once a chick performed a body-wing shaking display just after landing near other cranes, then one parent also gave this display about 20 secs later. Chicks also joined adult cranes in giving unison calls and driving off other cranes by adornment walking. Three times when the parents unisoned, the chick could be heard giving broken guard calls. These calls were of much higher frequency than adult guard calls, but had the same temporal patterning. Twice when parents adornment walked toward another crane

family, the chick walked with its parents, with tertials raised (Fig. 18). It was definitely joining in the display, though the intensity of its threat posture was not nearly as great as that of the adult adornment display. Twice, chicks were observed to initiate actual fighting. Once while adults of two families were adornment walking towards each other, the chick of one family attacked the chick of the other family. They jumped in the air, flapping their wings and kicking at each other for about 5 sec, then the attacked chick turned and ran away from the other in neck-retracted submissive posture (Fig. 25). Like captive chicks, the crowns of wild chicks were still at least partially feathered, and pinkish rather than bright red. Wild chicks also expanded their crowns when threatening other cranes.

Vocalizations

Although a number of vocalizations might have been covered appropriately in previous sections, such as agonistic or reproductive behavior, I have grouped them here for convenience and clarity.

Sandhill cranes have a large repertoire of vocalizations, some unique to either immatures or adults, and some given at all ages. I was able to recognize and observe the development of some but not all of these vocalizations. From hatching until about 42 weeks of age, chick vocalizations are given at about 2 to 5 kHz. At about 42 weeks of age, low frequency notes begin appearing in the chicks' vocalizations, and by 46 to 50 weeks, the vocalizations given contain the adult basal frequencies of less than 1 kHz. Walkinshaw (1949) also records that adult calls are acquired at just over 10 months of age (in March).

When a call is given by both the immature and the adult, the frequency at which the call is given is lower in adults, but the temporal

patterning and the context in which the call is given are evidence that the call serves the same function, and hence the same name is applied to both immature and adult forms of the call. The names used to identify calls are the same as those used by Archibald (1975) and Kepler (in prep.). Archibald (1975) provides the only printed sonographs to date. A lack of sonographs and careful description makes it difficult to refer to many earlier authors. Even though Walkinshaw (1949) gives extensive written descriptions of vocalizations, it is sometimes not possible to be absolutely certain about what call he is describing. Walkinshaw's "alarm call" is apparently the same as Archibald's "guard call," and Archibald's "alarm call" is not described by Walkinshaw. Several authors refer to the "alarm call" of cranes, but it is impossible to know to what vocalization they are referring.

The following descriptions are based largely on Archibald's (1975) observations as well as my own.

Contact Call (Fig. 30a-d)

The contact call is given by cranes of all ages and was one of three calls first heard during pipping. This call is a steady trill lasting 0.2 to 0.4 sec, and is given 1 to 2 times per sec. Archibald describes this call as "low amplitude" and "purr-like," and notes that it is given almost continuously by the chick during foraging and at the beginning of brooding. The contact calls given during pipping (Fig. 30a) were a slightly slower trill and at a lower frequency than those given after hatching (Fig. 30b). During the transition from immature to adult voice (Fig. 30c), the frequency decreased. Figure 30d shows the adult contact call given by a 48 week old chick, recorded in mid-April.

Figure 30

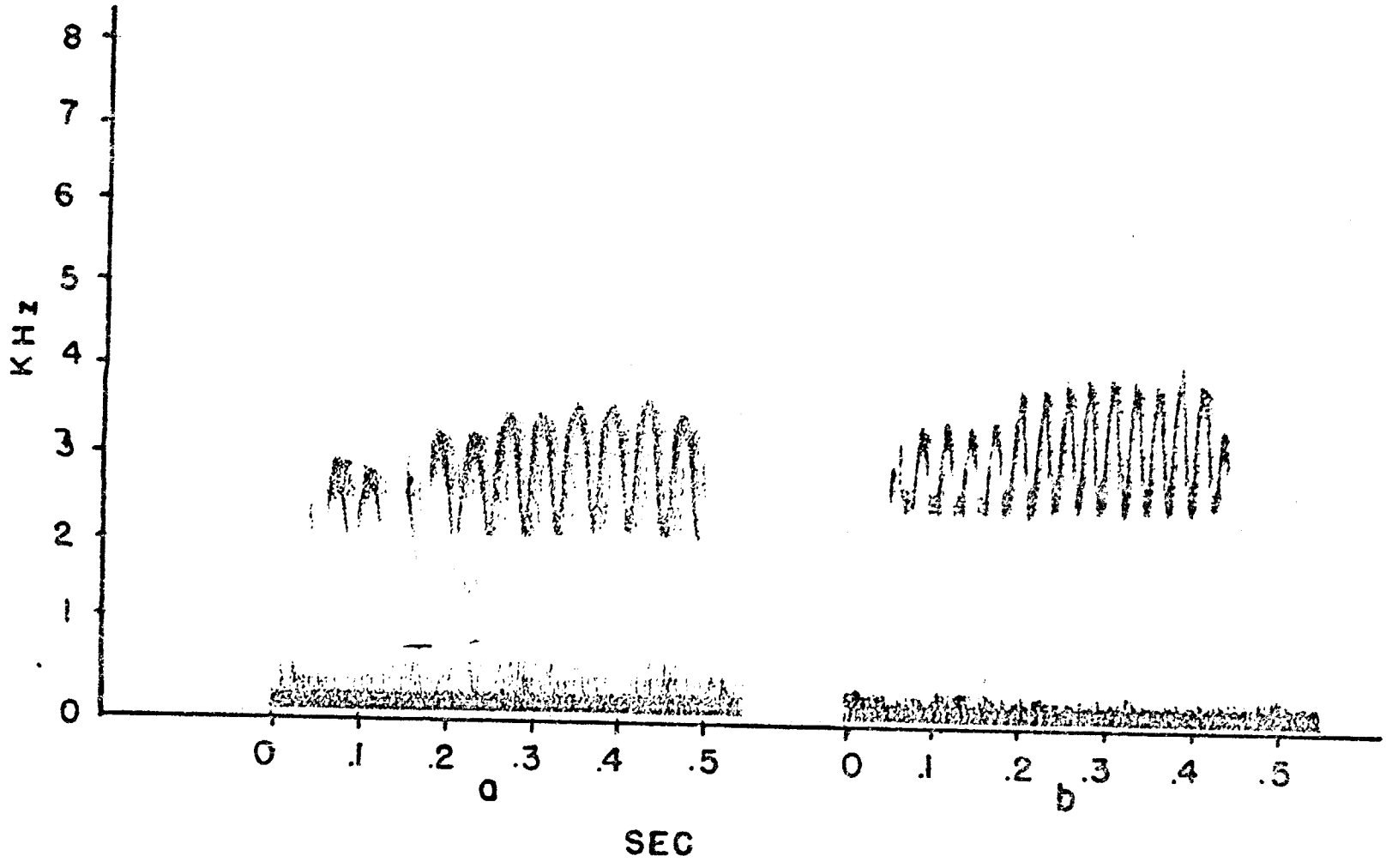
Contact call.

a) During pipping.

b) At 3 days of age.

c) Transition from immature to adult voice.

d) Adult contact call given by 48 week old chick.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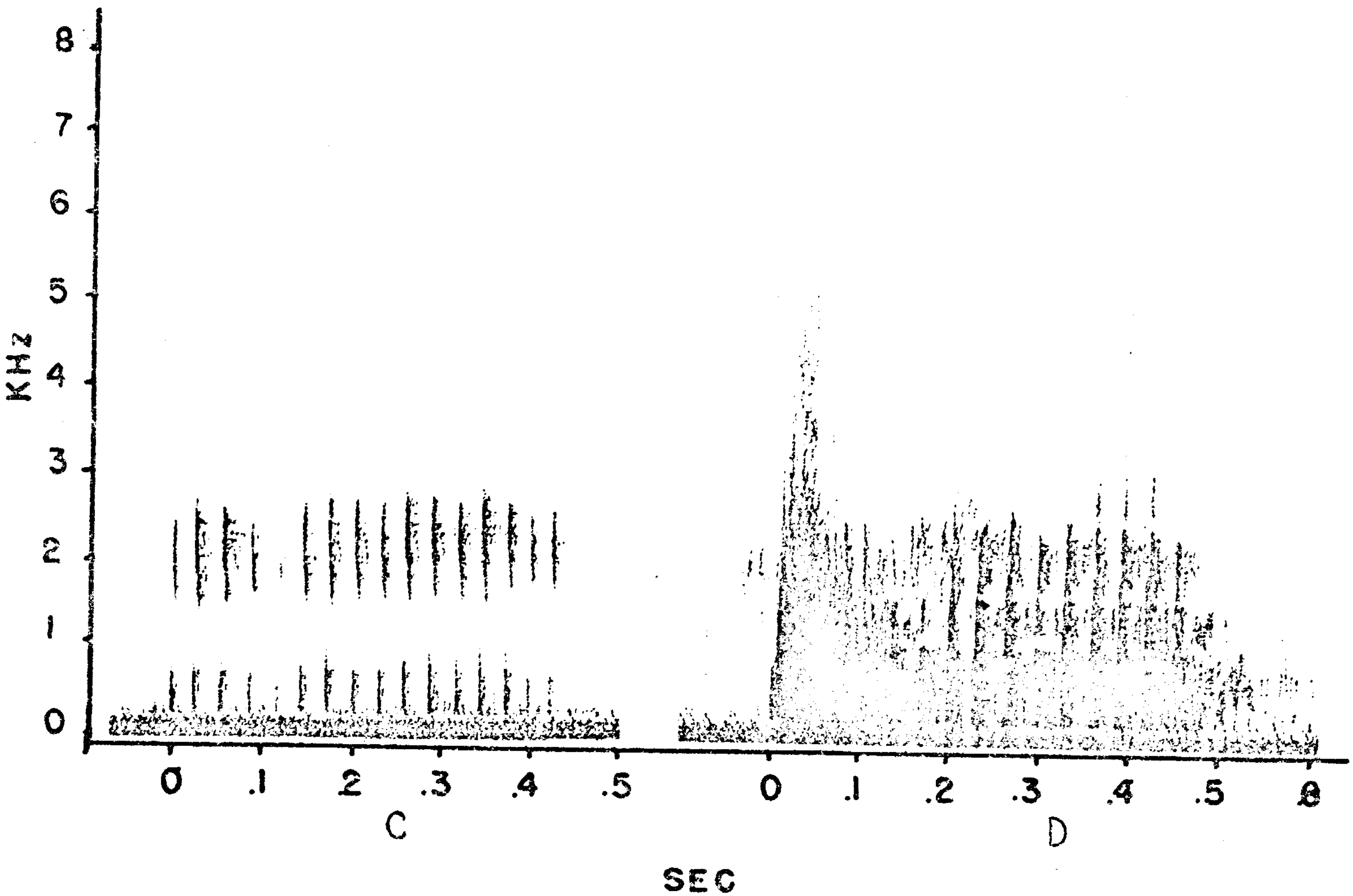
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Chicks give the contact call almost continuously, and it is even sometimes heard on the exhaled breath during sleeping. Contact calls are given very regularly although somewhat less frequently by adults than chicks. Distance made it nearly impossible to hear this call in wild birds. Archibald believes this call serves to keep pairs and families in auditory contact. This may be particularly important on the nesting territory when chicks are small and the habitat is dense, obscuring visual contact.

Pipping Call (Fig. 31)

A very low frequency, short, sharp peep was heard several times during pipping, but was never heard again after the chick had hatched. This was the lowest frequency call heard until the chick attained its adult voice almost 11 months later.

Stress Call (Fig. 32)

The stress call is the third call which first appeared during pipping. It is a plaintive ascending peep lasting about 0.2 sec, and is given about once per sec. It is a loud, unbroken call that is given when a chick is under a stress such as cold, hunger or abandonment. I observed chicks giving stress calls when caught under a wire mesh fencing and when being chased by other cranes. Chicks can give stress calls loudly enough to carry several hundred feet outdoors. I no longer heard this call when the chick began to attain its adult voice, although rarely an adult gives a stress call which is a "low, plaintive groan."

Food Begging (Fig. 33)

The food begging call is a loud, ascending peep which lasts about 0.2 sec, and is given about 3 times per sec. Archibald states: "The

Figure 31

Pipping call.

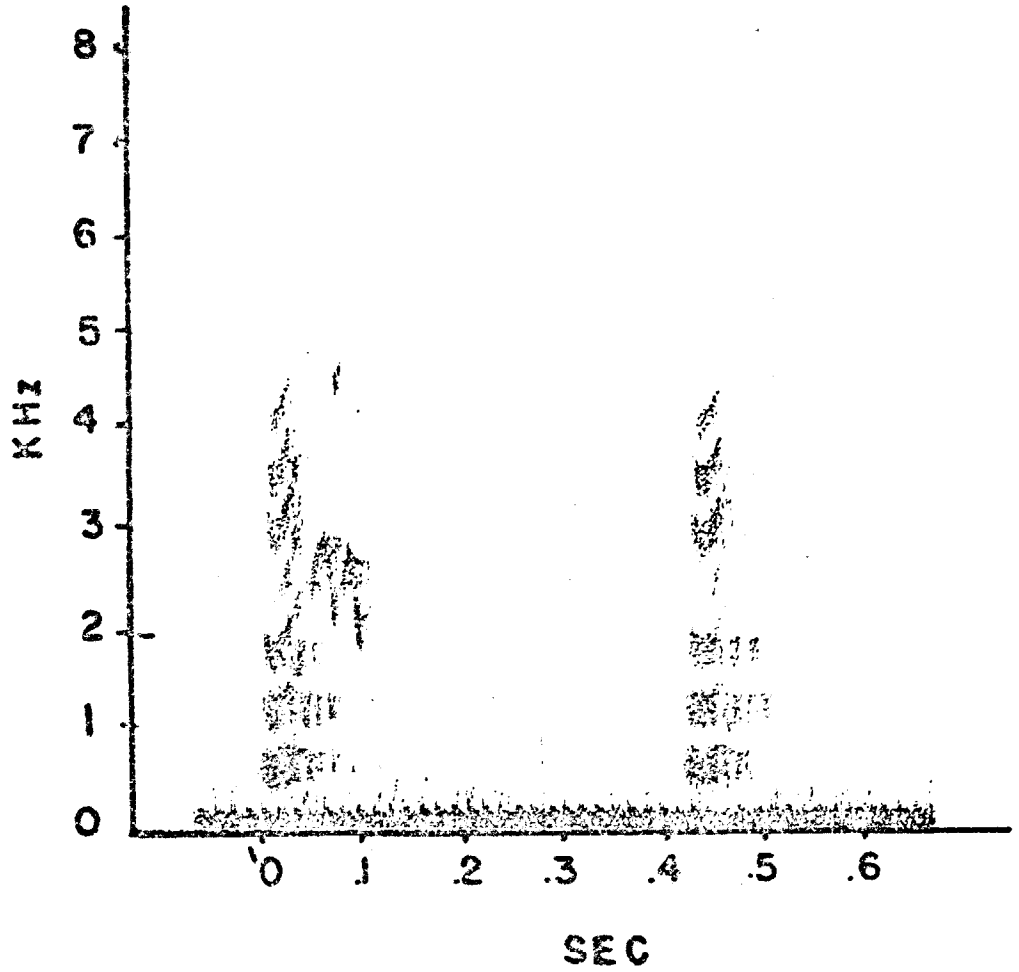
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Figure 32

Stress call.

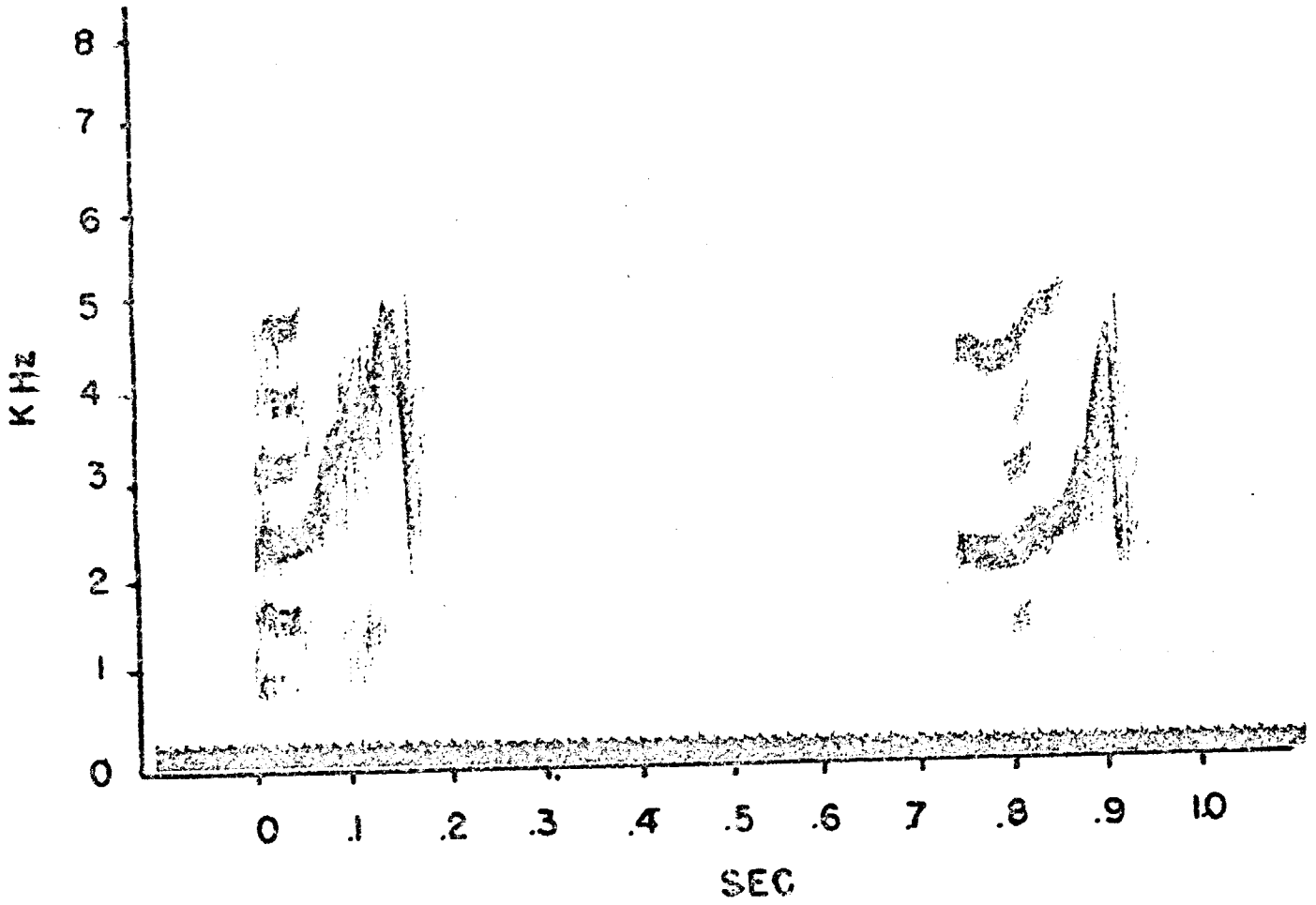
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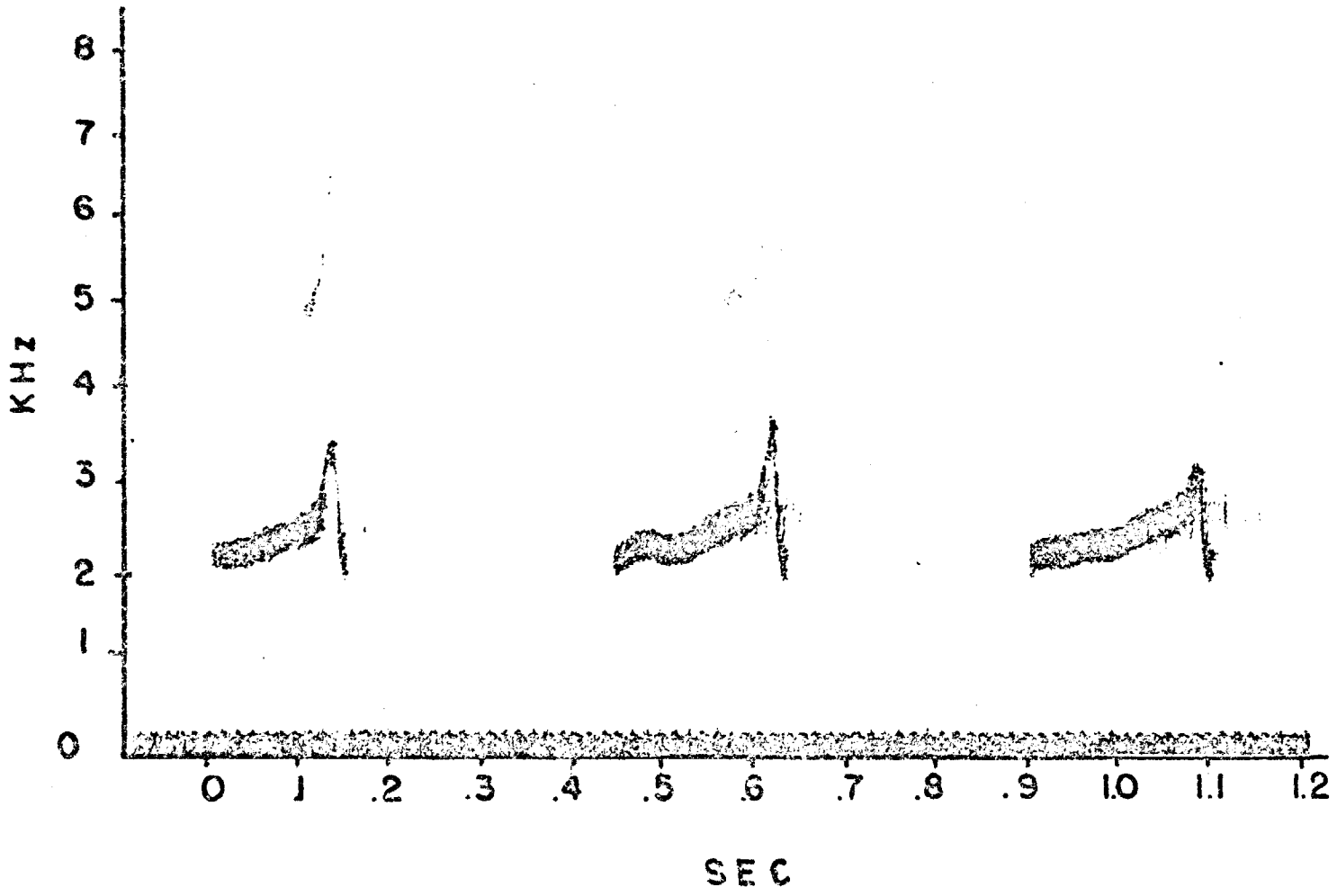
Figure 33

Food begging call.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food begging call is loud like the stress call, but rather than being a single shrill vocalization, it is a repeated 'plaintive-like' call."

This call is given from a day or two after hatching until the crane begins giving low frequency adult calls at about ten months of age. This vocalization apparently accompanies parental feeding of chicks throughout the winter. Chicks less than six weeks old beg for food by pecking at the parent's beak, while uttering a food begging call. After about six weeks of age, chicks usually assume the neck retracted submissive posture (Fig. 25) when food begging. The chick still frequently pecks at the parent's beak when the parent is holding a food item. If the parent is foraging by digging while the chick is food begging, the chick stands with its head low, very near the parent's head, rather than in neck retracted submissive posture, and the food begging call is given almost continuously.

In captivity, chicks will utter the food begging call at the approach of a human, and will give the food begging call continuously while pecking at bright objects held in the hand of a human.

Guard Call (Fig. 34a, b)

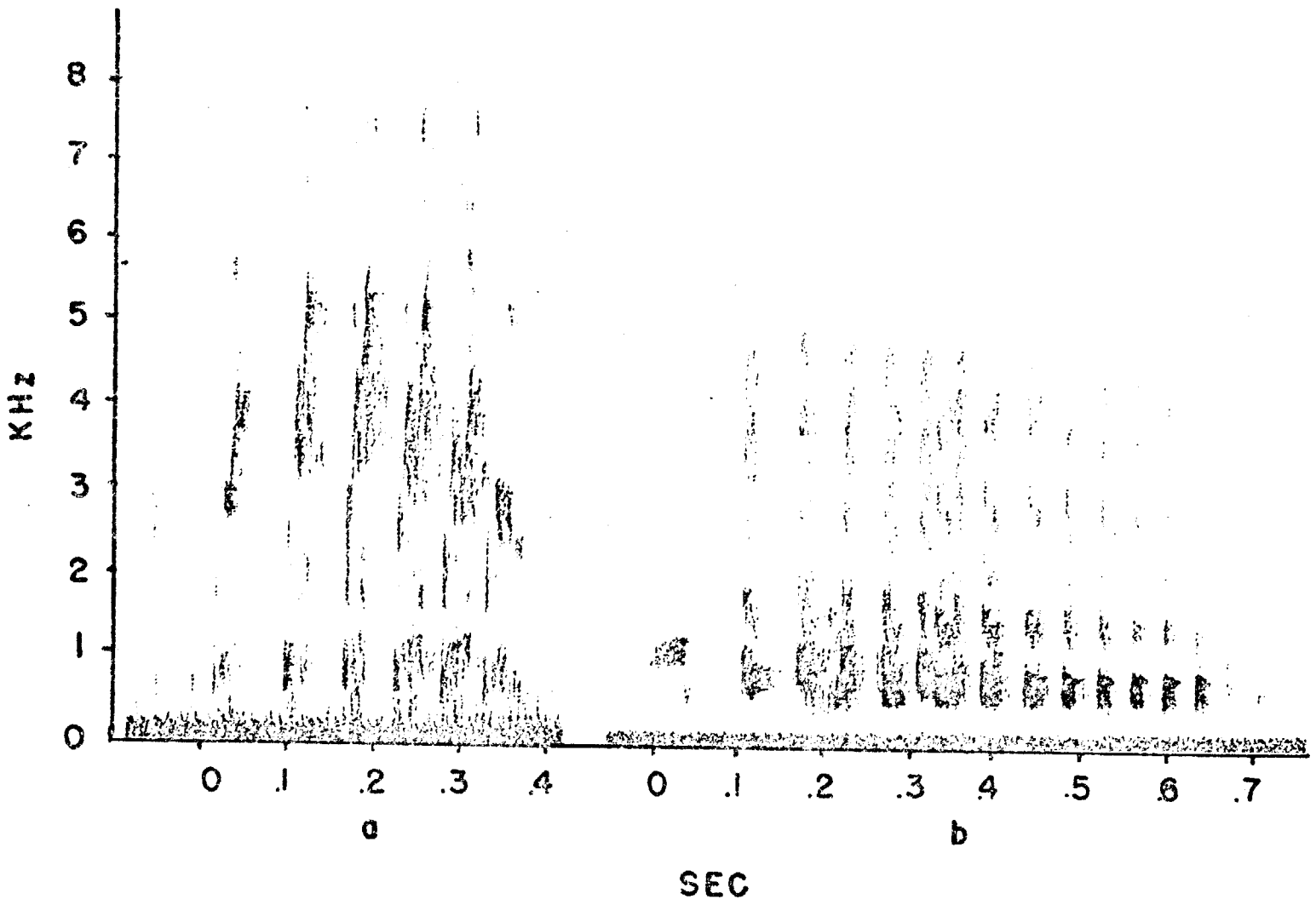
At nine to ten weeks of age, just before chicks begin to fly, they develop the guard call (Fig. 34a). This is a high broken call, which first ascends, then descends, and lasts about 0.45 sec. It was given by chicks in captivity accompanying guard calls of other adult cranes, frequently in response to the approach of dogs or strange humans, or to a hawk or crows flying overhead. Chicks giving this call almost always walked or stood in alert posture (Fig. 24).

Figure 34

Guard call.

a) Given by 40 week old chick.

b) Adult guard call.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b
SEC

As cranes attain their adult vocalizations, this call retains about the same temporal pattern, but becomes lower in frequency and slightly longer in duration (Fig. 34b). This call is usually repeated at 1 to 5 sec intervals.

Unison Call (Fig. 35a, b)

The unison call is an elaborate visual and vocal display given by crane pairs. Although the unison call develops soon after a crane acquires its adult voice, it is seldom given until about two years of age when pair formation begins.

Typically, the call consists of a species-typical introduction, then a series of calls repeated in synchrony by the male and female. According to Archibald (1975, p. 40-42), the female emits a short high unbroken introductory call, then:

> After her short high unbroken introductory call, the female immediately emits a long and lower broken call. From this call she shifts to a series of regular unbroken calls for the remainder of the unison call. After the female's unbroken introductory call, the male sometimes emits a long, low broken call with beak held in the vertical position. Sometimes this call is repeated several times at the beginning of the unison call, and occasionally at the end of the display. After the broken call introduction, the male emits a regular series of calls . . . .
>
> During the introduction, the female calls with beak raised about forty-five degrees above the horizontal. However, for the remainder of the call, she repeatedly moves her beak up forty-five degrees with each call, and then back to the horizontal between calls. Under high threat stimulation, the male calls with the beak in a vertical position throughout the display. With reduced threat the male calls with beak between forty-five degrees and the vertical. Wings of both sexes are closed throughout the unison call and the tertials are sometimes raised. Under extreme threat the male raises his back feathers and slightly lowers the elbows laterally, exposing the tail between the raised tertials, and slightly raises and lowers the elbows with

> each call. The tail is erected about fifty degrees above the horizontal and is conspicuous. (Fig. 35).

The unison call lasts 8.82 ± 4.76 seconds. Throughout the regular part of the unison call, the female emits two short calls (0.09 ± 0.03 seconds) for each of the male's longer calls (0.32 ± 0.03 seconds) (Fig. 35a). According to Archibald the guard call and the unison call are closely related in structure and function. The main difference between them is that the guard call is usually a single vocalization, independent of calls preceding and following it, while the unison call is a series of calls emitted in a fixed temporal sequence. According to Archibald (p. 21):

> Functionally, the Guard Call and the Unison Call overlap to some degree. Guard Calls are usually given when the bird is afraid but not afraid enough to flee: it holds its position and emits the Guard Call. With a greater element of threat in the encounter, most Gruinae species Guard Call and/or Unison Call.
>
> Guard Calls and Unison Calls are often given in association with sexual activities.

Unison calls are given at all times of the year under many different circumstances. On territories, they are given most frequently just prior to nesting, in association with other territorial defense activities. Walkinshaw (1965) reports that in areas where nesting densities are high, pairs unison call much more frequently than isolated pairs. In flocks, pairs unison call frequently while performing other threat displays.

Other Vocalizations

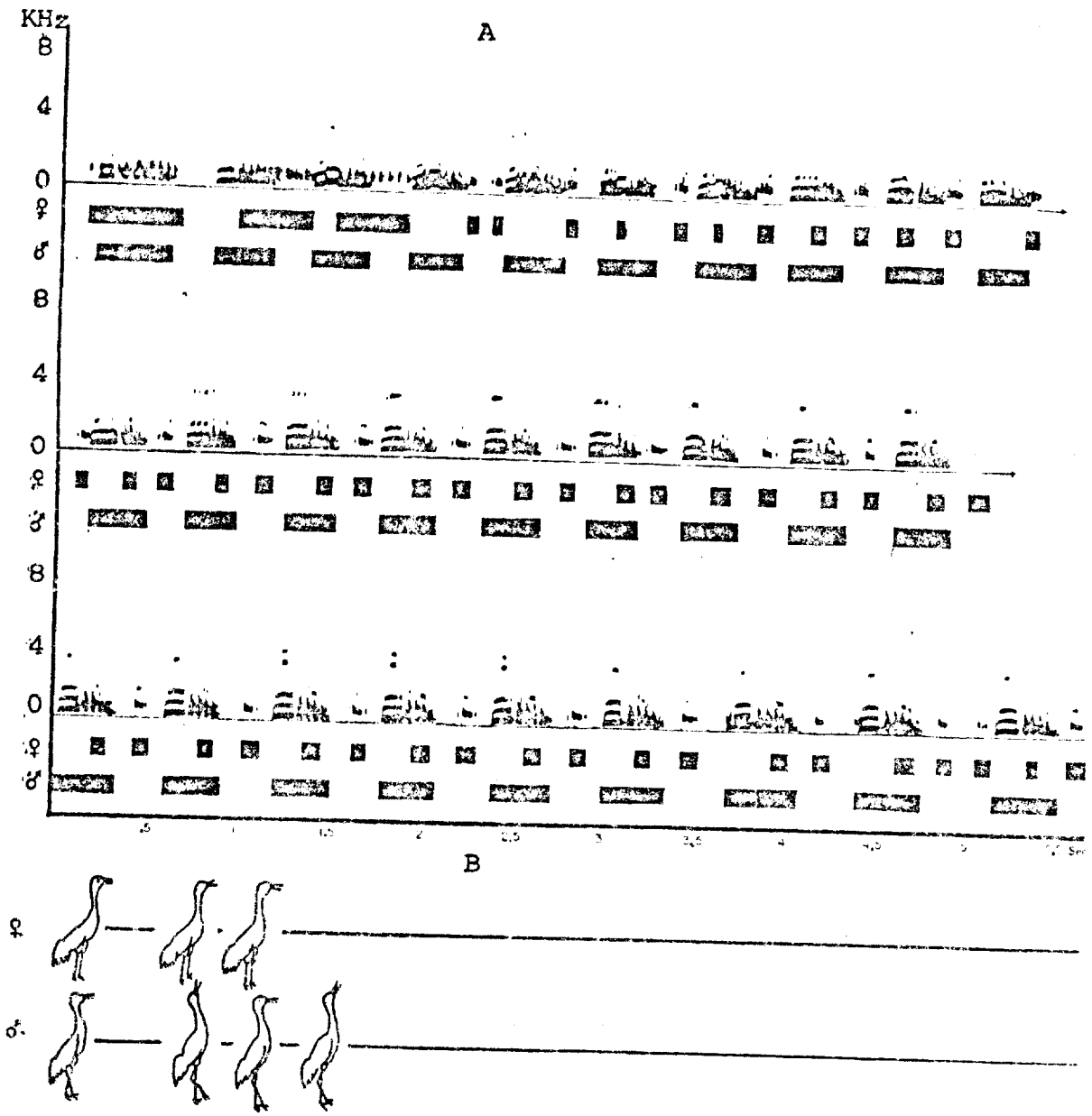
The following are vocalizations which are recognized in sandhill cranes, but for which sonographs are unavailable.

Figure 35

Unison call (from Archibald 1975, p. 41).

a) Sonogram of unison call.

b) Posture of male and female while calling.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Flight Intention Call. This call is first heard at about ten weeks of age, just as chicks begin to fly. This is a very brief, high frequency, unbroken call which is given as the chick stands in preflight posture (Fig. 15). In adults, the flight intention call becomes louder and lower.

Alarm Call. This call was first heard at 18 weeks of age in captive chicks. It is a low frequency, low volume, short broken call, usually given only once. This call was heard several times at close range from a bird near an area baited with corn at Necedah NWR, in response to a disturbance on my part, such as the protrudance of a camera lens, or the noise of a movie camera. An alarm call given by one to several cranes caused a flock of almost 100 cranes to assume preflight posture for several seconds, then to take flight almost simultaneously.

Location Call. This is a loud call, similar to the guard call, but less broken and more plaintive. It is given when a crane is separated from other cranes with which it is normally associated, and when one crane emits a location call, others respond with this call. This call is given only by adults.

Pre-Copulation Call. This call sometimes precedes, but usually follows voice change. The crane assumes the bill-raising pre-copulatory posture (Fig. 28), body slightly below horizontal, neck stretched upward and forward, with beak elevated about forty-five degrees above horizontal, and emits a regular series of short purr-like calls, gradually swelling in volume.

Nesting Call. This is a low "moan-like" call given by a crane pair as they build their nest and prepare to lay. According to Archibald: "Typically the pair stands together on or near their nest, heads lowered,

arranging the nesting materials and continually emitting this call. For several hours before a female lays an egg she emits long series of nesting calls. The function of the display is not known, but it is assumed to aid in reproductive synchrony of the mated pair.

Interactions With Other Species

Cranes were observed occasionally in close proximity to red-winged blackbirds (Agelaius phoeniceus), black terns (Chlidonias niger), great blue herons (Ardea herodias) and white-tailed deer (Odocoileus virginianus borealis). Both red-winged blackbirds and black terns frequently attacked cranes. They would frequently dive and peck at cranes vigorously enough to interrupt their activities. A crane would respond to their attacks by crouching slightly, withdrawing its neck so that its head was near its back, beak pointing upward. From this position the crane would attempt to jab at the attacking birds. Red-winged blackbirds would occasionally actually land on and peck at the backs of the foraging cranes. Boeker (1961) noted that red-winged blackbird harrassment could cause cranes to move from a favorite feeding area.

Great blue herons were occasionally observed within 10 m of both incubating and foraging cranes and crane families. In all instances, cranes and herons appeared to ignore each other completely.

A white-tailed deer was once observed grazing within 3 m of a foraging crane. The activities of the deer and the crane seemed to be unaffected by the presence of the other. Once, an obviously disturbed deer ran at top speed across the marsh, directly over the nest of pair A. The incubating male crane flew off the nest only when the deer was almost on top of it. The crane walked back to the nest within 2 min after the deer had

passed, worked for about 4 min with eggs and nest material, then resumed incubating.

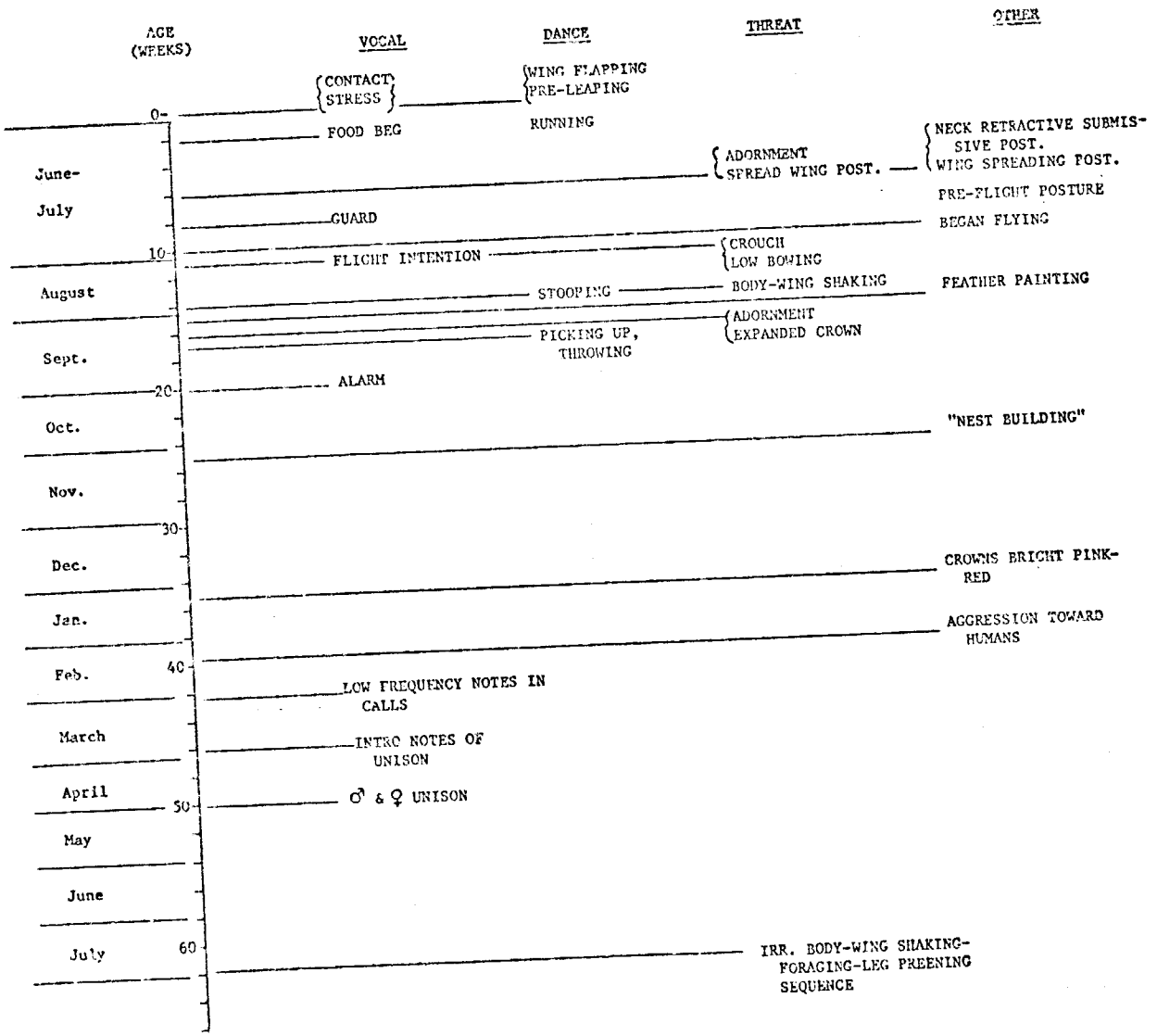
Lewis (1974) reports that cranes are very wary of coyotes. He also reports that crows (Corvus brachyrhynchos) will harrass cranes by swooping low over them, and that cranes were twice observed to threaten and chase crows. Every time bald eagles (Haliaeetus leucocephalus) flew over flocks of cranes near Fort Kearney, Nebraska, the cranes would fly. Drewien (1973) reports that at one nest an incubating male was killed and eaten by a gold eagle (Aquila chrysaetos).

Summary

Table IV summarizes the ages at which behavioral and other developments previously mentioned first occurred.

TABLE IV

APPEARANCE OF BEHAVIORS IN G. C. TABIDA CHICKS


AGE (WEEKS)
VOCAL
DANCE
THREAT
OTHER
CONTACT
STRESS
WING FLAPPING
PRE-LEAPING
RUNNING
0
FOOD BEG
June-
July
ADORNMENT
SPREAD WING POST.
NECK RETRACTIVE SUBMISSIVE POST.
WING SPREADING POST.
PRE-FLIGHT POSTURE
GUARD
BEGAN FLYING
10
FLIGHT INTENTION
CROUCH
LOW BOWING
August
STOOPING
BODY-WING SHAKING
FEATHER PAINTING
ADORNMENT
EXPANDED CROWN
Sept.
PICKING UP, THROWING
20
ALARM
Oct.
"NEST BUILDING"
Nov.
30
Dec.
CROWNS BRIGHT PINK-RED
Jan.
AGGRESSION TOWARD HUMANS
Feb.
40
LOW FREQUENCY NOTES IN CALLS
March
INTRO NOTES OF UNISON
April
50
♂ & ♀ UNISON
May
June
July
60
IRR. BODY-WING SHAKING-FORAGING-LEG PREENING SEQUENCE

IV. CAPTIVE CRANE OBSERVATIONS

CHANGES IN DAILY ACTIVITY PATTERNS DURING THE FIRST YEAR

Second-by-Second Record of Behavior

Captive sandhill crane chicks were observed regularly for extended periods of time throughout their first year (Table V) to document changes in daily time allotments for various activities, such as sleeping, preening, etc. It seemed likely that extensive observations might reveal changes over time, in how crane chicks budget their time. One might expect that changing growth rates, increasing body size and seasonal temperature and weather changes, as well as other factors, would affect time allotments for various activities.

Methods

Subjects. I made most observations on two sandhill chicks. In 1973, a G. c. tabida chick was observed from seven to 50 weeks of age. In 1974, a second chick was observed from zero to seven weeks of age. Chicks were housed as described in the methods section.

Apparatus and Procedure. I conducted most observations between 0700 and 1700 CDT (Fig. 36). Chicks less than one week old were observed every other day, then gradually less frequently as they aged (Table V). I was partially hidden from the chicks by a plywood or cardboard barrier during observations, and after an acclimatization period of several minutes, my presence did not seem to affect their behavior. Observations were recorded with a pencil, a watch with a second hand, and graph paper affixed to a clip board. Cross section paper ruled six squares to the inch (Ampad$_{tm}$) was used. The distance between vertical lines represented 10 sec intervals, and it was possible to record start and stop times of

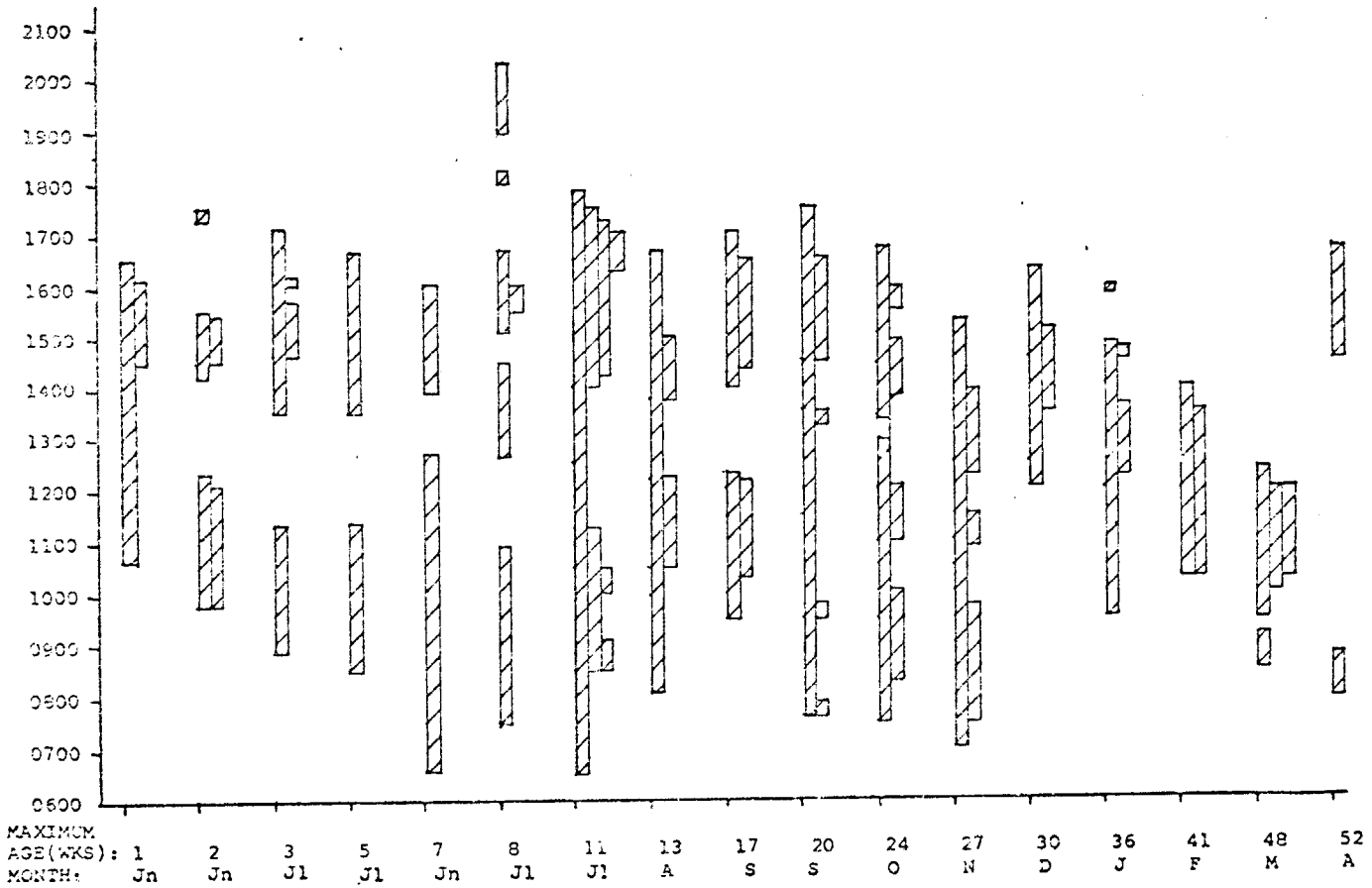
TABLE V

Ages, Dates and Hours of Observation
For 17 Age Intervals During the First Year

Age (Weeks)	Dates of Observation	Total Observation Time (Hours)
0-1	6-19-74 6-20-74 6-23-74	5.9
1.5-2	6-28-74 7-03-74	8.1
2.5-3	7-08-74 7-11-74	4.2
4-5	7-17-74 7-25-74	5.6
7	6-29-73	9.9
8	7-06-73	8.8
9-11	7-14-73 7-21-73 7-28-73	18.6
12-13	8-07-73 8-11-73	9.6
16-17	9-01-73 9-08-73	8.2
19-20	9-22-73 9-29-73	10.6
22-24	10-13-73 10-26-73	11.3
25-27	11-03-73 11-17-73	10.6
29-30	12-01-73 12-09-73	4.4
34-36	01-08-74 01-19-74	7.9
39-41	02-10-74 02-21-74	6.0
43-48	03-10-74 03-24-74 04-13-74	6.6
52	05-28-74	2.8

Figure 36

Time of day of continuous record of activities of observation.


2100
2000
1900
1800
1700
1600
1500
1400
1300
1200
1100
1000
0900
0800
0700
0600
MAXIMUM AGE(WKS): 1 2 3 5 7 8 11 13 17 20 24 27 30 36 41 48 52
MONTH: Jn Jn Jl Jl Jn Jl Jl A S S O N D J F M A

activities to within a 2 sec accuracy. Each sheet of cross section paper could be used for 10 min of observation time, and was immediately replaced with a new sheet when full. The various activities were assigned to horizontal lines and were permanently listed on the clipboard. When an activity occurred, start and stop marks were made on the appropriate horizontal line.

Analysis. The chicks' ages were divided into 17 time intervals, and all data collected within one interval were analyzed together. Each interval included, with one exception, a minimum of 4 hours of observation (Table V). The data within each interval were analyzed with the aid of a Datacraft computer to determine changes in 1) percent of time spent in a given activity, 2) frequency of bouts of a given activity, and 3) the average length of bouts $\pm$ 1 standard error. A bout was defined as the difference between the start time and the stop time of an activity, so long as this difference was greater than 2 secs. Certain activities, such as defecation, always lasted less than 2 secs and were, for purposes of analysis, defined as instantaneous activities. A bout was considered terminated when the activity ceased for longer than 2 secs. Pauses of 2 secs or less were ignored. Any behavior that could be recoguized as distinct from other behaviors was given a name and included in the activity list. Of the many behaviors recognized and recorded, only a few occurred frequently enough and in long enough bouts to be carefully analyzed by these methods. A discussion of the results of analysis of these activities follows.

Results and Discussion

Preening (Figs. 37 and 38). The percent of time spent preening increases greatly from zero to five weeks of age, then fluctuates at a

slightly lower level until about 17 weeks (Fig. 37). After about 17 weeks, the amount of time spent preening varies, but is less than prior to 17 weeks.

The number of bouts per hour increases greatly from zero to five weeks, remains steadily lower at about 10 bouts per hour from five to 17 weeks, then decreases to less than five bouts per hour after 24 weeks (Fig. 37). The average length of preening bouts increases throughout the first year (Fig. 38).

Hence, until five weeks of age, preening bouts become both longer and more frequent. After five weeks, bouts were less frequent, but longer.

Crane chicks grow very rapidly during the first four to five weeks. The down they had at hatching begins to be replaced by brown immature feathers by 2.5 to three weeks of age, and by five to six weeks the chick has a complete brown immature plumage, although downy plumes may still be attached to the tips of these feathers. The large increase in the percent of time spent preening during the first five weeks is probably due to the rapid growth of body feathers. As growth of immature body plumage is completed, rapid growth of flight feathers begins. From seven to ten weeks of age, primary and secondary feathers develop from about 10 cm quills to mature flight feathers. At 12 to 13 weeks, soon after growth of flight feathers was completed, the post-juvenal molt began. During this molt, the immature brown body plumage was replaced by adult gray plumage. This molt was completed by 20 to 22 weeks of age. Walkinshaw (1949) also described the molt of a captive greater sandhill crane. He found that the post-juvenal molt began at 83 days (12 weeks) and was completed by November (24 weeks).

Figure 37

Preening: the percentage of time and number of bouts per hour for 17 age intervals during the first year.

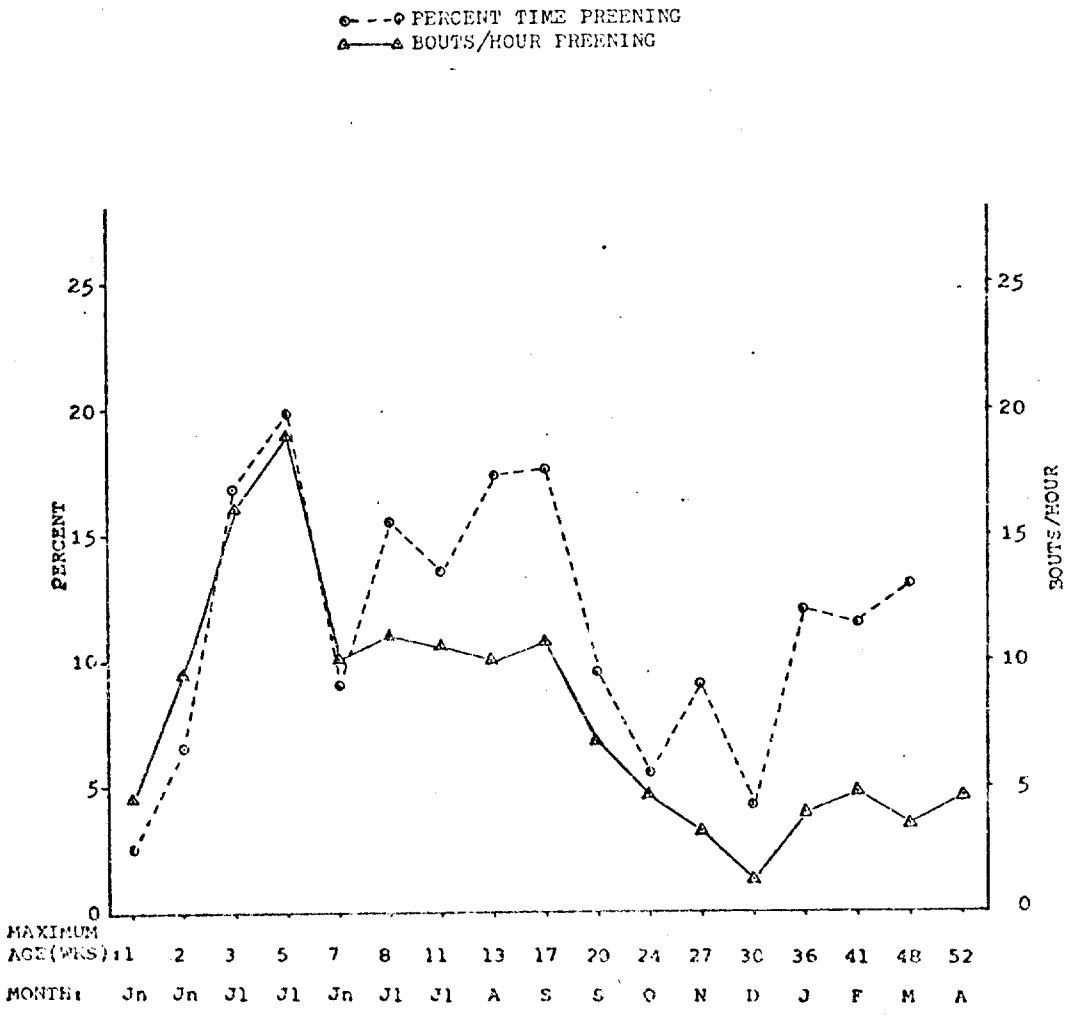
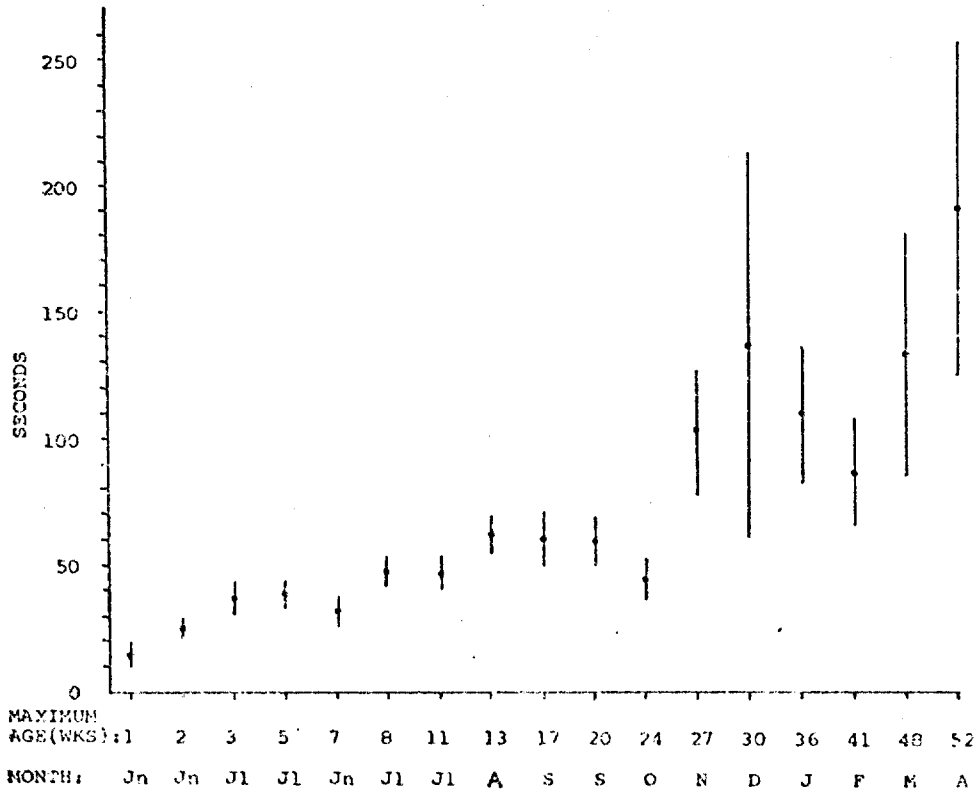


Figure 38

Preening: Average length of bouts ± 1 standard error for 17 age intervals during the first year.



In summary, either feather growth or molting occur almost continually from hatching to about 20 to 24 weeks of age. The highest percentages of time spent preening and greatest frequencies of bouts of preening occur until about this time, then both drop off. It seems quite likely that the amount of time spent preening and the frequency of preening bouts are related to feather growth and molting.

Sleeping. Three different sleeping postures were recognized in cranes. Chicks less than 2.5 weeks old slept exclusively in head out position. Young chicks were frequently observed attempting to assume a back sleeping or bill down position, but could not do so, probably because of small wing size and weak musculature. Chicks less than two weeks old spent by far the greatest percentage of time and had the greatest frequency of bouts of sleeping (Figs. 39 and 40). Once chicks were capable of assuming bill down and back sleeping positions, they no longer slept in head out position.

Throughout the first year, the percentage of time spent sleeping fluctuates greatly from one age interval to the next (Fig. 39). These fluctuations can be attributed largely to fluctuations in the amount of time spent in back sleeping position. The percent of total time spent sleeping in bill down position fluctuates much less, and is always less than five percent. Of 498.2 minutes of sleeping observed after 2.5 weeks of age, 84 percent are spent in back sleeping position and 17 percent in bill down position. At the same time, of 440 bouts of sleeping, only 36 percent are spent in back sleeping position and 64 percent in bill down position. While the average length of bouts of sleeping varied greatly for back sleeping position, they were usually much longer than bouts of sleeping in bill down position (Figs. 41 and 42).

Figure 39

Sleeping: the percentage of time spent in three sleeping postures for 17 age intervals during the first year.

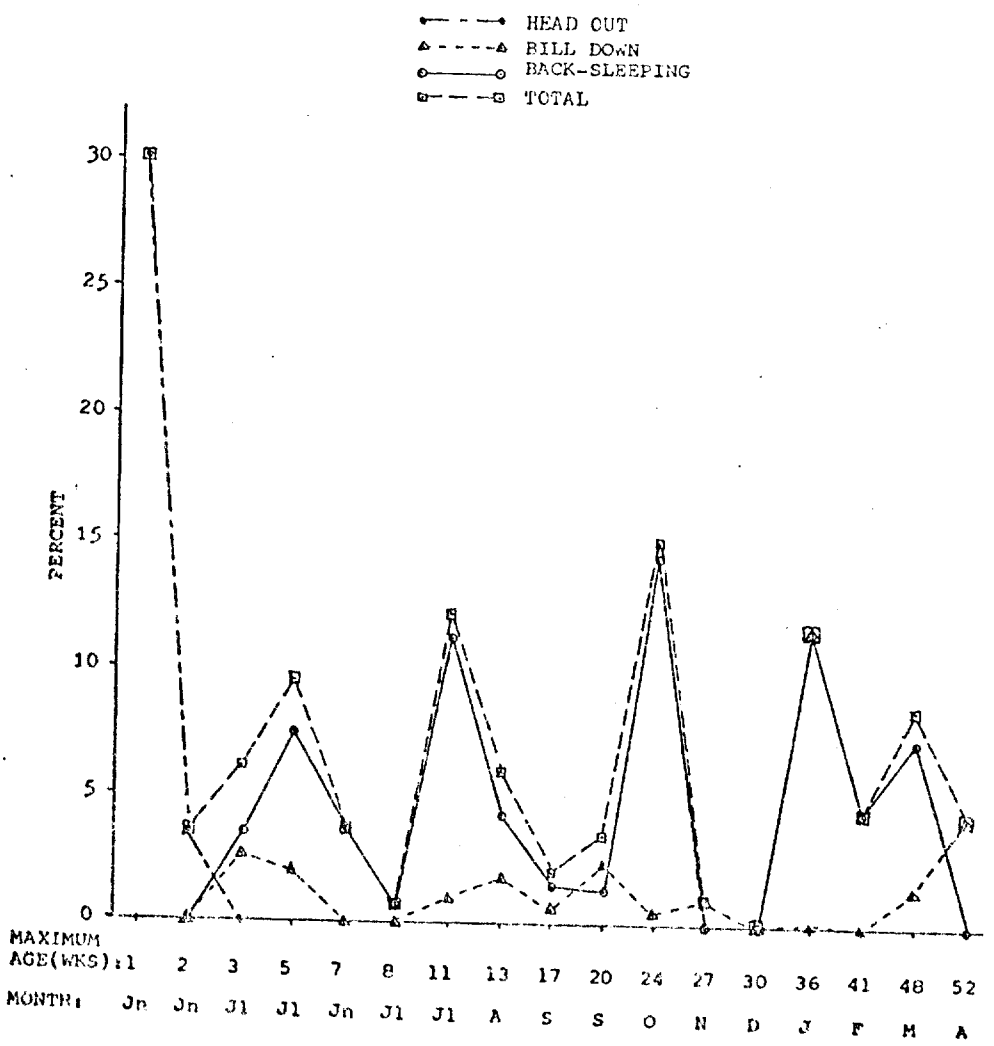


Figure 40

Sleeping: the frequency of bouts in three sleeping postures for 17 age intervals during the first year.

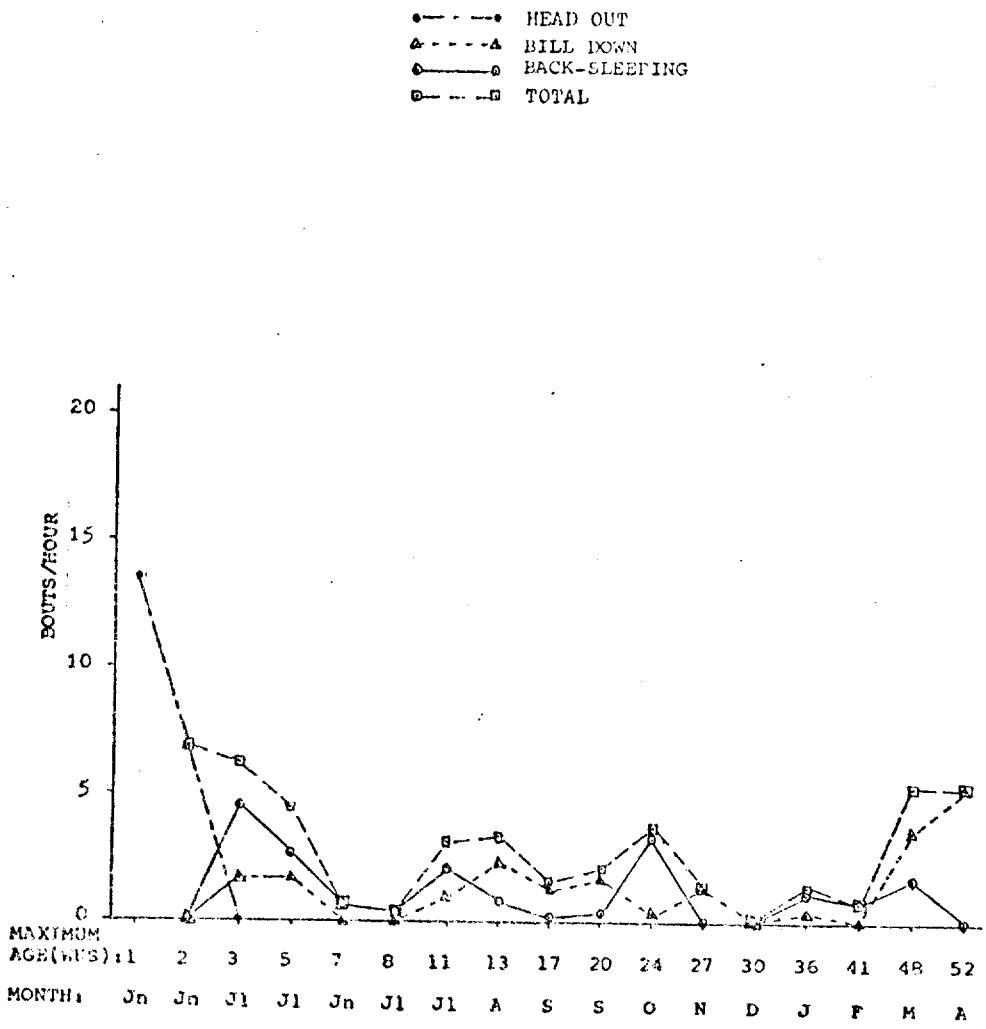


Figure 41

Sleeping, Head out and bill down positions: average length of bouts ± 1 standard error for 17 age intervals during the first year.

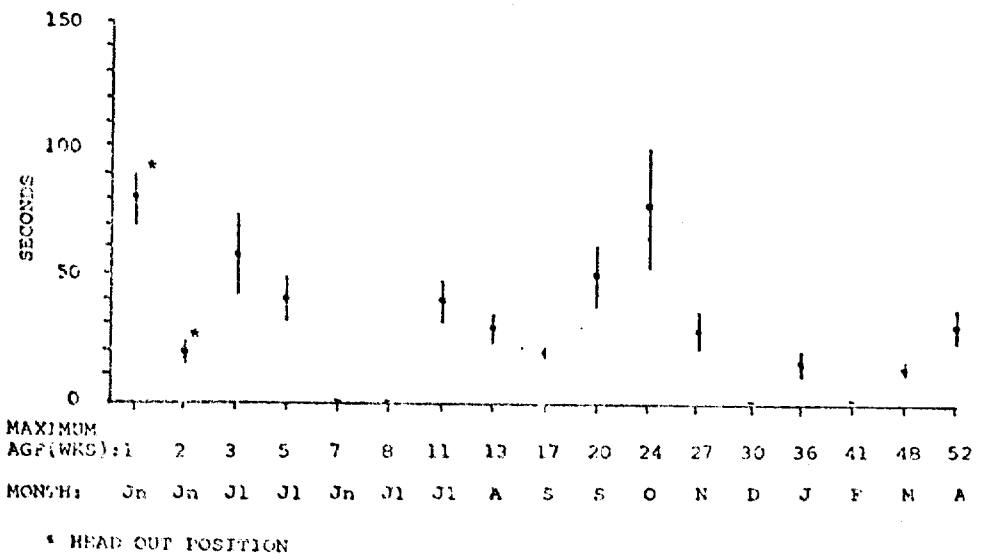
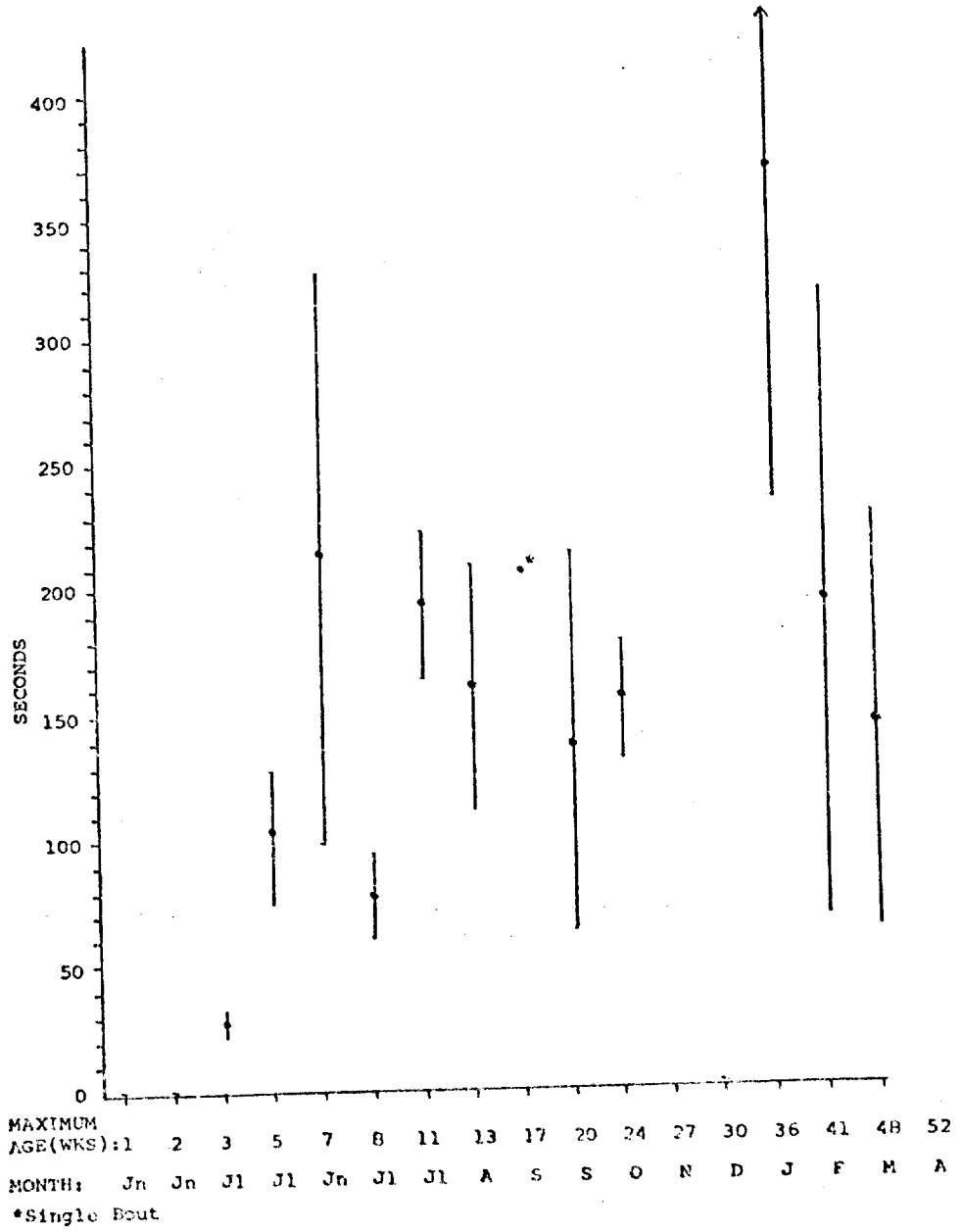


Figure 42

Back sleeping position: average length of bouts ± 1 standard error for 17 age intervals during the first year.



In summary, bouts of sleeping in bill down position tended to be short and frequent, while long bouts were spent in back sleeping position.

Because there is little fluctuation in the average number of bouts per hour of sleeping for each age interval (Fig. 40), the great fluctuation in total percent of time spent sleeping can be attributed to a relatively few long bouts spent in back sleeping position during certain age intervals. The reasons for these fluctuations are uncertain. There does not appear to be any direct relationship with temperature or weather conditions (Fig. 43).

Drinking, Feeding and Foraging. Food and water intake, as measured by time spent in drinking, feeding and foraging activities showed distinct trends over time. In addition to the second-by-second record of time spent on these activities, I recorded individual feeding and foraging pecks and drinks, and steps taken while foraging. The average number of steps, pecks or drinks taken per minute for the different age intervals was calculated (Fig. 44). Unfortunately this information was not recorded for 7 to 17 week old chicks, but data that were recorded give a good indication of the intensity of these activities. A drink was recorded each time the chick lowered its head to take in water then raised its head to swallow, as described earlier. Foraging pecks were somewhat more difficult to define, since chicks foraged in a number of different ways. When foraging consisted of quick individual jabs with the beak at objects, foraging pecks were easy to record. At other times, a chick would spend extended periods of time nibbling at one object, or digging with its beak in the ground. In these cases, each bout of nibbling or digging was recorded as a single peck. A bout was considered terminated

Figure 43

Range of temperatures, ground snow depths and weather conditions for observation dates in each age interval.

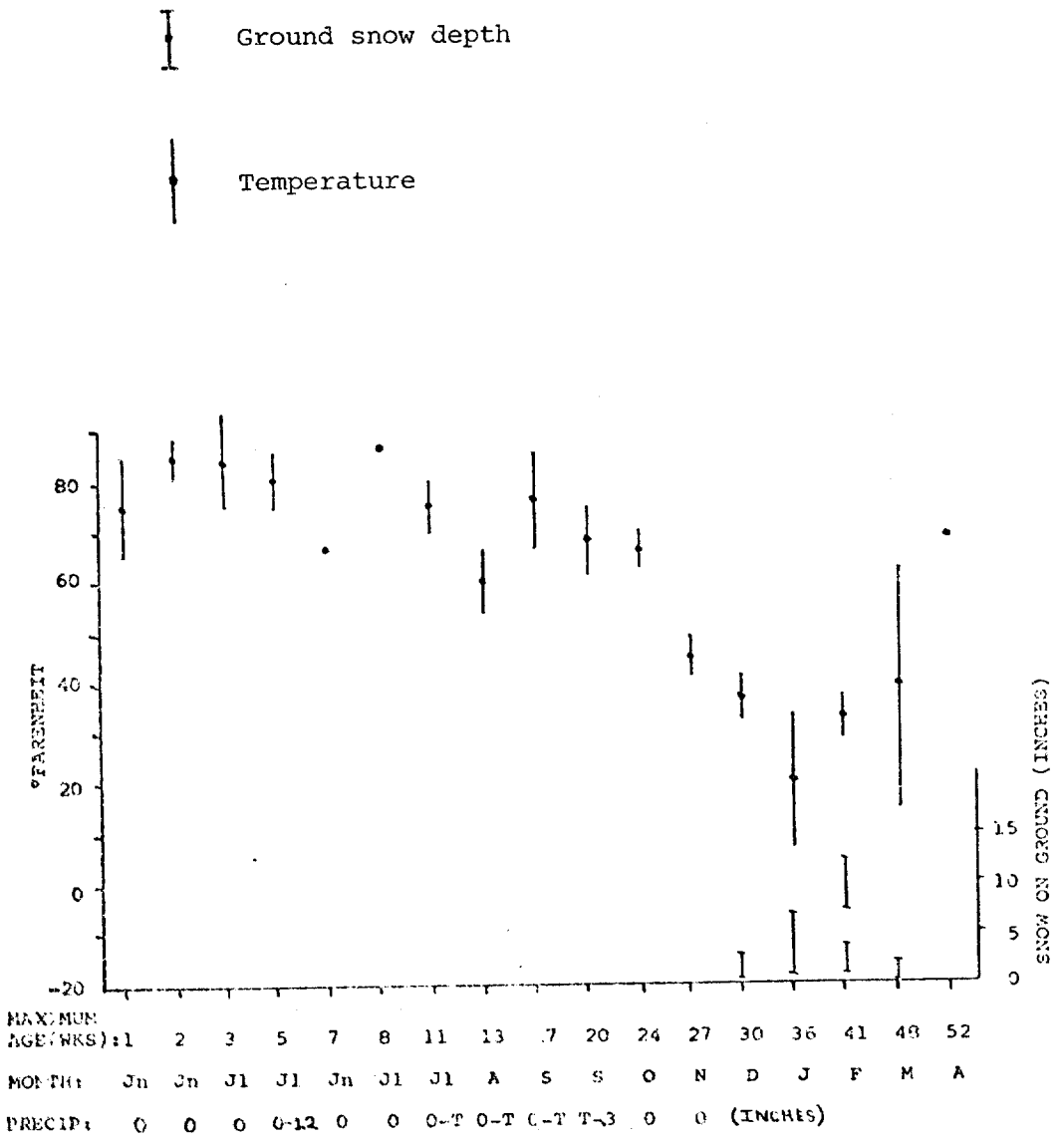
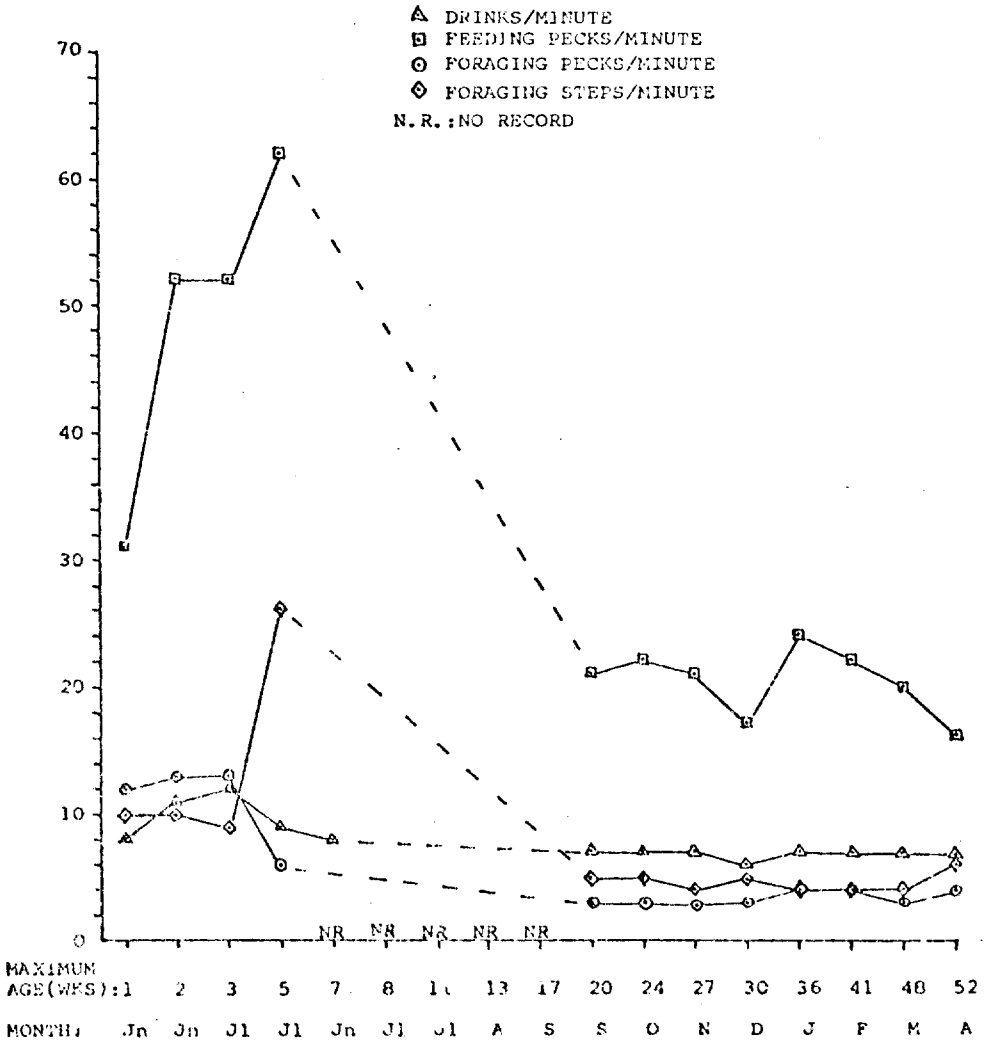


Figure 44

Frequency of drinks, feeding pecks and foraging pecks and steps for 12 age intervals during the first year.



and a new bout begun when digging or nibbling was interrupted for 2 sec or more, or if the site of nibbling or digging became greater than 15 cm from the site of nibbling or digging at the beginning of the bout. A step was considered to have been taken when a foot was lifted from the ground and placed a distance of at least 15 cm from its previous position. This distance was chosen because it was useful in distinguishing between steps which actually resulted in some directional movement, and the lifting and setting down of feet which often occurred while nibbling or digging, that did not result in any great movement of the crane.

No attempt was made to record actual swallowing of food objects while foraging. The distance between the observer and the chick, and obstructing vegetation often made it impossible to see the object a peck was directed at, or to observe whether something was swallowed. It was recognized though, that much foraging activity was not directed at food objects. Chicks spent much time nibbling and jabbing at wire fencing and wood chips in a manner that was indistinguishable from foraging for various invertebrates. I qualitatively observed that older chicks, especially after nine to ten months of age, spent less time pecking at nonfood objects. Chicks up to five or six months of age would peck for extended periods of time at almost any colorful, shining, or dangling object, while older chicks frequently would give an initial peck or two at these objects, then ignore them. The manner in which young chicks would peck at food and nonfood objects was quite similar. After catching an insect, such as a grasshopper or larva, the chick usually picked it up, dropped it, and jabbed at it many times before finally swallowing it. This was very similar to the way in which a chick manipulated a nonfood object, such as a key or wood chip. Although it was impossible to

observe wild chicks very closely, I would suspect that a wild chick would also initially handle many non-food objects with its beak, and that this activity may result in crane chicks becoming more adept, over time, at distinguishing food from non-food items.

Drinking. There seems to be less variation in drinking than in almost any other activity observed. The percent of time spent drinking (Fig. 45) is lowest in young chicks, then rises during late fall and winter. The average length of bouts (Fig. 46) shows a similar rise. The number of bouts per hour may also show a similar rise, though much variation for younger chicks makes this uncertain. It appears that water requirements and patterns of drinking are quite steady with a probable slight increase during colder months (Fig. 43).

Chicks less than seven weeks old may drink at a slightly faster rate (Fig. 44) than chicks 17 weeks old. By 17 weeks, the number of drinks per min is very steady. This is probably due to the maximum rate at which cranes can take individual drinks, since it took this crane at least 5 secs to take water into its mouth, raise its head to swallow the water, then again lower its beak to the water.

Feeding. Both the percent of time spent feeding and the average number of bouts per hour of feeding are rather variable, however, after about seven weeks of age, the percent of time spent feeding increases, while the bouts per hour decreases (Fig. 47). At about the same time (seven to eight weeks), the average length of bouts increases (Fig. 48). In general, it seems that feeding bouts become longer and less frequent after seven weeks of age, while the total amount of time spend feeding continues to increase until about 17 weeks of age. After 17 weeks of

Figure 45

Drinking: percent of time and frequency of bouts for 17 age intervals during the first year.

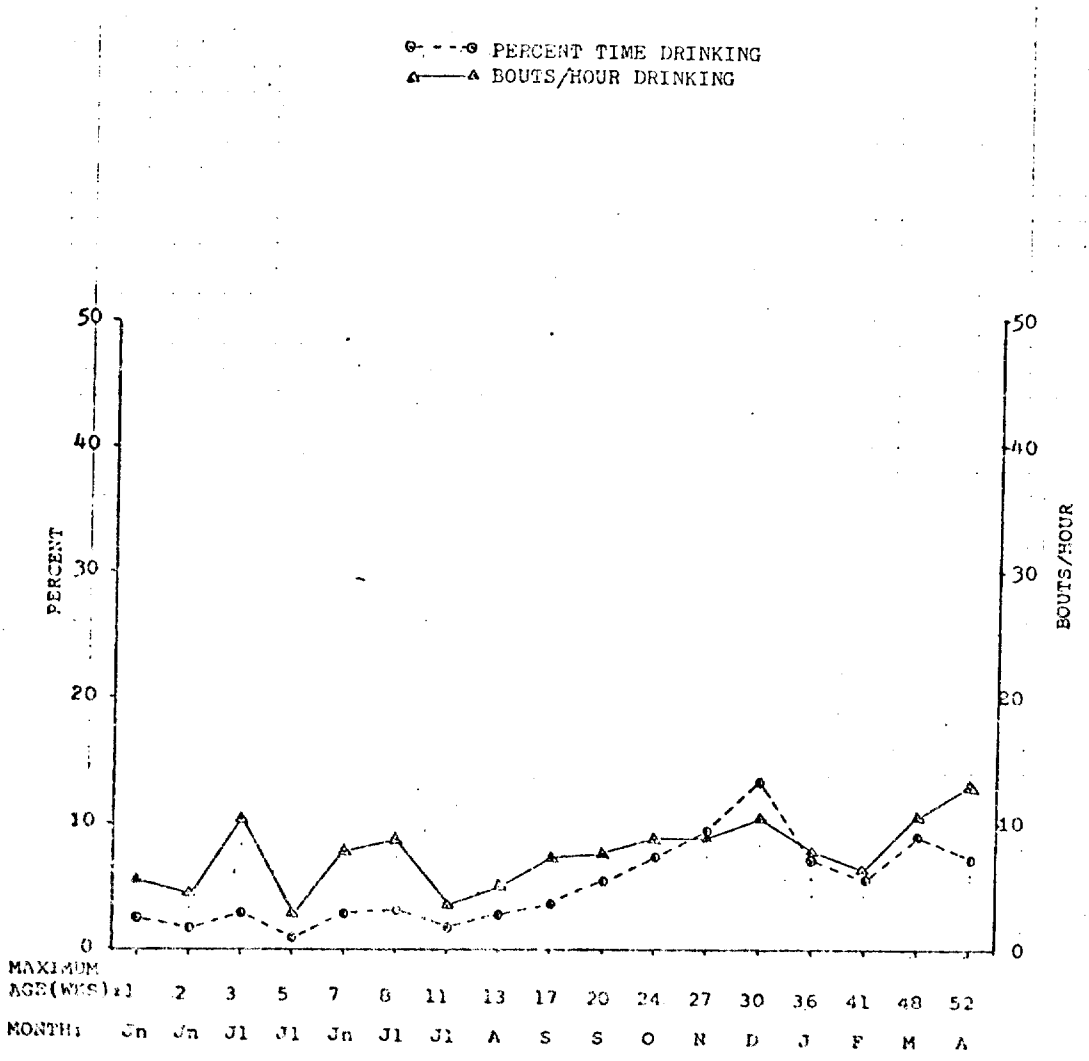


Figure 46

Drinking: average length of bouts ± 1 standard error for 17 age intervals during the first year.

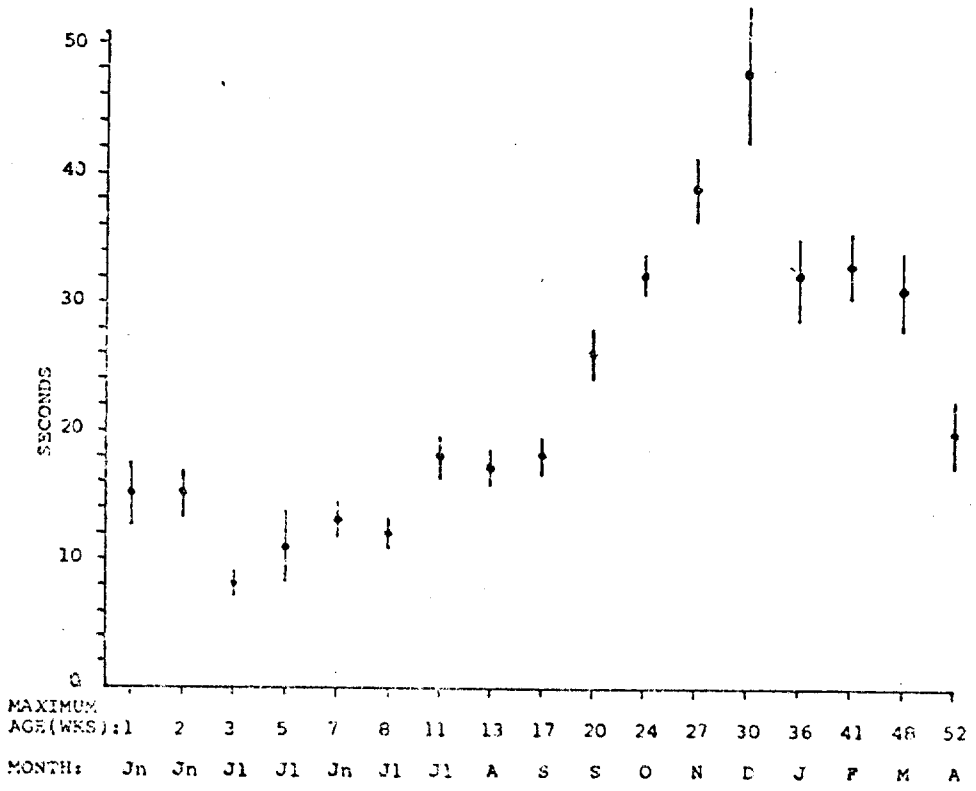


Figure 47

Feeding: percent of time and frequency of bouts for 17 age intervals during the first year.

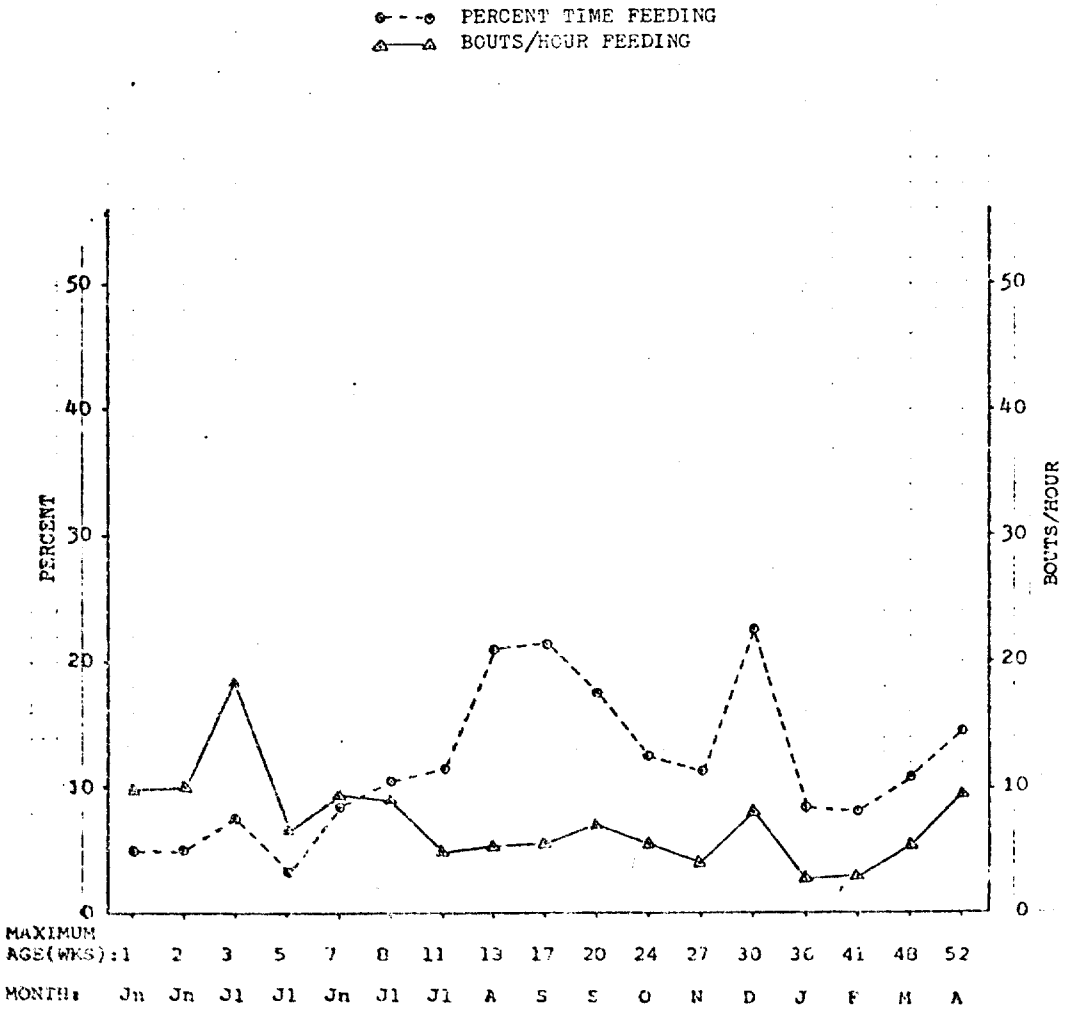
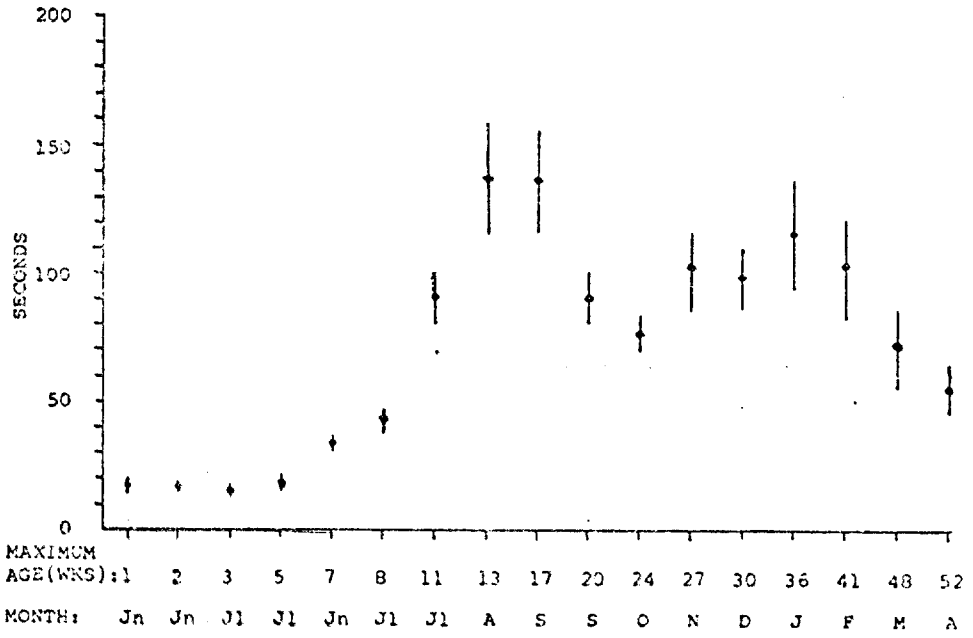


Figure 48

Feeding: average length of bouts ± 1 standard error for 17 age intervals during the first year.



age, the percent of time spent feeding and average length of bouts appears to decrease somewhat.

The rate of feeding (pecks/min) is much greater in chicks less than seven weeks old than it is in chicks over 17 weeks old (Fig. 44). There is no clear explanation for this, although possibly smaller chicks with their much shorter beaks and necks, are capable of picking up and swallowing food pellets more quickly than much larger chicks. Also, preliminary data (Baldwin, Ph.D. thesis, in prep.) indicate that the greatest rate of weight gain occurs between two and seven weeks of age. Perhaps this higher pecking rate reflects a need for greater food intake at this age.

Foraging. The amount of time spent foraging is very low in chicks less than two weeks old, but increases to a peak at seven weeks (Fig. 49). After seven weeks, the amount of time spent foraging decreases, although it remains variable. Both the number of bouts per hour and the average length of bouts (Fig. 50) increase to five to seven weeks of age, then the number of bouts per hour declines, while the average length of bouts increases slightly and remains high. In general, after seven weeks of age, bouts of foraging become longer and less frequent. Chicks less than two weeks old spend much less time foraging than at any other age. Very young chicks probably simply cannot afford to spend the energy required by foraging activity. They spend a large percentage of their time in various resting positions. Wild parents were observed spending a great deal of time carrying food to young chicks, hence it is probably not necessary that the chicks spend much time foraging.

Chicks spend more time foraging between five and 11 weeks of age than at any other time. Perhaps, as discussed earlier, chicks become more adept at distinguishing between food and non-food items after this

Figure 49

Foraging: percent of time and frequency of bouts for 17 age intervals during the first year.

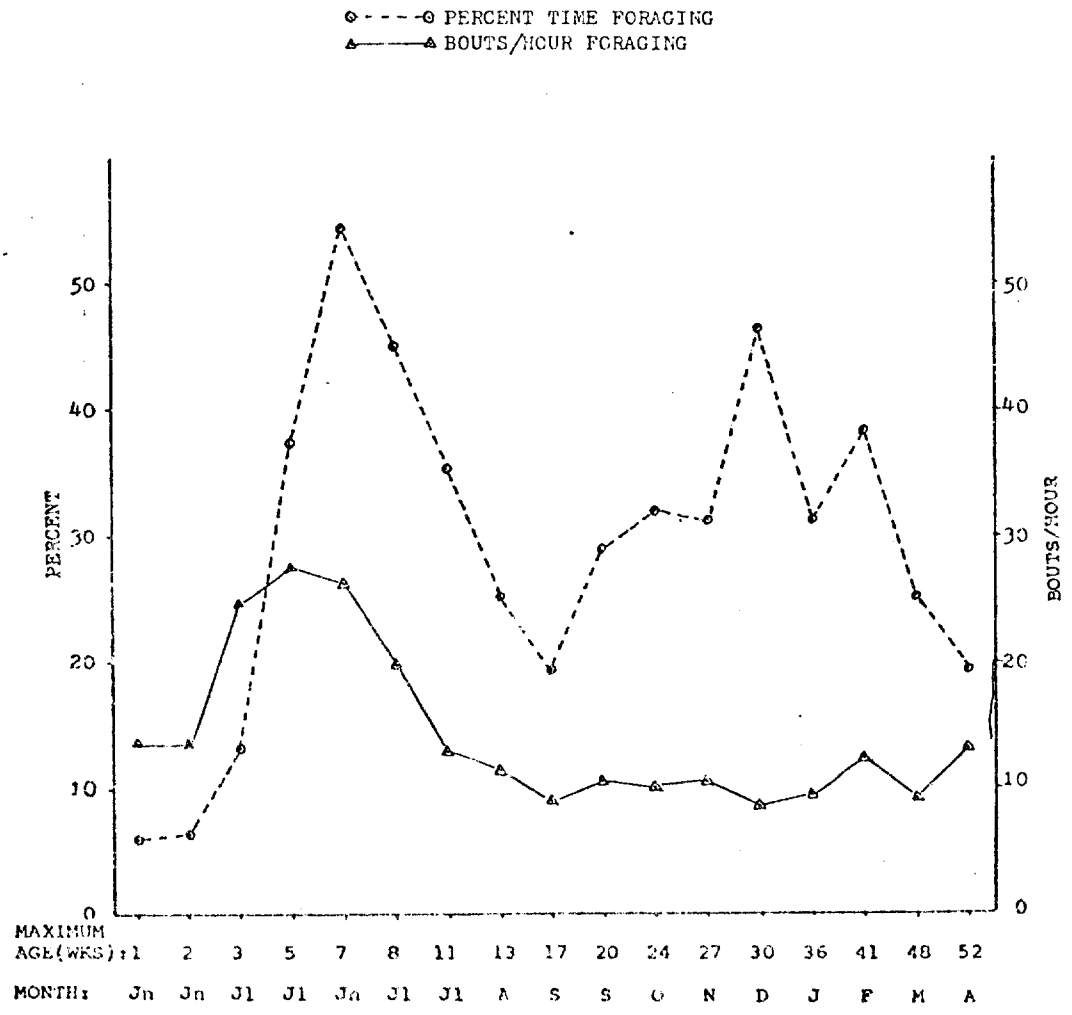
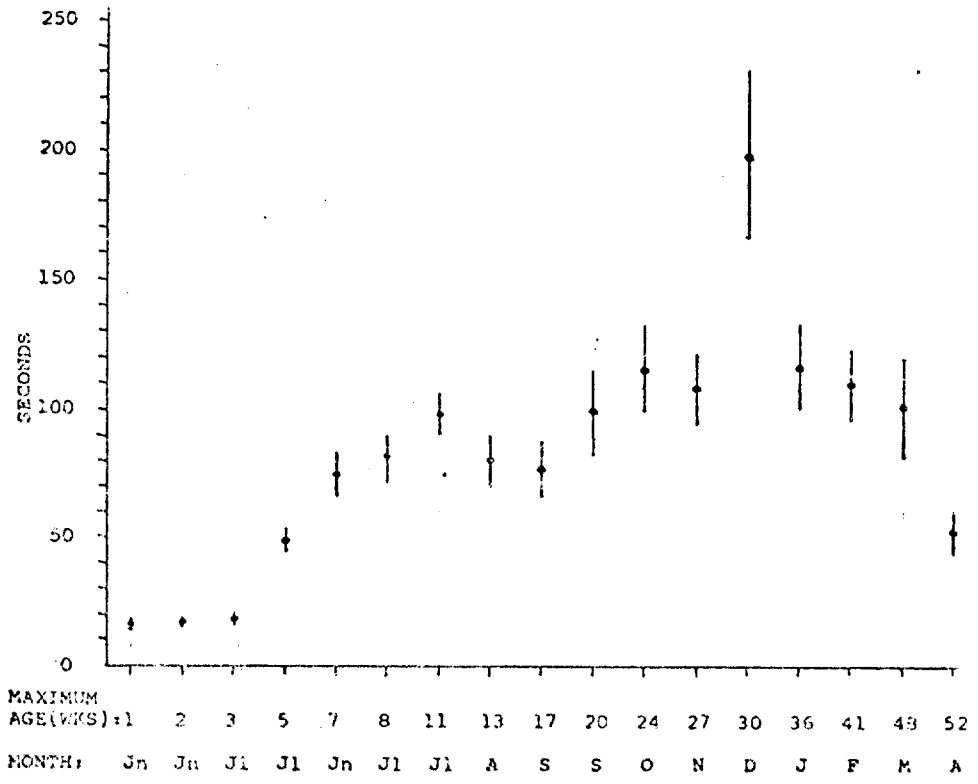


Figure 50

Foraging: average length of bouts ± 1 standard error for 17 age intervals during the first year.



time, and it is this period of much foraging activity which aids in development of this discriminatory ability.

Resting Positions

A chick was considered to be in a resting position any time it was sitting, in heel standing, unipedal or bipedal standing posture and not engaged in any other activity. Chicks less than two weeks old spent by far the greatest amount of time resting (Fig. 51). Bouts of resting also occur most frequently in younger chicks, decreasing sharply until about seven weeks of age (Fig. 51). The large amount of time spent resting and frequency of resting bouts in very young chicks is probably simply a result of the need of the rapidly growing chick for rest, and its relatively weaker musculature.

In addition to the trends seen in total amount of time spent resting, some interesting trends were observed in the four different resting postures.

Sitting and Heel Standing Postures. Chicks less than a week old spent much more time sitting than at any other age (Fig. 52) and more time sitting than in any other resting position. Bouts of sitting are also shortest and most frequent in young chicks (Figs. 52 and 53). Sitting probably requires less energy, and a less developed sense of balance than any other resting position: these factors probably account for its predominance in the early weeks. Sitting disappears entirely during November, December, January and February.

Bouts of heel standing posture tend to become longer and less frequent from hatching through 17 to 20 weeks of age, then decrease and disappear completely by November (Figs. 54 and 55). The days of observation in November, December, January, February and March were at least

Figure 51

Resting positions: percent of time and frequency of bouts for 17 age intervals during the first year.

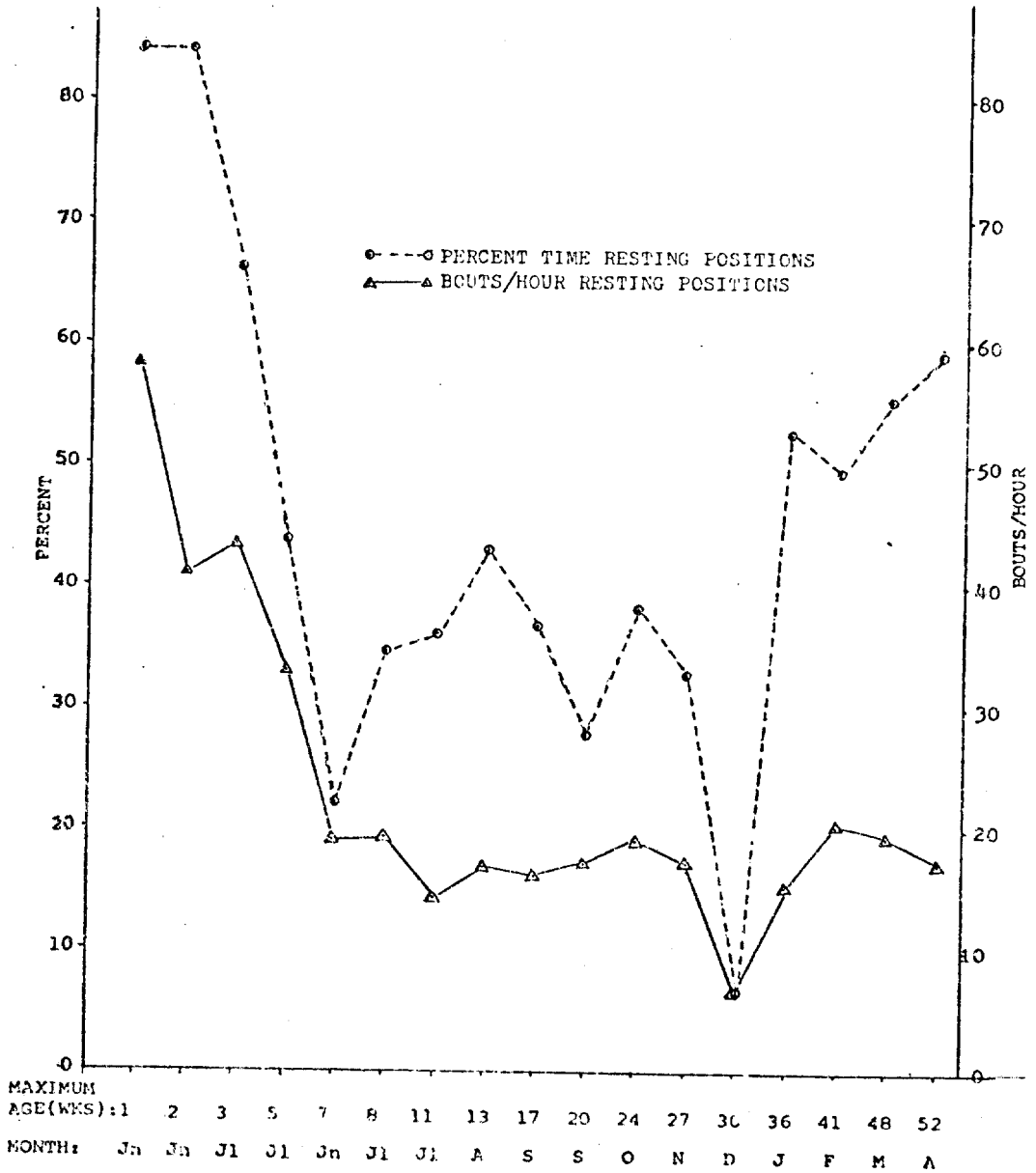


Figure 52

Sitting: percent of time and frequency of bouts for 17 age intervals during the first year.

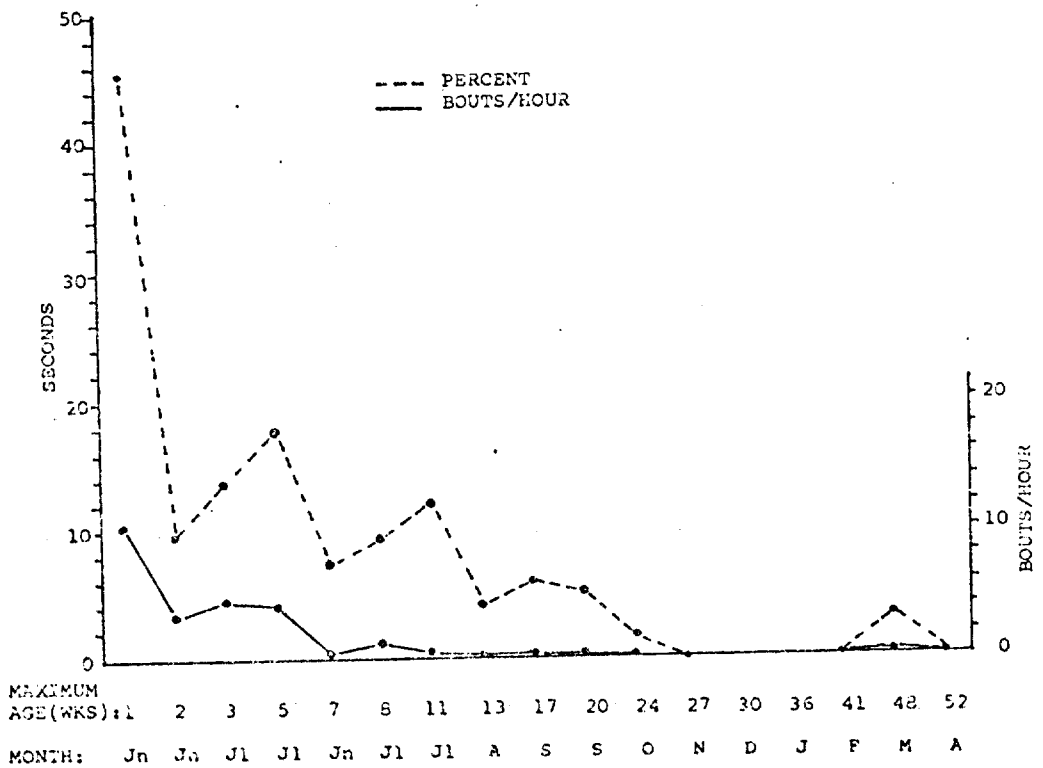
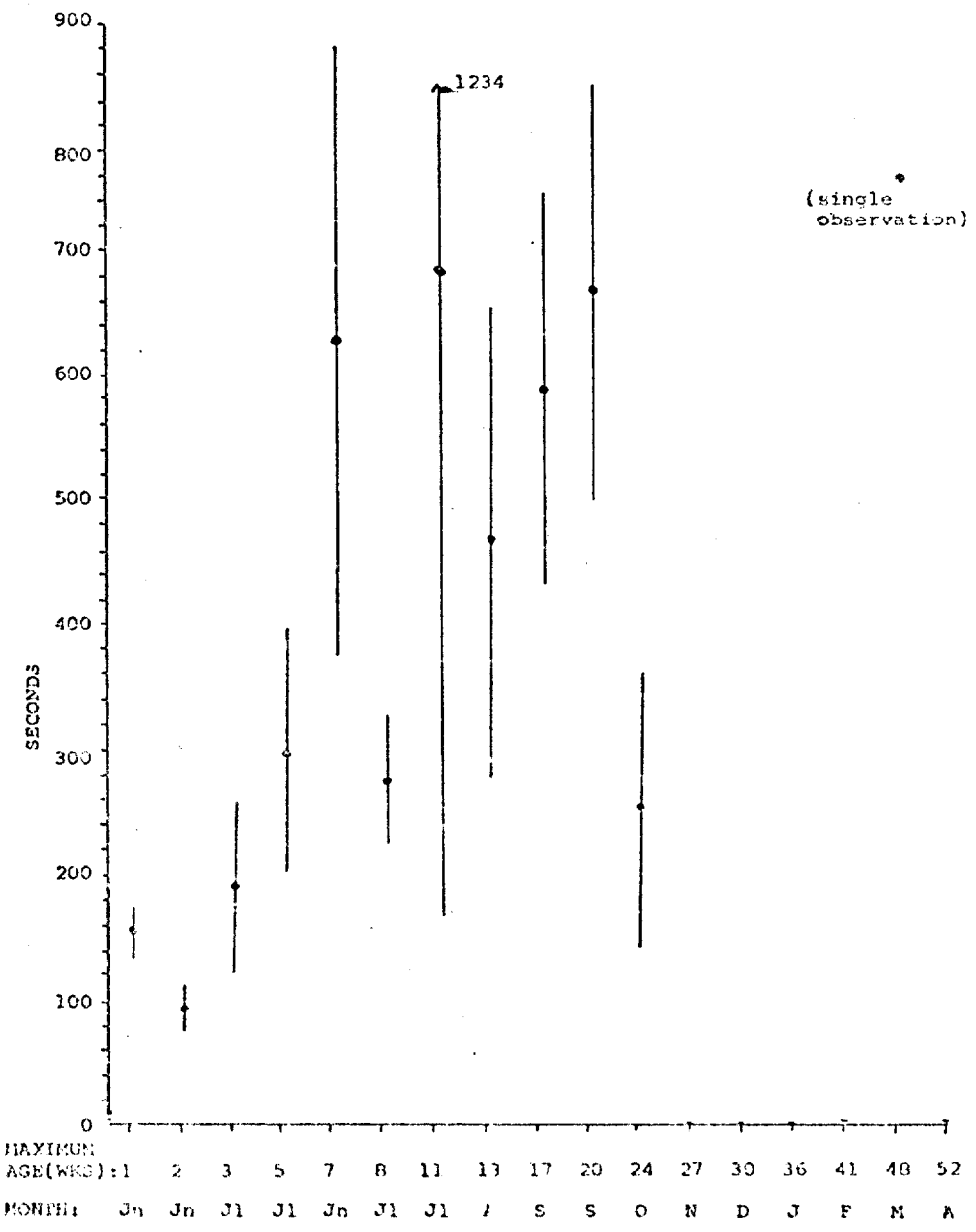


Figure 53

Sitting: average length of bouts ± 1 standard error for 17 age intervals during the first year.



20°F colder than any other observation days, and there was snow on the ground on these days (Fig. 43). Since sitting and hock posture both put large amounts of body and/or leg surface in contact with the ground, these resting positions probably would have incurred too much heat loss on these cold observation days.

Frith (1974) once observed 44 cranes sitting flat on the ground during a March blizzard, facing into a 38 m.p.h. wind. In this case, it seems likely that more energy was conserved by reducing the body surface area exposed to the wind than was lost through contact with the ground.

Bipedal Standing. Chicks less than three weeks old spent the greatest amount of time standing on two legs. After three weeks of age, the amount of time spent in this resting position varies, although it is less than before three weeks of age (Fig. 53). The frequency of bouts of bipedal standing is also greatest in chicks less than three weeks of age, decreases until about seven weeks of age, and varies thereafter, but remains less than before three weeks. The average lengths of bouts of bipedal standing are quite constant throughout the first year, usually 0.5 to 1 min long, and seldom more than 2 min long (Fig. 57). In general, bouts of bipedal standing tend to remain fairly constant in length, but become less frequent with increasing age.

Unipedal Standing. Chicks less than three weeks old spend no time standing on one leg. Although they occasionally attempted to assume this position, they lacked the ability to balance on one leg. Chicks only rarely stood on one leg until mid-September, spent 3 to 12 percent of their time in this position until January, then spent over 40 percent of their time in this position. Bouts of unipedal standing also occur much more frequently after December. There is considerable variation in the

Figure 54

Heel standing posture: percent of time and frequency of bouts for 17 age intervals during the first year.

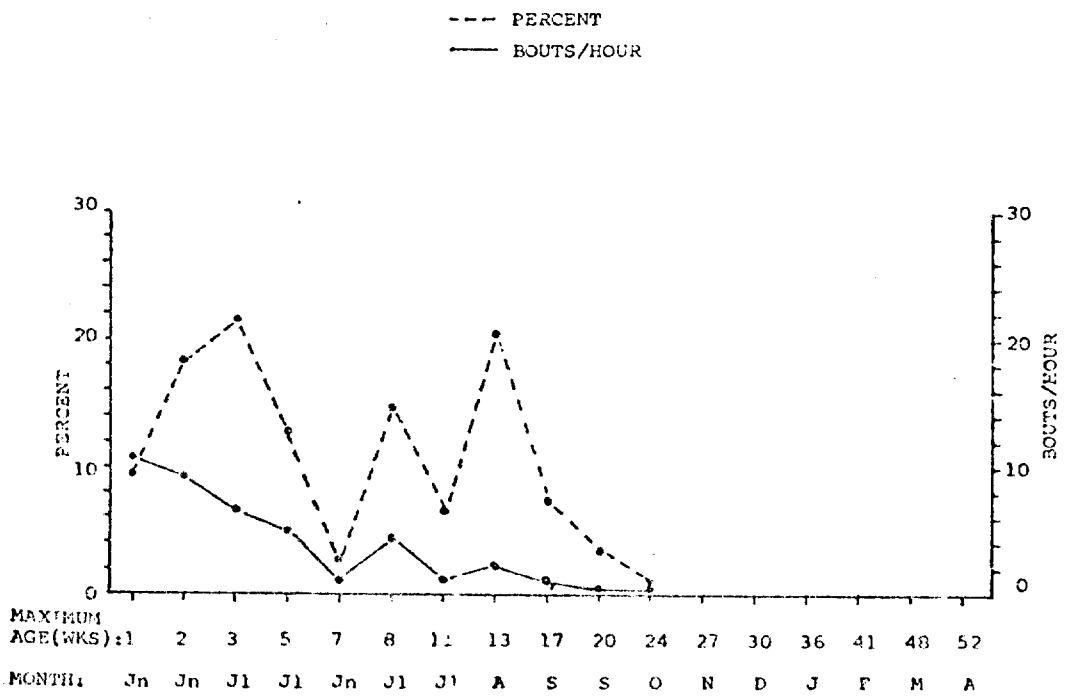


Figure 55

Heel standing posture: average length of bouts ± 1 standard error for 17 age intervals during the first year.

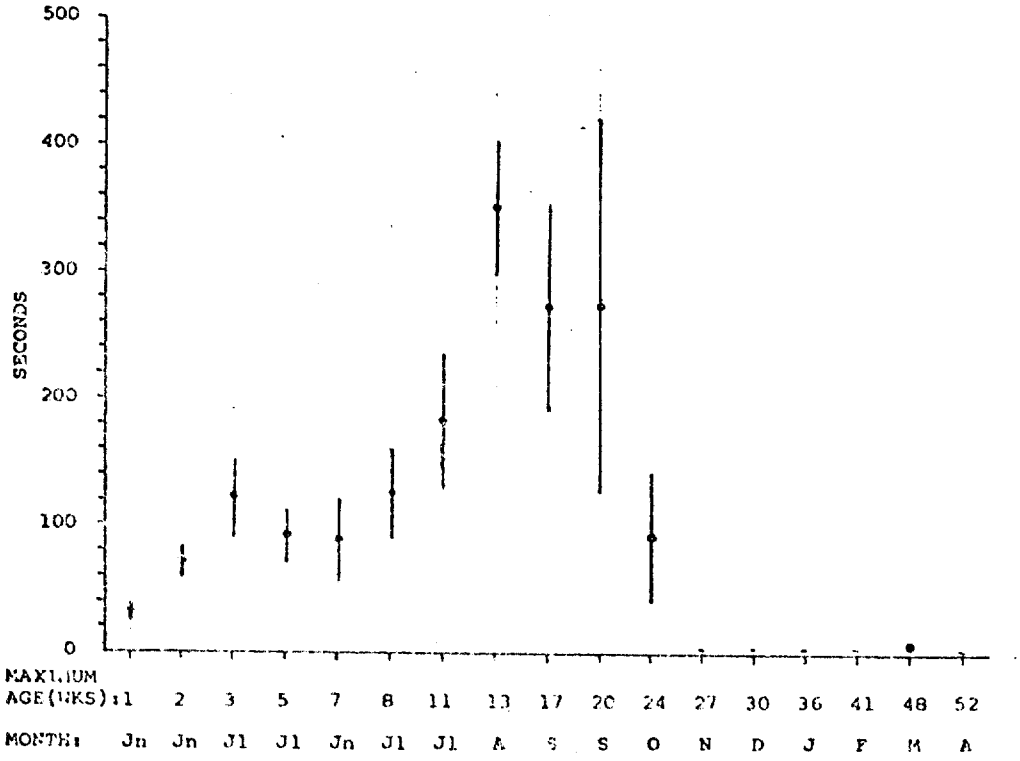


Figure 56

Bipedal standing: percent of time and frequency of bouts for 17 age intervals during the first year.

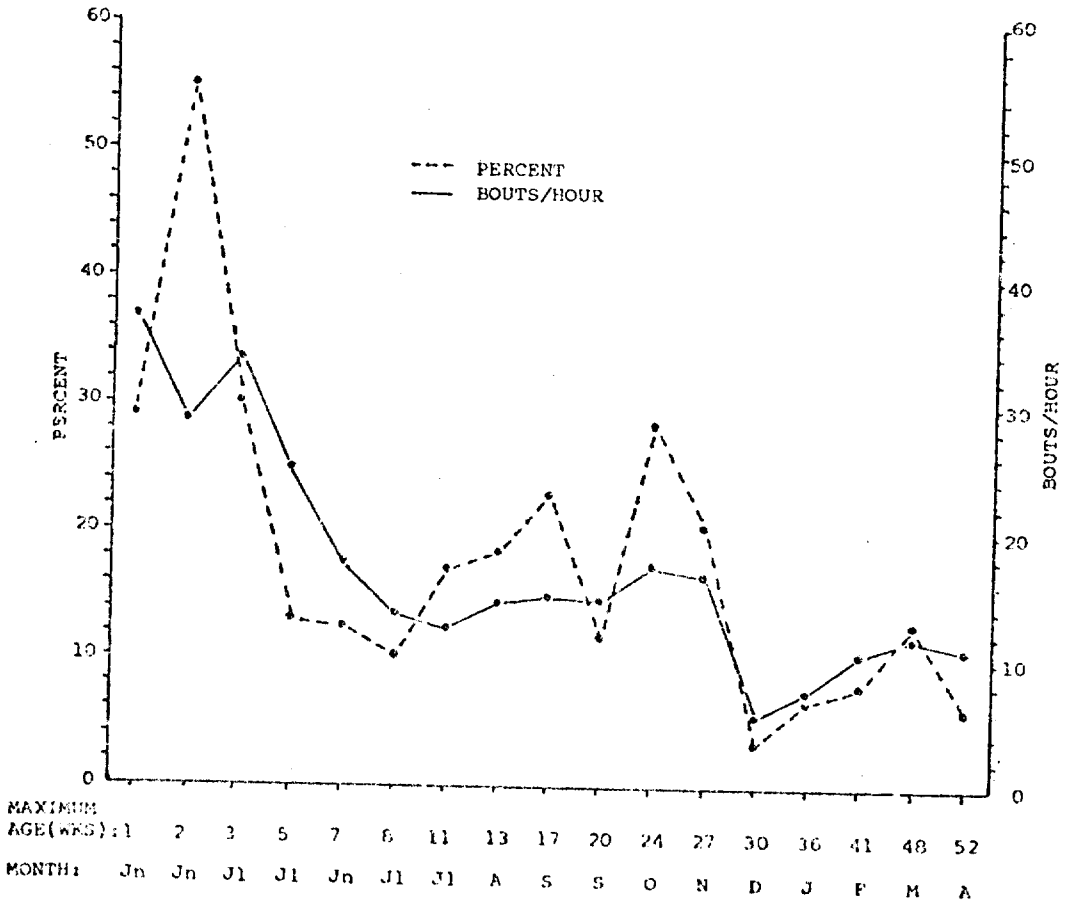
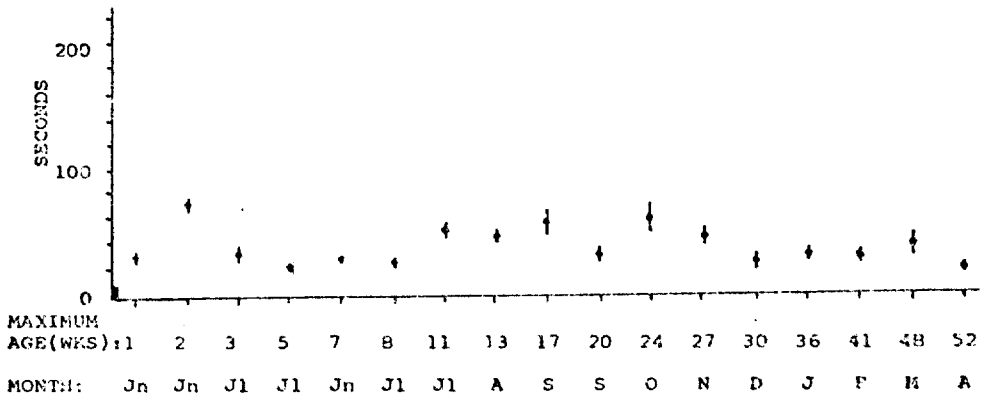


Figure 57

Bipedal standing: average length of bouts ± 1 standard error for 17 age intervals during the first year.



average length of bouts of unipedal standing, though they tend to be much longer than bouts of bipedal standing. There is an unexpectedly low percentage of time spent standing on one leg in December and an unexpectedly high percentage in May, but for other age intervals there seems to be a relationship between temperature and amount of time spent in this resting position (Fig. 43). Cranes probably experience less heat loss in this resting position than any other, since one leg can be completely insulated by body feathers, and there is a minimal amount of body contact with cold ground.

Figure 58

Unipedal standing: percent of time and frequency of bouts for 17 age intervals during the first year.

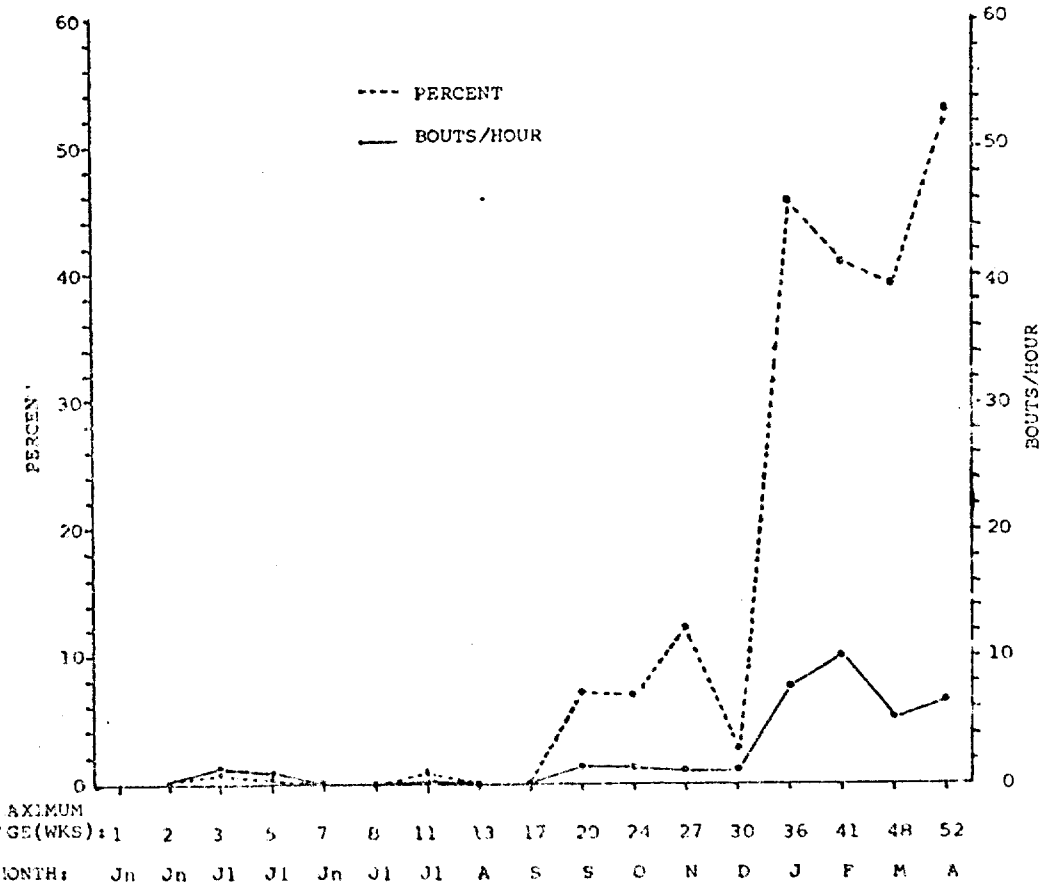
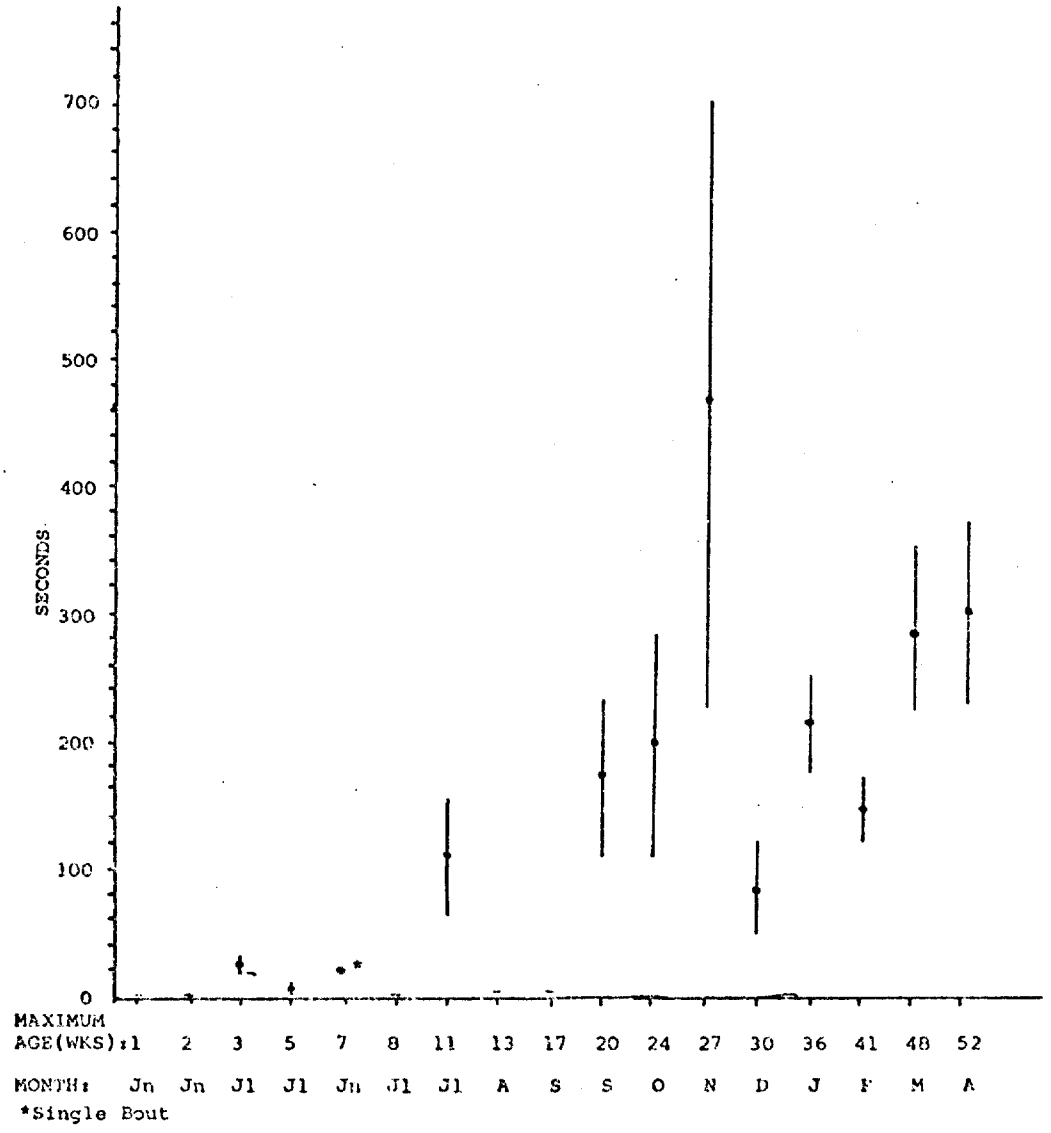


Figure 59

Unipedal standing: average length of bouts ± 1 standard error for 17 age intervals during the first year.



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