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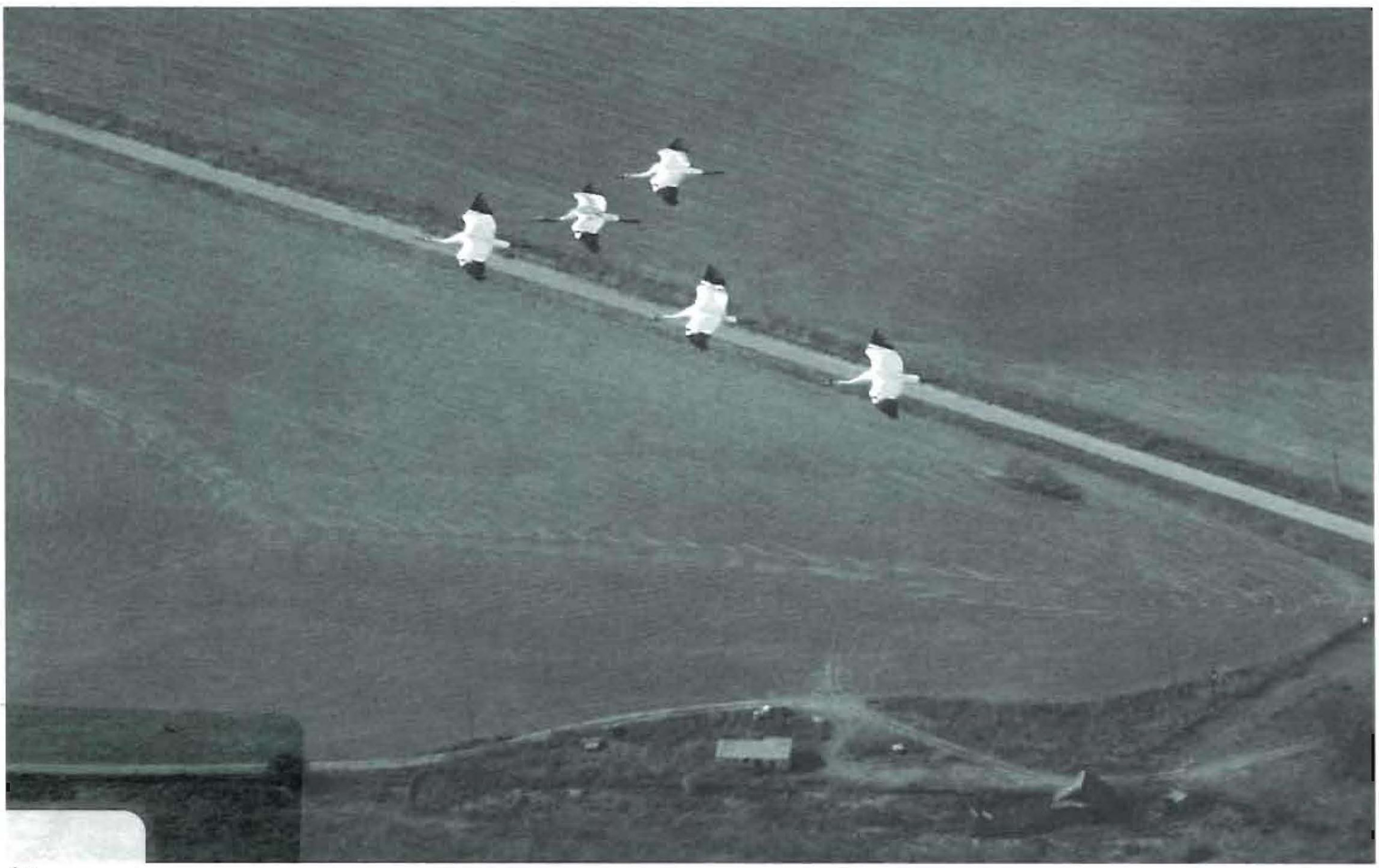

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Cover photo: Migrating Whooping Cranes near Byers Lake, Texas. Family 10/82 (top three birds, juvenile in centre) and an unbanded pair. (E. Kuyt)

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Abstract

From 1981 to 1984, Whooping Cranes *Grus americana* migrating between their summer range in and near Wood Buffalo National Park in Canada and their winter range on and near the Aransas National Wildlife Refuge in the United States were studied by means of radiotelemetry. Objectives of the aerial study included a precise determination of migration routes, duration of occupancy and location of stopover sites, and documentation of migrating crane behaviour and mortality.

In 1981, 1982, and 1983, 15 juvenile Whooping Cranes were captured on the breeding range and equipped with single radio transmitters weighing between 62 and 77 g each. Nine families, pairs, singles, or subadult groups in fall and five such aggregations in spring were monitored through all or part of their migration by teams of airborne and ground observers. The present report summarizes observations by the airborne radio-monitoring crews.

Radio contact with migrating cranes was maintained by means of leg-band radio transmitters, antennas attached to aircraft struts, and radio receivers carried in the aircraft. Radio signals could be picked up from distances up to 155 km, with shorter receiving ranges (up to 56 km) when cranes were on the ground. The radio system allowed operators to "home in" on cranes, and visual contact was maintained for up to 50% of the migration, enabling air crews to obtain data on flight behaviour.

Whooping Cranes do not all migrate simultaneously. Fall migration of yearlings and subadults began after the middle of September, with family groups and some paired adults following in early October. In spring, migration was under way by the middle of March, with family groups and paired adults leading, followed in April by subadults. Whooping Cranes usually migrated as pairs, family groups, singles, or small aggregates of up to four or five subadults. Sometimes pairs joined family groups for all or part of the migration.

Even though age-related differences in onset of migration and resumption of interrupted flights were evident, weather conditions were also important stimuli for the initiation or termination of migration flights. Southward fall departures from the nesting range coincided with northerly winds, rising barometric pressure, and good visibility. Weather conditions symptomatic of the passage of a low-pressure system (decreasing pressure, low ceiling, precipitation) forestalled departure of migration or forced migrating cranes to land. If fall departures were delayed, the birds might eventually begin their flight under less than ideal conditions (freezing, snowfall). Northward spring migration from the winter range was facilitated by the eastward passage of a high-pressure system producing warm southerly winds, relatively high barometric pressure, and good visibility. Weather conditions such as those enabling birds to begin fall and spring migrations also contributed to resumption of migration after unfavourable weather had forced down flying birds. Unfavourable weather conditions notwithstanding, onset or resumption of migration among experienced breeding pairs (with or without their juveniles) often occurred under less than ideal conditions, as if the birds were in a hurry to reach breeding territories. Yearlings and other subadults appeared to have a more "casual" approach to migration.

The period required to complete the 4000-km fall migration occupies a large part of the crane year. The migration, taking up to 50 days, consists of three parts: a two-day flight from the breeding range to the staging area in Saskatchewan; a one- to five-week staging period on prairie grainfields and wetlands; and a rapid week-long journey through the United States. Spring migration, particularly for established breeding pairs, may be completed in only 10–11 days, because no spring staging occurs.

The migration corridor followed by migrating Whooping Cranes measured 80 km at its narrowest and 300 km at its widest point. This corridor generally paralleled but did not cross the continuous 1000-m contour line that extends north from Mexico to the Northwest Territories.

Migrating Whooping Cranes display various forms of flight, such as relatively slow, low-level flapping flight and a rapid, high-altitude flight with little wing movement. The most common and undoubtedly most energy-efficient flight was a combination of spiralling and downwind gliding. This method of flight, resembling that of sailplanes, allowed cranes to utilize thermal updrafts and favourable winds during fair weather and resulted in rapid progress in the form of nonstop journeys of 9–10 hours and 700–800 km daily. During normal flying days, generally unaffected by weather disturbances, mean daily flight distance (and duration) and ground speed were about 400 km (7.5 hours) and 53 km/h. Spring migration flights were generally longer in distance and time than fall migration flights. Ground speeds of wind-assisted cranes reached over 100 km/h. Radio-tracked Whooping Cranes were observed as high as 1950 m above ground level, and, although migration at altitudes of 1500–1800 m was not uncommon, most flights occurred below 600 m.

The most common configuration of flying Whooping Cranes was the V-formation or modifications thereof. These formations were generally assumed by spiralling or gliding cranes. The echelon formation was also commonly observed, during wind-assisted high-altitude flights and low-level flapping flight. Although Whooping Cranes sometimes formed single flocks with other Whooping Cranes or Sandhill Cranes *Grus canadensis*, rarely did they appear to seek them out. In some instances crane families on spring migration remained intact until they reached the breeding range, whereas in other circumstances juveniles separated from their parents in Saskatchewan or at Aransas National Wildlife Refuge.

Whooping cranes are diurnal migrants: nocturnal flight was recorded rarely. When night flying did occur, it was done most often by nonbreeding birds and usually at the termination of long daytime migration flights. There was some evidence that birds recognized landscape features during daylight flights.

Six radio-equipped juvenile Whooping Cranes were found dead on the breeding range. Most likely these birds, not quite capable of sustained flight, died as a result of wolf *Canis lupus* predation. The remaining nine cranes were radio-tracked during the present study, and six of them died after contributing varying amounts of data. Two birds died as a result of power line collisions, and four were found dead or disappeared at the Aransas National Wildlife Refuge. Collision with power lines was the most serious threat to migrating Whooping Cranes.

Résumé

De 1981 à 1984, des Grues blanches d'Amérique *Grus americana* qui migraient entre leur aire d'été, située dans le parc national Wood Buffalo, au Canada, ou à proximité, et leur aire d'hivernage dans la réserve faunique nationale d'Aransas, aux États-Unis, ou à proximité, ont été étudiées au moyen de dispositifs de pistage radioélectrique. L'étude aérienne visait les objectifs suivants : établissement précis des voies migratoires, de la durée de séjour et de l'emplacement des haltes, et obtention d'informations sur le comportement et la mortalité des grues.

En 1981, 1982 et 1983, 15 Grues blanches d'Amérique juvéniles ont été capturées dans l'aire de reproduction, et un émetteur radio pesant entre 62 et 77 g leur a été fixé. À l'automne, des familles, des couples, des individus ou des subadultes (neuf groupes) de même que cinq regroupements de ce genre, au printemps, ont été suivis pendant toute la migration ou une partie seulement, par des équipes d'observateurs en vol et au sol. Le présent rapport résume les observations des équipes de radiorepérage.

Le contact radio avec les grues migratrices a été maintenu par des émetteurs radio fixés à la patte de l'oiseau, des antennes attachées sous les ailes de l'avion, et des récepteurs radio installés à bord de l'avion. Des signaux radio pouvaient être captés jusqu'à une distance de 155 km, avec des plages de réception plus courtes (jusqu'à 56 km) lorsque les grues étaient au sol. Le système radio a permis aux opérateurs de se « diriger sur » les grues, et le contact visuel a été maintenu pendant la moitié de la migration, ce qui a permis à l'équipage de recueillir des données sur le comportement en vol.

Les Grues blanches d'Amérique ne migrent pas toutes en même temps. La migration automnale est entreprise par les jeunes de l'année et les subadultes après le milieu de septembre, des groupes familiaux et quelques couples d'adultes suivant au début d'octobre. Au printemps, la migration commence dès le milieu de mars; des groupes familiaux et des couples adultes partent les premiers, suivis en avril par les subadultes. En général, chez les grues, la migration s'effectue par couples, groupes familiaux, individus, ou petits groupes de quatre ou cinq subadultes. Il arrive parfois que des couples se joignent à des groupes familiaux pour toute la migration ou une partie de celle-ci.

Même si des différences liées à l'âge étaient évidentes lorsque l'on considère le commencement de la migration et la reprise de vols interrompus, les conditions météorologiques constituaient également des stimuli importants pour le début ou la fin des vols migratoires. À l'automne, le départ de l'aire de nidification vers le sud a coïncidé avec des vents du nord, une augmentation de la pression barométrique et une bonne visibilité. Les conditions symptomatiques du passage d'un système de basse pression (pression à la baisse, plafond bas, précipitations) ont différé le début de la migration ou forcé les grues à se poser au sol. À l'automne, si les départs sont retardés, les oiseaux risquent, en fin de compte, d'entreprendre leur vol dans des conditions tout simplement défavorables (gel, chute de neige). Au printemps, la migration de l'aire d'hivernage vers le nord a été facilitée par le passage vers l'est d'un système de haute pression produisant des vents du sud chauds, une pression barométrique relativement élevée et une bonne visibilité. Des conditions météorologiques comme celles qui permettent aux oiseaux d'entreprendre les migrations automnale et printanière ont également contribué à la reprise de la migration après que des conditions défavorables eurent forcé les oiseaux à se poser au sol. Malgré des conditions défavorables, le début ou la reprise de la migration des couples reproducteurs établis (avec ou sans leurs jeunes) a eu lieu souvent dans de mauvaises conditions, comme si les oiseaux étaient pressés d'atteindre les territoires de reproduction. Les jeunes de l'année et d'autres subadultes semblaient avoir une approche plus « indifférente » face à la migration.

Chez les grues, une bonne partie de l'année est consacrée à la migration automnale de 4 000 km. La migration, qui peut prendre jusqu'à 50 jours, est divisée en trois parties : un vol de deux jours depuis l'aire de reproduction jusqu'à l'aire de repos ou halte en Saskatchewan; une période de repos d'une à cinq semaines dans les champs de céréales et les terres humides des Prairies, et un voyage rapide d'une semaine pour traverser les États-Unis. La migration printanière, notamment pour les couples reproducteurs déjà formés, peut prendre de 10 à 11 jours seulement parce qu'elle s'effectue sans période de repos.

Le couloir de migration emprunté par les Grues blanches d'Amérique migratrices a une largeur minimale de 80 km et une largeur maximale de 300 km. Ce couloir suit en général, mais sans la couper, la courbe de niveau continue de 1 000 m qui s'étend vers le nord depuis le Mexique jusque dans les Territoires du Nord-Ouest.

Les Grues blanches d'Amérique migratrices adoptent différentes formes de vol, comme le vol ramé à faible altitude, relativement lent, et le vol rapide à haute altitude avec peu de battements d'ailes. Le type de vol le plus courant et sans aucun doute le plus efficace combine le vol en spirale et le vol plané avec vent dans le dos. Ce type de vol, qui ressemble à celui des planeurs, permet aux grues d'utiliser les courants ascendants d'origine thermique et des vents favorables par temps clément; il entraîne donc une progression rapide sous forme de périples de 9 à 10 heures sans escale et le parcours d'une distance de 700 à 800 km par jour. Lors d'une journée normale de vol, en général sans perturbations météorologiques, les grues peuvent franchir une distance moyenne de près de 400 km en 7,5 heures, à une vitesse de 53 km/h. Les vols migratoires printaniers couvrent en général une distance plus grande et durent plus longtemps que les vols migratoires automnaux. La vitesse des grues qui volent vent dans le dos atteint plus de 100 km/h. Le pistage radioélectrique a permis d'observer des Grues blanches d'Amérique à une altitude atteignant 1 950 m, et bien que la migration à des altitudes de 1 500 à 1 800 m soit assez fréquente, la plupart des vols s'effectuent à moins de 600 m.

La formation de vol la plus courante chez les Grues blanches d'Amérique est le vol en V ou des variations de ce dernier. Ces formations sont adoptées en général par des grues qui effectuent des vols en spirale ou du vol plané. La formation en oblique est aussi fréquemment observée au cours de vols à haute altitude avec vent dans le dos et de vols ramés à faible altitude. Même si les Grues blanches d'Amérique se joignent parfois à d'autres Grues blanches d'Amérique ou des Grues du Canada *Grus canadensis* pour former une seule volée, il semble qu'elles les cherchent rarement. Dans certains cas, pendant la migration printanière, des familles de grues demeurent entières jusqu'à ce qu'elles atteignent l'aire de reproduction, tandis que dans d'autres cas, des juvéniles quittent leurs parents en Saskatchewan ou à la réserve faunique nationale d'Aransas.

Les Grues blanches d'Amérique sont des oiseaux migrateurs diurnes : on a rarement observé des vols nocturnes, et ceux-ci étaient le plus souvent effectués par des oiseaux non reproducteurs, en général, à la fin de longs vols migratoires de jour. Il y a lieu de croire que les oiseaux reconnaissent les caractéristiques morphologiques du paysage pendant leurs vols de jour.

Six Grues blanches d'Amérique juvéniles auxquelles on avait fixé des émetteurs radio ont été trouvées mortes dans l'aire de reproduction. Il est fort probable que ces oiseaux, encore inaptes au vol soutenu, ont été la proie de loups *Canis lupus*. Les neuf grues qui restaient ont été suivies par radio au cours de la présente étude, et six d'entre elles sont mortes après avoir fourni un certain nombre de données. Deux oiseaux sont morts après avoir heurté des lignes de transport électrique, et quatre ont été trouvés morts ou ont disparu dans la réserve faunique nationale d'Aransas. Les lignes de transport électrique sont la menace la plus grave pour les Grues blanches d'Amérique au cours de leur migration.

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Disclaimer

The data contained herein were obtained during joint aerial investigations by the Canadian Wildlife Service, Environment Canada, and the United States Fish and Wildlife Service, Department of the Interior. Opinions and conclusions in this report are those of the author and do not necessarily represent the views of other participants in the aerial radio-tracking work or of those involved in the planning or coordinating of the project. Mention of a product, manufacturer, or service company does not necessarily constitute endorsement of these products or companies by the author or his employer.

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R.C. Drewien (Idaho Cooperative Wildlife Research Unit, Moscow, Idaho) advised and assisted during each year's Whooping Crane colour-banding project in Wood Buffalo National Park (WBNP), and I am indebted to him for his great contribution. For assistance during banding and installation of radios between 1981 and 1984, I also thank Drewien's co-worker K. Clegg, the late B.M. Biederman, and volunteers J. Kuyt, G. Drewien, and C.A. von Treuenfels. J.P. Goossen and B.E. Johnson of the Canadian Wildlife Service (CWS) served as aerial observers during banding work. The United States Fish and Wildlife Service (USFWS) provided the major share of manpower, financial, and equipment support during the actual radio-tracking. Design and coordination of the project were provided by L. Thomas and M.A. Howe (USFWS). M. Anderson, W. Jobman, and L. Smith (USFWS) were points of contact for field crews, which often involved telephone calls at late hours. E.G. Bizeau (Idaho Cooperative Wildlife Research Unit, Moscow, Idaho) secured required telemetry equipment.

CWS contributed my services and those of J.P. Goossen for all or portions of aerial tracking from 1981 to 1984. B.W. Johns (CWS) assisted in several capacities for brief periods in Saskatchewan. The present paper is based on individual radio-tracking reports prepared earlier by the author, J.P. Goossen, L.S. Young, and S.E. Labuda (USFWS).

Although all USFWS and chartered pilots provided excellent support, two pilots deserve special mention for long and dedicated service, and I gratefully acknowledge the outstanding cooperation of USFWS pilot-biologists G.F. Steffen and D.S. Benning. For work on the breeding range and elsewhere in northern areas, I thank pilots of Loon Air Ltd., Fort Smith, NWT, especially B. Bourque, for many years of productive and dependable service. In this project, the pilots constituted the backbone of the aerial tracking, and without their dedication and skill the work could not have been carried out. Others who contributed to the project for generally brief but important portions included commanding officers of military reservations and employees of Flight Services at many airports in Canada and the United States. CWS employees S. MacEachran, L. Strembitsky, and M. Regnier contributed drafting, typing, and proofreading services. R. Edwards, J.P. Goossen, H.J. Boyd, and F.G. Cooch (CWS), J.C. Lewis and T.V. Stehn (USFWS), S.A. Nesbitt (Florida Game and Fresh Water Fish Commission), R.C. Drewien, G.F. Steffen, D.S. Benning, L.S. Young, and S.E. Labuda reviewed and improved the manuscript, but any errors remaining are the responsibility of the author. H. Ouellet (Canadian Museum of Nature, Ottawa) prepared the French translation of the abstract. I thank all of the above contributors.

Many of the cooperators unfortunately could not witness the glorious spectacle of migrating Whooping Cranes, but their contributions were as important as those of the privileged crews who flew with the cranes.

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1.0 Introduction

Whooping Cranes *Grus americana* spend up to two months each fall and a shorter period in spring on their semiannual migrations between their summer range in Wood Buffalo National Park (WBNP) in Canada and their winter range on the Aransas National Wildlife Refuge (ANWR) in the United States. Although considerable information is available from studies on their breeding and winter ranges, relatively little is known about the ecology and behaviour of migrating Whooping Cranes. In 1977, the United States Fish and Wildlife Service (USFWS) initiated a Whooping Crane migration monitoring program, which is now coordinated with the reporting network of the National Audubon Society (NAS), Canadian Wildlife Service (CWS), and various states along the migration route (U.S. Fish and Wildlife Service 1986).

In 1981, a cooperative USFWS–CWS–NAS project was launched to radio-track Whooping Cranes moving between their summer and winter ranges. The project had been preceded by radio-tracking studies of Greater Sandhill Cranes *Grus canadensis tabida* migrating between Minnesota and Florida (Crete and Toepfer 1978; Toepfer and Crete 1979; Anderson et al. 1980) and of Sandhill Cranes *G. canadensis* in Manitoba (Melvin and Temple 1980). To test radiotelemetry techniques and equipment and to study the effects of radio-tagging on juvenile Whooping Cranes, Drewien and Bizeau (1981) captured five juvenile Whooping Cranes reared at Grays Lake, Idaho, by foster-parent Greater Sandhill Cranes. By means of radios attached to the legs of the young Whooping Cranes, observers were able to follow the migrating Sandhill Cranes from their breeding range to the vicinity of the Monte Vista National Wildlife Refuge in Colorado. During the 1979 tracking project and subsequent studies of radio-tagged Whooping Cranes, Drewien and Bizeau (1981) found no adverse effects of the radio-tagging on juvenile Whooping Cranes. Weaknesses in the transmitter design were identified and improvements suggested.

USFWS and CWS approval was given to begin the radio-tracking study of Whooping Cranes migrating from WBNP in fall 1981. A single Whooping Crane family was to be radio-tracked from WBNP to ANWR by a team of aerial observers cooperating with a ground crew in a vehicle. Objectives of the project were to (1) determine, by means of radiotelemetry, the precise fall migration route of a Whooping Crane family leaving WBNP in 1981; (2) identify and describe habitat and stopover sites used by the cranes during migration; (3) document crane behaviour and identify sources of mortality; and (4) provide information to develop a plan of action for future migration monitoring studies.

The present paper analyzes, expands, and summarizes completed or incomplete reports, handwritten field notes, and maps covering portions of the 1981 pilot project and subsequent aerial tracking of Whooping Cranes migrating in fall or spring between WBNP and ANWR (Kuyt 1982, 1984a, 1984b, 1986a, 1986b; Goossen 1982, 1986a, 1986b, 1987a, 1987b, 1987c; Labuda 1983; Young 1984). Reports covering habitat studies and behaviour of cranes occupied with feeding, roosting, and resting during staging periods and stopovers (objectives 2 and 3 above) were prepared by the ground crews and have been published elsewhere (Howe 1987, 1989; Ward and Anderson 1987).

2.0 Methods

2.1 Summary of field work and logistics

2.1.1 Wood Buffalo National Park

Descriptions and nomenclature of nests or composite nesting areas (CNA) from which colour-banded and radio-equipped juvenile Whooping Cranes originated are given in Kuyt (1981a) and Kuyt and Goossen (1987). In this report, the Whooping Crane family from CNA Klewi 1 (or nest 2/81) is referred to as "F 2/81," the yearling from nest 10/82 is called "Y 10/82," and a Whooping Crane from nest 6/82 is called "crane 6/82." Juvenile birds on their first northward migration may be referred to as "yearlings."

Kuyt (1984b) provided details on distribution of Whooping Crane family groups in WBNP and colour-banding (including installation of transmitters), and Kuyt (1984b) and Goossen (1986a, 1986b) reported on postbanding and premigration aerial surveys.

All but one of the Whooping Crane nests found between 1981 and 1984 are located between 4 and 22 km north of Highway 5, the only road west of Fort Smith, NWT (Fig. 1), and virtually the entire Whooping Crane population crosses this road twice each year. As we did not have a vehicle equipped with a radio receiver in Fort Smith, it was not possible to monitor the onset of migration from the ground, and we had no alternative but to make brief daily flights from Fort Smith to the breeding range to ensure that radio-equipped cranes had not yet begun migration. In 1983, the last family group to migrate from WBNP left sometime after 18 October, when the entire country was already in the grip of winter.

2.1.2 Wood Buffalo National Park to south-central Saskatchewan

There are few usable roads in northern Alberta and northern Saskatchewan. In 1981, the ground crew waited for the southward-flying cranes and the tracking aircraft in the Cold Lake–Meadow Lake area of west-central Saskatchewan. The exact route taken by migrating cranes and the location and length of stopovers in northern areas were unknown. To enable us to land in isolated areas, float-equipped aircraft were used initially. In 1981 and 1982, we learned enough about the migration route and nature of stopovers in northern areas to become comfortable with using wheeled aircraft there in 1983 and 1984.

Once the cranes had landed on a lake in the North Battleford area, the radio-tracking antennas were transferred from the float aircraft to wheeled aircraft. These aircraft were used for the balance of the fall tracking. Only wheeled aircraft were used during northward radio-tracking in 1983 and 1984.

2.1.3 Saskatchewan to Aransas National Wildlife Refuge

The USFWS provided aircraft and pilots for fall tracking between Saskatchewan and ANWR. Ground and air crews were able to work in close cooperation by means of two-way radios. When tracking aircraft were grounded during unfavourable weather or when migrating cranes flew too fast for the ground crew vehicle to keep up, air and ground crews maintained contact by telephone or through the cooperation of airport Flight Services.

2.2 Equipment

2.2.1 Radio transmitters

The use of radio transmitters was a sequel to the Whooping Crane colour-banding program, which began in WBNP in 1977 (Kuyt 1979; Drewien and Kuyt 1979). Three transmitters were placed on prefledged Whooping Cranes in 1981, and six radios were used each year in 1982 and 1983 (Table 1).

Radio transmitters in earlier crane studies were back-mounted packages (Nesbitt 1976; Toepfer and Crete 1979; Melvin and Temple 1980), but later investigations (Drewien and Bizeau 1981; Melvin et al. 1983) indicated that leg-band radios were safer than backpack radios and required less time for installation. As leg-band radios were deemed preferable for use on juvenile Whooping Cranes, only these radios were used in the present study. Solar- and battery-powered radio transmitters, manufactured by Telemetry Systems Inc. (Mequon, Wis.), were provided by Drewien (Drewien and Bizeau 1981). The transmitters were mounted on standard 80-mm coloured lynnply (Lynn Plastic Sales Co. Inc., Cambridge, Mass.) bands by means of two 1.6 × 12.7 mm stainless steel bolts and nuts, as described by Melvin et al. (1983). The metal parts were expected to corrode in several years, allowing the radio (no longer expected to be functional) to fall away.

Weights of radio packages (colour band, radio, and antenna) ranged from 62.0 to 76.5 g (Table 1), 1.3–2.2% of the body weight of juvenile Whooping Cranes at time of application. We have no information to show that the cranes were inconvenienced by the radio transmitters attached to their legs; birds equipped with backpacks, on the other hand, sometimes show abnormal behaviour (Nesbitt 1976).

Handling time of birds ranged from 11 to 25 minutes. During that time, the birds were measured, weighed, banded, and photographed; in 1981 and 1983, blood samples were taken. After installing the radio transmitters, we made frequent survey flights over the nesting area to become familiar with the equipment and with the various radio signals and detection ranges.

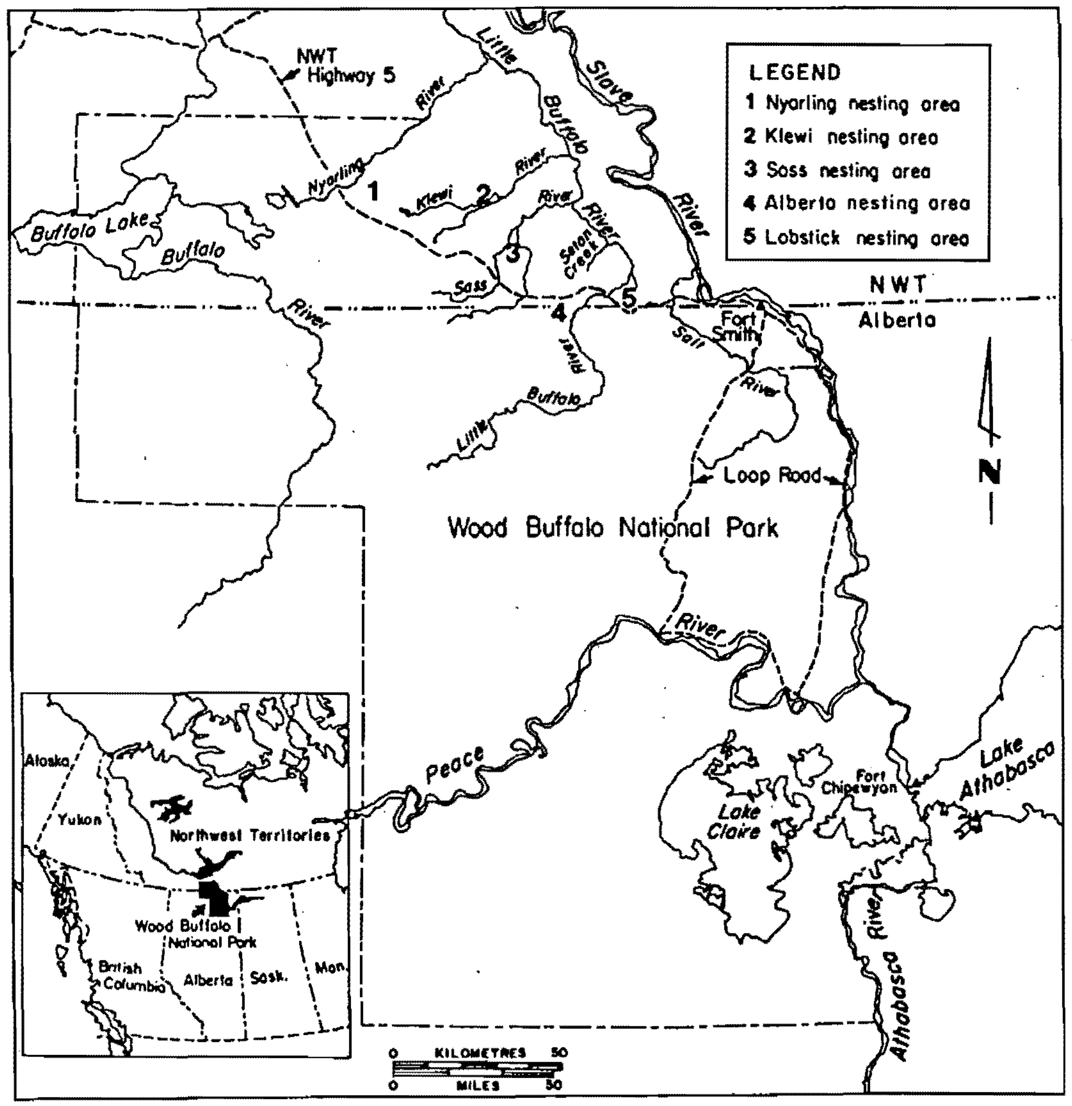
The manufacturers estimated a transmitter life of two to three years (Drewien and Bizeau 1981). In 1985, radios attached on birds 3/81, 10/82, and 19/83 (Table 1) still functioned, although the signals had weakened considerably. On 13 May 1986, we could no longer hear the radio on crane 3/81 during a flight directly over the bird in WBNP. On 29 July 1986, we failed to detect the signals of 10/82 and 19/83 (a mated pair) when we flew directly over them. In December 1986, T. Stehn (pers. commun.) advised that the radio on bird 10/82 could not be heard and that it appeared to have separated from the plastic colour band. Radios on 19/83 and 3/81 could still be heard at a range of 200–400 m. Although the life span (five years and four months for radio 3/81) considerably exceeded earlier estimates, it is highly unlikely that the radio could still have been used for practical radio-tracking. The remaining two radios stopped transmitting in 1987, although transmitters minus the antennas were last observed by T. Stehn (pers. commun.) on 30 January 1990 (bird 3/81) and on 7 April 1988 (bird 19/83).

2.2.2 Receiving antennas

We used light-weight aluminum four- and two-element yagi directional antennas (Drewien and Bizeau 1981). The four-element antennas were stronger and provided better signal reception than the two-element H-shaped antennas. The former were used almost exclusively after 1981.

Antennas were mounted on aircraft struts by means of strut cuffs and aeroseal clamps and cross-braced to the aircraft wing. The main axis of the four-element antenna was tilted about 15° (outboard end low) for maximum reception range of the transmitter signal (Gilmer et al. 1981). The radio receiver in the aircraft's cockpit and the two antennas were connected by coaxial cables that were fed through the air intake in the leading edge of the wing.

Figure 1
Whooping Crane nesting areas in Wood Buffalo National Park



2.2.3 Radio receivers

Various radio receivers were at our disposal during the 1981–84 aerial tracking project. A Telonics scanner-receiver (Telonics Inc., Mesa, Ariz.) and a Cedar Creek scanner-receiver (Cedar Creek Bioelectronics Lab., University of Minnesota, Bethel, Minn.) were used in 1981. After 1981, ATS scanner-receivers (Advanced Telemetry Systems Inc., Isanti, Minn.) were used as the primary equipment. AVM receivers (AVM Instrument Co., Champaign, Ill.) were carried in tracking aircraft each year as backup receivers.

The memory capability of the scanner-receiver proved useful, because it allowed all our transmitter frequencies to be programmed into the memory circuit. Frequencies could be recalled by means of a switch or scanned automatically by an internal and variable timing device. A left–right switch installed between the coaxial cables and the radio receiver enabled the operator to monitor the difference in signal strength picked up by the two antennas and hence to "home in" on the transmitter-instrumented crane.

2.2.4 Reception of radio signals

Our ability to receive radio signals was influenced by many variables, including make and performance of equipment, altitude, radio signal interference, weather, topography, possibly smoke from forest fires, and proficiency of operators. Although it was impossible to eliminate all biases, it was important to have an understanding of maximum distances at which signals could be received. Knowing transmitter tolerances enabled us to carry out "blind" searches for radio signals in the most economic grid pattern when a radio-equipped bird became lost during tracking.

Ground and flight tests to determine radio transmitter signal strength and range were carried out several times (Kuyt 1982, 1984a, 1986a, 1986b), usually before the beginning of migration.

2.2.4.1 Ground-to-ground signal reception

Preliminary testing in the WBNP area before migration began in 1981 indicated maximum ground-to-ground (g–g) distances of 4–5 km (Kuyt 1982; Goossen 1982). Testing of radios before they were placed on cranes gave even lower reception values. Testing after application was possible only in fall 1981, when a portable receiver was available for a brief period and when a Whooping Crane family (F 3/81) occurred within range of Highway No. 5, the only road in the area. Drewien and Bizeau (1981) reported g–g distances of 2.5–8 km in Idaho. I have no information on the effect that differences in forest cover in Idaho and WBNP may have had on radio signal range. Melvin et al. (1983) found a g–g range of 2.4–6.4 km in flat to hilly terrain.

2.2.4.2 Ground-to-air signal reception

I frequently tested reception ranges of the three radios in fall 1981 as we flew over the breeding range. As a result of heavy smoke from forest fires in WBNP during the second week of August 1981, flying conditions were often marginal, and we were unable to operate from high enough

Table 1
Banding and radio transmitter data for juvenile Whooping Cranes banded in Wood Buffalo National Park, 1981–1983

Bird No.	Date banded	Weight (g) at banding: Bird	Weight (g) at banding: Radio	Radio as % of body weight	Range of radio frequency (MHz)	Fate of bird
2/81	9 Aug. 1981	4550	76.5	1.68	164.425	Died 18 Oct. 1981, Saskatchewan, after colliding with power line
3/81	11 Aug. 1981	4700	63.5	1.35	164.605–164.607	Still alive as of March 1991
7/81	9 Aug. 1981	4400	76.0	1.73	164.545	Found dead under power line, 16 Oct. 1982, Waco, Texas
1/82	15 Aug. 1982	3775	68.0	1.80	164.655	Found dead ANWR, 2 Feb. 1983; suspected disease, followed by coyote predation[a]
2/82	15 Aug. 1982	4050	68.0	1.68	164.621–164.623	Found dead ANWR, 15 Nov. 1984; suspected avian predation[a]
3/82	15 Aug. 1982	5075	64.5	1.27	164.525	Found dead WBNP, 19 Aug. 1982; believed killed by wolves
4/82	15 Aug. 1982	4450	66.5	1.49	164.471	Found dead WBNP, 19 Aug. 1982; believed killed by wolves
6/82	15 Aug. 1982	3850	68.5	1.78	164.645	Found dead ANWR, 4 Jan. 1983; cause of death unknown[a]
10/82	15 Aug. 1982	4875	65.0	1.33	164.565–164.568	Still alive as of March 1991
2/83	1 Aug. 1983	3738	62.0	1.66	164.340–164.345	Remains found WBNP, 16 Sept. 1983; believed killed by wolves
3/83	1 Aug. 1983	3538	62.0	1.75	164.265–164.269	Remains found WBNP, 16 Sept. 1983; believed killed by wolves
6/83	1 Aug. 1983	4735	65.0	1.37	164.825–164.826	Remains found WBNP, 15 Sept. 1983; believed killed by wolves
9/83	1 Aug. 1983	3132	68.0	2.17	164.750–164.751	Disappeared at ANWR, 21 Nov. 1984
19/83	1 Aug. 1983	3534	66.0	1.87	164.440–164.444	Still alive as of March 1991
21/83	1 Aug. 1983	3138	62.0	1.98	164.295–164.300	Remains found WBNP, 16 Sept. 1983; believed killed by wolves

[a] Data from T. Stehn (pers. commun.)

altitudes to determine maximum reception. It is also possible that the thick smoke interfered with radio signal reception.

Ground-to-air (g–a) detection distances ranged between 20 and 28 km under those conditions. Drewien and Bizeau (1981) reported a g–a range of 25–35 km. Melvin et al. (1983) reported a range of 15–35 km, and Labuda (1983) recorded 22.4 km while flying at 150 m above ground level (agl) under conditions of lowered visibility.

During tests of the radio signal strength for crane 7/81 in Saskatchewan in October 1981 (Kuyt 1982), I recorded g–a distances of 25–35 km with the aircraft at 850 m agl, 16–18 km at 640 m agl, and 13–14 km at 400 m agl. These figures were obtained under satisfactory weather conditions. Goossen (1982) noted an improvement in signal detection from 19.3 km at about 1600 m agl to 29 km at about 2200 m agl, followed by a reduction to 22.5 km at 2500 m agl.

Throughout the testing, it was noted that best signal reception was obtained by flying the aircraft with a wing (i.e., the long axis of the antenna) pointing towards the radio. Reception was unreliable when flying directly to or from a radio. Gilmer et al. (1981) described radio signal patterns as received by side-looking yagi antennas of the same type as used in our tracking studies.

Weather conditions at ANWR were excellent in late March 1983 (Kuyt 1986a). Detectable signals were received up to 48 km with the aircraft at 900 and 1200 m agl but only up to 32 km at 1500 m agl. At 50 km from the transmitter and with the aircraft descending from 1500 m agl, signals remained at the same strength until we dropped below 750 m agl. Signals then weakened and had disappeared when we reached 300–450 m agl.

On 19 September 1982, I tested radio signals in south-central Saskatchewan under excellent weather conditions (Kuyt 1984a). Reliable signals were picked up from 48 km with the aircraft in level flight at 1200 m agl and from 40 km at 1800 m agl. Improved reception ranges (up to 56 km at 1200 and 1800 m agl) were obtained by flying the aircraft in a tight 360° turn. These signals were usually faint, but this method of detecting signals at extreme distances was useful, and the direction of the radio signal source could be determined by recording the compass bearing at the moment when the signal was loudest. While circling at about 2400 m agl, Young (1984) detected a faint signal from one of two cranes he was tracking and subsequently located 70 km from where he first heard the signal. He suggested this was probably the maximum g–a distance of the signal. It is also possible that the crane had made a brief flight and Young had picked up the air-to-air signal then.

Occasionally, a flying radio-equipped crane was detected when the tracking aircraft was on the ground. Although useful information was sometimes received under these conditions, I was of course unable to measure the air-to-ground distance between the flying bird and the parked aircraft.

2.2.4.3 *Air-to-air signal reception*

Accurate air-to-air (a–a) detection of radio signals could not be determined in WBNP prior to the start of migration, as Whooping Cranes rarely fly in summer, and then for only a few minutes at a time at low altitudes. Goossen (1982) found an average a–a detection distance of 59 km during four tests. In September 1981, while searching in central Saskatchewan for "lost" family 2/81, I heard a weak signal and later found the birds 75 km from where the signal was first heard (Kuyt 1982). Although the birds were in a small pond when found, it is likely that they had been in the air when the signal was picked up.

During tests in central Nebraska, I found that a–a reception distances ranged between 45 and 86 km (Kuyt 1982). Drewien and Bizeau (1981) found a–a distances of about 80 km. On 17 September 1982, while landing at a site near Jackfish Lake, Saskatchewan, I continued to monitor the radio signal of crane 7/81, which we had left in flight near Radisson, Saskatchewan (Kuyt 1984a). As we approached the landing, I still heard the signal of the crane, then estimated to have been 132.5 km away. It was in the same area that Goossen (1986b), on 14 October 1982, picked up the signal of crane 1/82 at a distance of about 155 km from where the crane was believed to have been in flight at the time. Melvin (1980) gave a similar figure (160 km) for maximum a–a reception distances.

2.2.5 Aircraft

Single-engined fixed-wing aircraft (Cessna 172, 180, 182, 185, or 206) on wheels, on floats, or with amphibious landing gear were used for aerial tracking. The roomy Cessna 206 was the preferred aircraft, particularly during long tracking sessions or when an extra passenger was carried (e.g., for filming purposes). Several times in northern Alberta, floats proved useful, as they allowed us to land near cranes at stopovers. Extra fuel carried in containers in the aircraft turned out to be a wise precaution when landings were made in isolated areas.

2.2.6 Aircraft–ground vehicle communication

Radio communications between air and ground crews varied from occasionally poor to frequently excellent. In 1981, I had serious problems when the aircraft's radio-transmitting range was only 8 km, although we could receive ground crew messages from 125 km. In spring 1983, a two-way radio installed to accommodate a film crew did not allow me to listen to the crane's signal and communicate with the ground trackers simultaneously. In both years, modifications were made in the communications system that enabled us to carry out our work satisfactorily.

Atmospheric conditions also affected radio communications. During marginal visibility, when we had difficulty tracking the birds with the aircraft and when it was imperative to let the ground crew know where we were, the conditions were also poor for radio communications. Fortunately, under those conditions, the cranes were reluctant or unable to fly far, and we usually relocated them soon after the weather improved.

2.2.7 Maps and record keeping

The aerial observer's most important tasks were to maintain radio contact with the transmitter-equipped birds when cranes were flying and to advise the ground crew about the position of the tracking aircraft and location, course, and progress of the migrating cranes. When tracked birds were in sight, the aerial observers recorded altitude and speed of flying birds and their flight behaviour. Young (1984) recorded aspects of crane migration flight every 10 minutes and obtained 172 samples.

While aloft, we were unable to record any weather data other than air temperature. Information on wind speed, wind direction, and barometric pressure was obtained from Flight Services along our route. I also collected weather résumés from daily newspapers en route and found these useful in later summaries of weather patterns as they related to crane migration. During flight, locations of cranes were plotted on 1:250 000 topographic maps or (rarely) on 1:500 000 sectional aeronautical charts. Canadian maps were obtained from the Department of Energy, Mines and Resources, U.S. maps from the U.S. Geological Survey and U.S. Department of Commerce.

Description of flight formations follows that of Heppner (1974) or was modified from that study. Flight altitude of birds under observation was determined from the aircraft's altimeter or (rarely) estimated visually.

All times in this report are Central Standard Time. The metric (SI) system is used throughout the report. Although vertical measurements of altitude were made in feet (to facilitate readings from maps and aircraft instruments), here they are converted to metres.

Migration routes in this report (Figs. 3–8, 10–16) show mainly combined routes transposed from Kuyt's and Goossen's tracking reports, augmented by data extracted from Labuda (1983) and Young (1984).

3.0 Results and discussion

3.1 Influence of weather on migration

Weather has a profound effect on migration of Whooping Cranes. In this study, weather indirectly influenced habitat conditions on the breeding range and so may have dictated earlier or later than usual seasonal departures. Unfavourable weather interrupted flights or precluded initiation of migration. Weather factors may also determine the duration and speed of flights.

3.1.1 Fall

3.1.1.1 Departure from Wood Buffalo National Park

From reports by many observers along the migration route (Stephen 1979; B. Johns, pers. commun.), it was known that Whooping Cranes usually migrate in small flocks consisting of family groups or perhaps pairs. It was not, therefore, unexpected that the departures of Whooping Cranes we witnessed during radio-tracking involved individual families (two adults and single chick) or small numbers of subadults (Tables 2 and 3).

There were individual and age-related differences in timing of migration departures. This became apparent when cranes did not leave the summer range simultaneously, even though weather conditions on any one day did not differ greatly in that relatively small area.

Family 2/81 left WBNP at about 10:00 on 17 September 1981 (Fig. 2), but this departure, early for a family group, may have been related to exceedingly dry conditions in WBNP that year. Daily temperatures between 16 and 20 September averaged 12.9°C, equalled those of the period 6–10 September, but were more than double those of the periods 1–5 September and 21–30 September (Goossen 1982). The next family to leave (F 7/81) departed on 4 October, when the daily temperature had dropped to -2.1°C (average daily temperature for 1–5 October was 2.4°C). A third family (F 3/81) was observed on its summer range (B. Bourque, pers. commun.) as late as 15 October, only a few days before freeze-up. Of these three families, F 2/81 probably contained the oldest breeding pair (Table 4); the pair in F 3/81 began nesting only in 1977, six years after F 7/81.

Two subadults, the earliest known fall migrants, left the crane summer range on 15 September 1982. Just before migration, the two birds were 45 km apart in WBNP, and they began migration independently: Y 7/81 with three other Whooping Cranes (including a two-year-old and a five-year-old bird), and Y 3/81 with a five-year-old bird. The advantage to young cranes of migrating with older, experienced birds is obvious.

All radio-tracked birds except F 7/81 departed from WBNP on northerly winds (Table 4), generally during rising barometric pressure and with good visibility. Family 7/81 left on 4 October 1981 when winds were from the west (265°), and the three birds flew 306 km that day at a ground speed of about 35 km/h. The following day winds swung south (225°), and the cranes interrupted their migration. They resumed their southward migration on the morning of 8 October when the wind again had a northern aspect (065°). The cranes covered only 210 km in 5.5 hours of flying under poor weather conditions. The 5–8 October wind shift, slightly increasing temperature, decreasing barometric pressure, low ceiling, precipitation, and poor visibility are characteristic of a cyclone (a low-pressure system).

In addition to northerly wind, snowfall may also trigger fall migration. In 1981 and 1983, several families began fall migration shortly after the first snowfall (Table 4). Cranes delaying their migration for whatever reasons until late in the season may eventually begin migration under less than ideal conditions (Melvin and Temple 1981). The latest known departure date for Whooping Cranes from WBNP was after 18 October 1983, when snow and ice covered almost all of the summer range (Table 4). Invariably, the last birds to depart were family groups or breeding pairs.

During years with good habitat conditions, fall migrations from WBNP have been comparatively late. If food resources remain plentiful and accessible, there appear to be no reasons for the cranes to leave WBNP early. Eventually, cold weather, culminating in late October freeze-up, will drive the last cranes out.

3.1.1.2 Departure from Saskatchewan staging areas

On 20 October 1981, F 7/81 continued its migration after an 11- to 12-day staging period in southwestern Saskatchewan. The barometric pressure had peaked, temperatures during the previous four days had been declining, the first snow of the season had fallen the previous night, and the winds were favourable (Table 5). The remnants of the weather disturbance (i.e., blowing snow, low ceiling, poor visibility) allowed only relatively slow progress by the cranes that day (Kuyt 1982), but the cranes progressed rapidly on the afternoon of 21 October and during the next day.

After a 24-day period on the Saskatchewan staging area (Kuyt 1984a), Y 7/81 and three older companions resumed fall migration on 11 October 1982, when the weather was unsettled. Weather data from 2.5 hours before the cranes' departure are shown in Table 5. Barometric pressure, although not recorded on 11 October, was known to have been high (102.7 kPa) two days earlier. Yearling 7/81 and its three companions left the staging area at an unusual time (14:30), and their flight over Last Mountain Lake was erratic, including northward flights of five and 24 minutes and several landings (Kuyt 1984a). After the final landing, the cranes took off at 18:29 and flew south. Darkness fell, and we were unable to follow the birds. The cranes continued their unusual nocturnal flight for an undetermined period, and neither ground nor air crew could locate the birds the following day.

In fall 1982, four crane families were monitored in Saskatchewan, two by each of the two tracking teams. The four families were at least 50 km distant from one another and not in visual or auditory contact. When the four families resumed their southward migration on the same day, weather conditions (Table 5) were similar in all four areas, and the continuation of migration was probably precipitated by an abrupt wind shift, increasing barometric pressure, and decreasing temperature. Family 10/82 (near North Battleford) and F 1/82 (near Saskatoon) departed at 10:16 and 10:45, respectively, followed by F 6/82 and F 2/82 at approximately 14:29–14:50 and 15:00, respectively. This schedule of departure was not surprising, because the wind direction changed earlier for the first two families.

Table 2
Summary of identification data for Whooping Cranes radio-tracked in fall, 1981–83

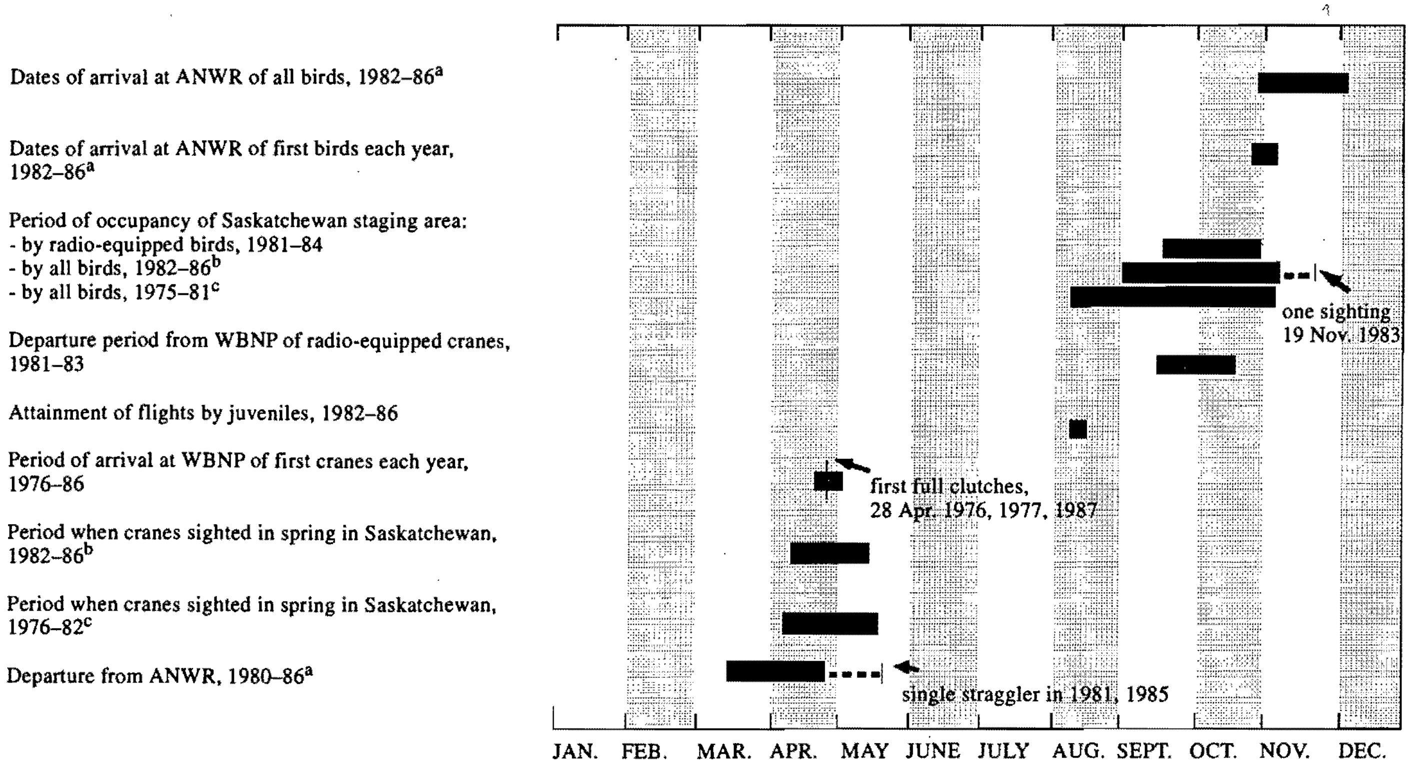
Bird No.	USFWS band	Colour band[a]	When tracked	Comments
2/81	629-01808	R/W–Green	Fall 1981	Tracked with parents; collided with power line Midnight Lake, Saskatchewan, 11 October, and died Saskatoon, 18 October
3/81	629-01809	Green–R/W	Fall 1982	Incidental signals picked up 16, 17, 18 Sept., 28 Oct.; located roosts 16 Sept., 12 Oct., observed in flight 3 Nov. near Waco, Texas
7/81	629-01807	White–R/W	Fall 1981	Tracked with parents, WBNP to ANWR, briefly accompanied by two other Whooping Cranes
			Fall 1982	Tracked with three other birds, including Red–Red and Red–R/W, WBNP to Last Mountain Lake, Saskatchewan; found dead 16 Oct. near Waco, Texas
1/82	629-01811	W/R–Green	Fall 1982	Detected 14 Oct., Alberta–Saskatchewan border, tracked with parents and two other birds to Saskatoon area roost; left area with three adults, 27 Oct., tracked to W of Regina; signals heard 70 km SE of Regina, 27–28 Oct.; found dead at ANWR on 2 Feb. 1983
2/82	629-01812	Green–W/R	Fall 1982	Detected 20 Oct. with parents, near Redberry Lake, Saskatchewan; tracked to area SW of Weyburn, Saskatchewan, 27 Oct. incidental signals to ANWR
			Fall 1983	Tracked with Y 10/82 from WBNP to ANWR
6/82	629-01815	B/W–Red	Fall 1982	First detected Redberry Lake, 21 Oct., with parents; tracked to ANWR; found dead ANWR 4 Jan. 1983
10/82	629-01810	White–Red	Fall 1982	Tracked with parents WBNP to ANWR
			Fall 1983	Tracked with Y 2/82 WBNP to ANWR
19/83	599-09822	R–Yellow	Fall 1983	Migrated with parents from WBNP about 16 Oct.; first detected Glaslyn, Saskatchewan, 18 Oct.; family with two, later three additional adults tracked to Oklahoma and again from Matagorda Bay, Texas, to ANWR

[a] R, W, B, Y are 40–mm bands; Red, White, Green, Yellow are 80–mm bands.

Table 3
Summary of identification data for Whooping Cranes radio-tracked in spring, 1983–84

Bird No.	USFWS band	Colour band[a]	When tracked	Comments
3/81	629-01809	Green–R/W	Spring 1983	Observed on ground, Minton, Saskatchewan, 25–27 April
			Spring 1984	Bird 3/81 and companion joined by F 19/83 and companions, 15 Apr., near Wakeeney, Kansas; bird 3/81 separated from tracked flock next day near Swan Lake, Nebraska
2/82	629-01812	Green–W/R	Spring 1983	Tracked with parents, ANWR to WBNP
			Spring 1984	Tracked with other two-year-old 10/82, ANWR to WBNP; died ANWR about 15 Nov. 1984
10/82	629-01810	White/Red	Spring 1983	Tracked with parents, ANWR to Meadow Lake, Saskatchewan, briefly accompanied by one and two other Whooping Cranes
			Spring 1984	Tracked with two-year-old 2/82, ANWR to WBNP
9/83	599-09832	Yellow–Y/R	Spring 1984	Tracked incidentally, ANWR to Kansas; observed in flight 6 Apr., Gatesville, Texas, and on roost 8 Apr., Temple, Oklahoma
19/83	599-09822	R–Yellow	Spring 1984	Tracked with parents, pair of cranes (2/80 and 11/80), and another pair (including 3/81) from ANWR to WBNP; first pair separated in North Dakota, second pair in Nebraska, where single adult may have joined; separated from other three birds near Turtleford, Saskatchewan; Observed separately from parents, WBNP, 7 May 1984

Figure 2
Whooping Crane arrival and departure dates: Aransas National Wildlife Refuge, Saskatchewan staging area, and Wood Buffalo National Park



[a] Data from T. Stehn, pers. commun.
[b] Data from B. Johns, pers. commun.
[c] Salyer (1982)

Table 4
Weather conditions during departure of radio-equipped Whooping Cranes from Wood Buffalo National Park, 1981–84

Date and time migration started	Identification of birds	Age (est.)[a] of adults (yr:mth)	Wind direction and speed: Wind direction (° true North)	Wind speed (km/h)	Barometric pressure (kPa)[b]	Barometric pressure during previous 4–5 days	Temperature (°C)	Visibility	Other
17 Sept. 1981, est. 10:00	F 2/81	>17	290	12.6	101.6	Rising	17	Poor, smoke	No snow cover
4 Oct. 1981,[c] est. 10:15	F 7/81	>14	265	12	101.8	Rising	-2	Fair to good	First snow (2.6 cm) fell 3 Oct.
After 4 Oct. 1981	F 3/81	>8	n.d.[d]	n.d.	n.d.	n.d.	n.d.	n.d.	Freeze-up occurred 17–20 Oct.
15 Sept. 1982, est. 08:15	Y 7/81 and Y 3/81	1:3.5	320–340	26–31	101.4	Rising, slight decline 14–15 Sept.	12	Good	No snow on ground
8 Oct. 1982,[c] est. 10:00	F 10/82	4:3.5	295	10	98.9	Variable, but slight increase from 7 to 8 Oct.	±2	Good	No snow on ground
24 Sept. 1983, est. 11:00	Y 2/82 and Y 10/82	1:3.5	220–300	9	100.3	Decline, slight increase from 23 to 24 Sept.	6	Good	No snow on ground
16 Oct. 1983, 09:00	F 19/83	>6	360	9	102.3	Rising	-7	Poor	16-cm snowfall 14 and 15 Oct.; all lakes frozen
After 18 Oct. 1983	F 9/83	>18	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	All lakes frozen

[a] Age estimate by breeding area tenure.
[b] 1 kPa = 7.5 torr (1 standard atmosphere = 760 torr = 101.325 kPa).
[c] Goossen (1982, 1986b).
[d] n.d. = no data.

Table 5
Weather conditions in fall during departure of radio-equipped Whooping Cranes from Saskatchewan, 1981–84

Departure time	Identity of birds	Age of birds (yr:mth)	Wind direction and speed: Wind direction (° true North)	Wind speed (km/h)	Barometric pressure (kPa)	Temperature (°C)	Visibility	Other
20 Oct. 1981, 08:54	F 7/81	>17	350	18	102.7	0	Fair (2 km) but decreasing	5 cm of snow fell during the night
11 Oct. 1982, 14:30	Y 7/81, three other birds	1:5	140	8–10	–	10–12	Unlimited	Weather data from 12:00
27 Oct. 1982, 10:16	F 10/82	4:5	290	24	93.6, rising	12	Good	Thin high cloud, light haze
27 Oct. 1982, 10:45	F 1/82	>19	290	24	93.6, rising	12	Good	Thin high could, light haze
27 Oct. 1982, est. 15:00[a]	F 2/82	>15	310	19–24	93.6, rising	10.6	Good	–
27 Oct. 1982, 14:29–14:50[a]	F 6/82	>16	310	19	93.6, rising	10.6	Good	–
11 Oct. 1983, 09:45[b]	Y 2/82 Y 10/82	1:5	315	>20 (est.)	95.2	-6.7	Unlimited	Sunny, clear; temperature at 1700 m asl
7 Nov. 1983, 07:48[c]	F 19/83	>6	280	28	93.2, rising	0.7	Good	10% cloud cover

[a] Goossen (1987a).
[b] Young (1984).
[c] Goossen (1987b)

3.1.1.3 Resumption of flights after weather disturbances in the United States

When F 7/81 left the staging area on 20 October 1981, winds en route remained almost entirely from the north or northwest until the birds reached the vicinity of Broken Bow, Nebraska (Kuyt 1982). On 23 October, adverse winds delayed the birds somewhat; winds were northerly by the next day, and the cranes continued their migration. Low ceiling, fog, and light rain kept the cranes grounded during the morning of 25 October; although the birds resumed their migration in the afternoon, weather conditions may have been only marginal, because the cranes made four intermediate stops that day.

From 27 to 31 October, F 7/81 remained at Byers Lake, Texas, after having been exposed to strong head winds on 27 October. When the frontal system passed, the cranes resumed their migration with favourable winds aloft and increasing barometric pressure (Table 6). They reached the Texas coast on 3 November without further interruptions.

On 28 October 1982, one day after its departure from Saskatchewan, F 10/82 encountered deteriorating weather in North Dakota. The cranes deviated 30° off course, likely as a result of strong northwesterly winds, and were relocated on the ground only after a lengthy aerial search under poor weather conditions (Kuyt 1984a). Family 6/82, tracked by Goossen (1986b) on the same day but slightly farther west, continued its flight without deviation.

The following morning, visibility had improved; with rising barometric pressure, F 10/82 continued its migration, although winds were from the southwest. These adverse winds may have accounted for a one-hour stopover in the early afternoon and for the relatively early (15:26) termination of the cranes' 251-km flight to Hausauer Lake, South Dakota.

Family 6/82 was tracked on 29 October 1982 (Goossen 1986b) to the area northeast of Colome, South Dakota, about 180 km south of F 10/82's landing site. These birds, too, landed early in the day (est. 10:40) after having flown only 138 km. There is little doubt that the weather strongly influenced the flight behaviour of both family groups. From 30 to 31 October, head winds prevailed, and F 10/82 made little progress. The unfavourable winds also affected Sandhill Cranes, a pair of Whooping Cranes, and large numbers of geese roosting near F 10/82 on Swan Lake, South Dakota (Kuyt 1984a). On 1 November, with a return of favourable winds (Table 6), the five Whooping Cranes and several hundred Sandhill Cranes resumed their southward migration.

Family 6/82 covered only 129 km on 30 October. The cranes flew into light head winds all day and made one intermediate stop. The following day, F 6/82 did not travel but rested and fed under overcast skies and practically calm conditions. Sky and visibility were below optimum on 1 November, but northerly winds apparently were an overriding factor, and F 6/82 and F 10/82 resumed migration within an hour of each other. Aided by northerly winds, they completed the remainder of their fall migration in long, daily, nonstop flights.

From 14 to 22 October 1983, the two birds (Y 2/82, Y 10/82) monitored by Young (1984) remained near Enid, Oklahoma. Strong southerly winds kept the two subadults (each 16.5 months old), a family of Whooping Cranes, and approximately 20 000 Sandhill Cranes at Great Salt Plains Lake. Rain, low ceilings, and lowered visibility occurred on several days. The wind swung back to the north on 20 October, but occasional rain and low cloud kept the cranes grounded. On 22 October, weather conditions improved, allowing the five Whooping Cranes to leave. The two subadults continued their migration without further interruptions and reached the winter range on 25 October. An aerial survey that day by staff at ANWR located the two birds as well as the family seen earlier by Young on Great Salt Plains Lake.

On 8 November 1983, a flock of six Whooping Cranes tracked by Goossen (1987b) landed near Pierre, South Dakota, in the early afternoon, most likely as a result

Table 6
Weather conditions upon resumption of interrupted southward migration of radio-equipped Whooping Cranes

Date/time	Identification of birds	Location	Wind direction and speed: Wind direction (° true North)	Wind speed (km/h)	Barometric pressure (kPa)	Temperature (°C)	Visibility	Other
27–31 Oct. 1981	F 7/81	Byers Lake, Texas	118–288	5–36	101.4–101.7	15–20	Poor to excellent	Passage of front, shift to NW winds late on 31 Oct.
1 Nov. 1981	F 7/81	Byers Lake, Texas	228	9	102.2	10	Excellent	Birds departed 08:00; winds aloft at 40 km/h
1 Nov. 1982	F 10/82	Pierre, South Dakota	330	11	101.3 rising	10	Excellent	High, thin cloud
1 Nov. 1982[a]	F 6/82	O'Neil, Nebraska and area	270–320	9–15	–	–	Excellent	F6/82 continued flight into evening under full moon
22 Oct. 1983[b]	Y 2/82 Y 10/82	Enid, Oklahoma	N	–	–	–	Poor to fair	Low ceiling; precipitation stopped
9 Nov. 1983[c], 07:43	F 19/83, three other birds	Pierre, South Dakota	330	22	–	–	Fair	Low ceiling, snow on ground, winds increasing in strength

[a] Goossen (1987a).
[b] Young (1984)
[c] Goossen (1987b).

Table 7
Weather conditions during departure of radio-equipped Whooping Cranes from Aransas National Wildlife Refuge, 1981–84

Date and time migration started	Identification of birds	Wind direction and speed: Wind direction (° true North)	Wind speed (km/h)	Barometric pressure (kPa)	Temperature (°C)	Visibility	Other
12 Apr. 1982,[a] 10:00–11:00	F 3/81, F 7/81	180	29, gusts to 42	101.8	25	Excellent	Visibility >24 km
9 Apr. 1983, 10:21	F 2/82	250	10–13	102.0	18	Excellent	Calm at 08:00, then start of southerly winds
11 Apr. 1983,[b] 08:40	F 10/82, one additional bird	150	35	101.6	26.5	Excellent	Winds up to 50 km/h later in day
5 Apr. 1984, 10:00	F 9/83	080	13	102.2	22	Excellent	Head winds aloft at 40 km/h N of ANWR; birds returned to ANWR
6 Apr. 1984, 09:00	F 19/83	130	22	101.9	30	Excellent	Slight haze, some broken cloud
9 Apr. 1984,[a,c] 10:38	Subadults 2/82, 10/82	170	34	101.2	30	Excellent	Visibility >24 km

[a] T. Stehn and K. Butts (pers. commun.).
[b] Labuda (1983).
[c] Goossen (1987c).

of rain and poor visibility. Low ceilings on 9 November (Table 6) made it impossible for the aerial trackers to follow the cranes, but the birds made excellent progress, the benefits of strong northerly winds apparently overriding the disadvantage of the low ceiling. It is likely that the cranes, taking advantage of powerful tail winds on 9 and 10 November, made an 830-km nonstop journey from northern Oklahoma to the Texas coast, where they were located by Goossen the following day.

3.1.2 Spring

3.1.2.1 Departure from Aransas National Wildlife Refuge

One of the few observations of Whooping Cranes departing from ANWR (Shields and Benham 1968) provides weather data. On 6 April 1966, a clear, sunny day with southeasterly winds of 29–32 km/h, 23 birds flying in pairs, family units, and groups of five and seven left between 09:00 and 09:14.

Extreme dates of departures of Whooping Cranes from ANWR given by Allen (1952) for the period 1938–45 were 23 March and 5 May; median dates were between 11 and 15 April. These median dates are, not surprisingly, somewhat later than those given in Table 7, because the radio-tracking crews departed with the earliest migrants. Allen (1952) did not provide many weather details for days on which Whooping Cranes began spring migration, and he suggested that, although weather was an important influence in producing variation in departure dates, the gonadal cycle of normal birds was primarily responsible for migration departures. Our radio-tracking studies, of course, were not designed to provide documentation of the physiological aspects of bird migration.

Northward radio-tracking from ANWR was carried out only in spring 1983 and 1984, but available data are augmented by observations of departing radio-equipped cranes made by staff of ANWR (Table 7).

Weather conditions during departures of Whooping Cranes from ANWR were associated with the eastward passing of high-pressure systems (anticyclones) and characterized by warm southerly winds, relatively high barometric pressure, and excellent visibility. Bagg et al. (1950) provided detailed information on the eastward progression of anticyclones through the United States and their effect on bird migration.

Most of the conditions conducive to spring migration prevailed on 5 April 1984, when F 9/83 departed from ANWR. Winds at ground level, however, were from the east (Table 7); upon encountering head winds aloft about 40 km north of ANWR, F 9/83 turned abruptly and flew back to ANWR. The following day, aided by southeasterly winds (Table 7), many cranes initiated spring migration.

Sandhill Cranes begin spring departure from Florida (Nesbitt 1975) under weather conditions similar to those prevalent when Whooping Cranes leave ANWR (rising barometric pressure, warm temperature, southeasterly winds, and clear skies).

3.1.2.2 Resumption of flights after weather disturbances

On 11 April 1983, F 2/82 completed its daily migration under adverse weather conditions and for the next two days remained grounded near Hoxie, Kansas (Kuyt 1986a). With rising barometric pressure and temperature and under clear skies, the cranes resumed migration on 14 April, although winds were northerly at 24–32 km/h (Table 8). Rarely have Whooping Cranes initiated the day's flight into head winds. On 14 April, F 2/82 laboured for over five hours at 16 km/h, and another unproductive day followed on 15 April. A frontal system passed through the Callaway, Nebraska, area on 16 and 17 April, keeping F 2/82 on the ground. Improved migration conditions (Table 8) returned on 18 April, and migration resumed. No further weather disturbances occurred between Callaway and WBNP, and F 2/82 completed its spring migration to WBNP on 22 April, having flown 346, 494, 609, and 395 km daily during its last four days of migration (Kuyt 1986a).

The adverse weather that grounded F 2/82 near Hoxie also kept F 10/82 on the ground from 13 to 15 April near Kiowa, Kansas (Labuda 1983). The three birds resumed migration on 16 April but progressed only 135 km at 33 km/h. Lack of favourable winds undoubtedly accounted for their limited advance (Table 8). In spite of deteriorating wind conditions the next day (Table 8), the cranes departed, flying in weather similar to that influencing F 2/82 during its 14 April departure from the Hoxie area. The cranes struggled into the wind, flew laboriously all day, made two landings, and by the end of the day had covered only 165 km at about 22 km/h. With an improvement on 18 April, F 10/82 flew nonstop for about 500 km, then landed on the shore of a lake near Minton, Saskatchewan, where they remained until 30 April.

On 6 April 1984, F 19/83 flew 655 km from ANWR to Henrietta, Texas, under excellent flying conditions. A low- pressure system entered the area that night, bringing heavy rain, low overcast, occasional lightning, and tornado warnings on 7 April. On 8 April, the cranes attempted to carry on, aided by improved visibility; opposed by a strong head wind, they covered only 75 km. With a return to suitable conditions on 9 April (Table 8), the cranes flew 445 km (Kuyt 1986b). On 10 and 11 April, another low-pressure system moving west to east passed through, and the cranes remained on the ground near Dighton, Kansas, for three days. Subadults 2/82 and 10/82 tracked to the Pratt, Kansas, area were influenced by the same weather system and remained on the ground from 12 to 17 April (Goossen 1987c).

It appears that subadults were more reluctant than family groups to continue their migration under less than optimum weather conditions. Two subadults remained in the North Platte, Nebraska, area from 19 April to 8 May (Goossen 1987c); although visibility during this period was good, crosswinds or head winds occurred during most mornings, and suitable winds usually occurred only on isolated days. The unsettled weather continued for a few more days, and the two cranes moved accordingly. On 14 May, conditions finally improved, and the two cranes, as if making up for lost time, made their longest flight of the

Table 8
Weather conditions during departure of radio-equipped Whooping Cranes after weather-enforced stopovers or weather-shortened flights

Date and time migration resumed	Identification of birds	Wind direction and speed: Wind direction (° true North)	Wind speed (km/h)	Barometric pressure (kPa)	Temperature (°C)	Visibility	Other
14 Apr. 1983, 11:30	F 2/82	360	24–32	102.3, rising	4	Clear	–
18 Apr. 1983, 11:04	F 2/82	170	24	101.2	–	Mostly clear	Fog dissipated by 10:00; maximum temperature for 17 Apr. was 15°C
16 Apr. 1983,[a] 10:10	F 10/82	350	<2	102.2	4	Clear	Sunny weather, numerous thermals
17 Apr. 1983,[a] 08:55	F 10/82	335	40	–	–	Good	Good thermals at midday
18 Apr. 1983,[a] 10:51	F 10/82	135	8–24	–	–	Fair to good	Low overcast dissipated and thermal activity by 10:00
30 Apr. 1983,[a] est. 07:50	F 10/82	120	24–32	101.4	-2	Clear	Good thermals most of day, winds shifting to N, lowered ceiling in late afternoon
9 Apr. 1984	F 19/83	070–090	13	101.2, rising	>18	Excellent	Ceiling 640 m; broken cloud, wind swinging S

[a] Labuda (1983).

1984 spring migration, flying 696 km nonstop from Last Mountain Lake, Saskatchewan, to Cowper Lake, Alberta.

3.1.2.3 Departure from Saskatchewan

There is little information to show that northward-migrating Whooping Cranes linger in Saskatchewan for extended periods. Family 2/82 stopped overnight on 20 April 1983 near Biggar, Saskatchewan, but continued into Alberta the next day. Family 19/83 migrated into Saskatchewan on 18 April 1984 and landed northeast of North Battleford. The birds resumed their migration the following day in normal fashion; during the course of the day, however, they made several unexpected course changes, and they terminated their flight earlier than usual. Weather conditions on 19 April were conducive to continued migration, but the cranes remained in the same area until 26 April, even though the weather on 20 and 21 April was ideal for continued migration. Separation of adults and young occurred on 26 April, shortly after the family resumed its migration. The juvenile bird made an unusual solo flight to the southeast and remained near Krydor, Saskatchewan, until 9 or 10 May.

Family 10/82 remained near Minton in southern Saskatchewan from 20 to 30 April, even though several favourable flight days passed. Another radio-equipped crane (two-year-old 3/81) was found by Labuda (1983) only 14 km from F 10/82 on 25 April and remained in the area until the morning of 27 April. Factors other than weather were apparently keeping F 10/82 in the Minton area. The family resumed flying on 30 April under favourable weather conditions (Table 8); although the weather began to deteriorate in late afternoon, the cranes completed a 614-km nonstop flight to the Meadow Lake area (Labuda 1983). The weather was unsuitable for migration on 1 May (wind 320° at 33–36 km/h, barometric pressure 101.25 kPa, snow flurries, 150-m ceiling).

By 3 May, F 10/82 had not yet arrived on the breeding range (its breeding site at Lobstick Creek is well known; Fig. 1). During a 9 May 1983 survey, I saw pair 10/82 on its nesting territory of the previous year. I sighted Y 10/82 (the pair's 1982 chick) on 28 May, about 13 km south of its parents' 1983 nest site. It is not known when the three cranes returned to their summer range or whether the three cranes arrived as a family group or independently.

3.2 Migration

For many species of migratory birds, the traditional travel in spring and fall between winter and breeding ranges occupies a significant portion of the year. The time required for Whooping Cranes to complete their 4000-km migration usually ranges from two to four weeks but may take as long as 50 days. The duration of migration depends on date of departure, weather conditions en route, habitat conditions on summer and winter ranges, and experience (age) of the birds. Individual differences and other factors may also play a part. In fall, migrating Whooping Cranes can reach the Saskatchewan agricultural area two days after their departure from WBNP. The cranes may spend from several days to a month on a staging area (see Section 3.2.6) in Saskatchewan before leaving on a relatively rapid crossing of the central United States to reach the winter range on the Texas coast.

Melvin and Temple's (1981) generalized model of Sandhill Crane migration and their three basic categories of migration habitat (staging areas, traditional stopover areas, and nontraditional stopover areas) generally apply to the Whooping Crane fall migration. A major difference is that adult Whooping Cranes in the same area do not form a single flock, each pair or family usually remaining a separate unit.

Subadults have a greater tendency to move around during the staging period than do mated pairs or family groups, and they are also more likely to form flocks. As many as 12 birds in a flock (but rarely more than six) were observed in Saskatchewan. Melvin and Temple (1981) discussed the physiological and social benefits of staging areas to Sandhill Cranes. The interactions of subadult Whooping Cranes on the staging area could also play an important social function—for example, in establishing and reinforcing pair bonds.

After the cranes leave the staging area, the remainder of the migration usually consists of daily flights, terminated each day in a stopover. These stopover areas, where birds often roost for the night in small wetlands, are likely selected opportunistically as time of day and weather conditions dictate. The infrequent use of large wetlands, as pointed out by Howe (1989), may simply reflect their scarcity in many areas.

Spring migration of Whooping Cranes occurs within the same general corridor as fall migration. There are no spring staging areas near the winter range (as exist along the Platte River for Sandhill Cranes), and northward migration of breeding pairs and families through the United States is generally rapid if weather conditions allow it.

Although some northbound Whooping Cranes may linger for a few days on the fall staging area, there is no indication of a spring staging period in Saskatchewan comparable with that in fall. Delays are generally weather-related, and cranes are capable of reaching the breeding range in WBNP on the second day after departure from the Saskatchewan grain belt.

3.2.1 Premigration movements

It is unusual to see a Whooping Crane flying in spring and summer, except in the immediate vicinity of the nest. The reasons may vary: from late April until early August, breeding cranes are involved in nesting activities and care of flightless young. Many of the adults and subadults may be flightless during the latter part of that period as a result of moulting of major flight feathers. Moult is completed by early August, and family groups will then be involved in continuous foraging to prepare for fall migration. If local food resources are sufficient, there is little need for cranes to fly.

As little was known about fall departure dates of migrating cranes, the frequency of fall aerial surveys over WBNP was increased greatly in 1981 to maintain contact with radio-equipped cranes. Despite the increased aerial surveillance, tracking crews' sightings of flying cranes in WBNP were few, and most were of subadult birds. Two-year-old 3/81 moved 34 km between 28 May and 21 June 1983 (Kuyt 1984b), when radio signals of crane 3/81 and Y 10/82 were received from the same wetland; although neither bird was observed, the two cranes were probably together. Crane 10/82 later became associated with a different bird, and we did not locate 3/81 in WBNP again that fall.

I determined some of the movements of other subadult birds in summer 1982 by means of radiotelemetry (Kuyt 1984a). In June and July, yearlings 3/81 and 7/81 were often detected in various parts of the cranes' summer range. The yearlings were originally observed alone; by the middle of August, however, each had begun associating with one or several Whooping Cranes, and they eventually began the fall migration with these birds. Yearling 3/81 began a gradual southward drift on or about 11 August, passed through its parents' home range on 12 September (where it became associated with a five-year-old crane), then continued to drift south on 13 and 14 September. The two birds began migration from the summer range the following day.

In 1983, Y 2/82 (alone) and Y 10/82 (with a single Sandhill Crane) were frequently detected in WBNP (visually or by radio signals). On 14 September, Y 2/82 left its summer range between Sass and Klewi rivers and moved 51 km southeast into the home range of nesting pair 17/83. A short distance north of former nest 17/83, Y 2/82 encountered Y 10/82, the 1982 chick of pair 17/83. The two yearlings became associated and, on 19 September, flew 60 km northwest. The following day, the two birds began a leisurely return; on 24 September, I found them in the same wetland from which they had departed on 19 September. The two birds initiated fall migration from this marsh in the late morning of 24 September (Kuyt 1984b; Young 1984).

These seemingly random movements sooner or later result in subadults encountering each other and forming associations. In almost all instances when groups of two, three, four, or five cranes not known to be associated with a nest were observed on the summer range, colour-band information showed the flocks to consist of subadult birds. Single Whooping Cranes, often yearlings (presumably recently separated from their parents), which are seen occasionally in spring, are rare during the summer.

Aggregations including colour-banded birds are also known to have migrated as units. These and other associations are maintained or newly formed on the Saskatchewan staging area (Kuyt 1984b). This mechanism probably plays a role in future formation of pairs leading to permanent breeding pair bonds.

Flying on the summer range is even more uncommon in family groups than among subadults. Juveniles do not become able to fly until about the middle of August (Fig. 2).

Family groups maintained home ranges that varied in size from 1.32 to 9.56 km², and the birds were usually found within 4.5 km of the nest site (Kuyt 1984b; Goossen 1986a, 1986b). When families began moving, they did so in progressive stages. Over a 42-day period (4 August–16 September) in 1983, F 19/83 moved 4 km southeast from its chick's 1 August banding site. On 18 September, 27 September, and 9 October, the family moved south in progressively greater increments. Daily distances moved during the last 10 days of the premigration period were greater than during earlier 10-day periods (Kuyt 1984b). When migration began on 16 October, F 19/83 had progressed about 9 km southeast of the nest site. Daily moves made by family groups were as long as 4.5 km but averaged less than 2 km. Probably most of these moves were made on foot.

Quite a different movement was made by F 1/82 in 1982. This Sass River family had a relatively small home range of 2.40 km². On 15 September, F 1/82 was found by Goossen (1986b) 17 km south of its home range, but the birds returned to their home range on the following day. On 24 September, the birds were found near the Klewi River, 17 km northwest of the nest area, where they remained in an area of 1.69 km² until at least 8 October. In 1983, F 20/83, which in that year occupied the same composite nesting area (Kuyt 1981a) as F 1/82 in 1982 (and therefore is assumed to contain the same pair of adults), moved from its Sass River home range on 17 September. This movement of 18.5 km was easily the longest 1983 premigration movement of a family group. The family used the same general area in 1983 as in the previous year. Other premigration movements were noted in 1983 (Kuyt 1984b), when Klewi River families 7/83, 19/83, 15/83, and 18/83 moved 2.5–3.5 km south of their respective home ranges, then gradually drifted south to the north end of the nonbreeder area (Kuyt 1979). Migration from this area is believed to have occurred on 16 October.

I was not able to demonstrate any pronounced southward premigration movement by the only family (F 9/83) remaining in the Sass River portion of the breeding range (the other family F 20/83 had flown to the nonbreeder area). Family 9/83 and two pairs of adult cranes in the Sass area moved out after 18 October and were the last birds to migrate in 1983.

3.2.2 Departure dates

The earliest documented departure date during the period 1981–83 was 15 September 1982, when Y 3/81 and Y 7/81 (with their respective companions) left WBNP during the morning (Table 4). Whooping Cranes were observed in Saskatchewan as early as 27 August 1981 (Johns 1987), 7 August (no year given; Salyer 1982), and even 7 July 1977 (Stephen 1979). It is possible, therefore, that some Whooping Cranes depart from WBNP at earlier dates than radio-tracking crews were able to document from 1981 to 1983. Some or all of the early sightings in Saskatchewan may have involved birds summering there.

Yearlings and other subadults are among the earliest departing cranes. Family 2/81 also left WBNP early in 1981, when dry conditions (contributing to record forest fires in the park that summer and fall) may have forced some cranes to depart earlier than in years with better habitat conditions.

The latest departures of Whooping Cranes from WBNP occurred after 18 October 1983, when two pairs of adults and F 9/83 were last observed in the Sass area (Table 4). At the time, the entire area was snow-covered, and all ponds were frozen. The seven birds were roosting and foraging in still ice-free running water of Preble Creek and nearby streams.

3.2.3 Fall migration route

The migration corridor used by the radio-tracked birds on their departure from WBNP is about 80 km wide (the approximate east–west extension of the breeding range), and its axis is oriented NNW–SSE (about 340°–160°). This corridor widens gradually as the birds proceed south; except for the flight track of F 7/81, the corridor would be much narrower, particularly through Alberta and Saskatchewan (Figs. 3–5). Family 7/81, originating from the westernmost part of the breeding range, maintained its orientation on the western border of the migration corridor until reaching central Oklahoma. Family 10/82, originating from the easternmost portion of the breeding range, maintained a central position in the corridor, except in North Dakota, where it was briefly forced east by weather conditions, and in Oklahoma and Texas, where it maintained its orientation on the western border of the migration corridor until ANWR was reached.

Most of the cranes tracked seemed to follow the Athabasca River south during their first migration day. As several of these flights were made when visibility was poor (smoke and low ceiling in 1981), it is unlikely that all the low-flying cranes were visually guided by the Athabasca River.

In Saskatchewan, most of the tracked birds veered east upon approaching the North Saskatchewan River (Fig. 4), generally causing a narrowing of the migration corridor (except for F 7/81) to a crossing in the vicinity of Borden, northwest of Saskatoon (Fig. 5). In this area, the southeasterly direction of the North Saskatchewan River valley and the abrupt northeasterly bend of the river near Borden (where most crossings occurred) may play a role in orienting the cranes' migration route.

A similar situation exists in North and South Dakota, where the valley of the Missouri River may be used as a navigation aid by the cranes. Several tracked cranes, forced east of the river in this area by weather conditions, swung back west in the Pierre, South Dakota, area and returned to a route west of the river (Fig. 6). In fall 1981, F 7/81 appeared to follow the Cimarron River valley in Oklahoma (Fig. 7) for about 70 km (Kuyt 1982).

The narrowest part of the fall migration corridor (excluding both ends) occurs along the Platte River, an area 80 km wide between Lexington and Grand Island, Nebraska (Fig. 7). This area was used by Whooping Cranes more in the past than today (Lingle 1985). The widest part of the fall corridor (about 300 km) occurs near the Kansas–Oklahoma border (Fig. 7), immediately south of the narrowest part near the Platte River. The apparent widening of the corridor is due entirely to the easterly deviation of F 6/82 on 1 November 1982, when the cranes continued flying after sunset, possibly because of loss or reduction of visual orientation (Goossen 1987a). Similarly, F 19/83 flew after sunset on 9–10 November 1983 (Goossen 1987b) and may have been pushed off course by strong northwesterly winds. This deviation could have accounted for the birds reaching the coast at Matagorda Bay, well to the northeast of ANWR (Fig. 8), resulting in a wider than expected migration corridor at the southern terminus.

Figure 9 shows the fall migration corridor in its entire length, as based on the data obtained during 11 fall trackings (Table 2). Average widths at 10 evenly spaced points along the corridor (excluding the first and last 100 km of the migration route) produce a mean corridor width of about 200 km, which might be increased with a greater number of tracking data.

Also shown on Figure 9 is the continuous 1000-m contour line between the Northwest Territories and Mexico.

Figure 3
Fall migration routes of radio-tracked Whooping Cranes: Wood Buffalo National Park to Fort McMurray area

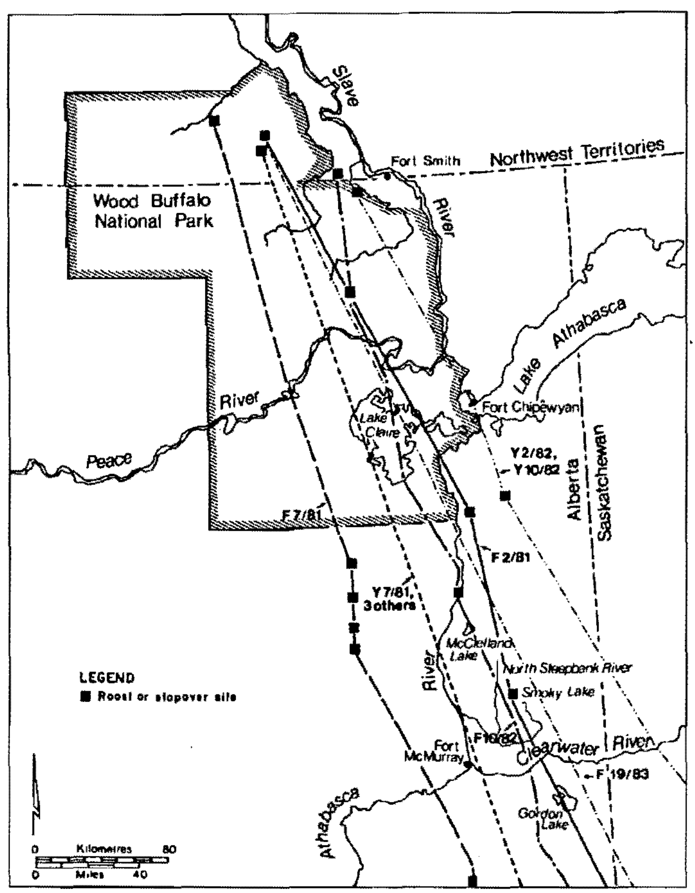


Figure 4
Fall migration routes of radio-tracked Whooping Cranes: Fort McMurray area to west-central Saskatchewan

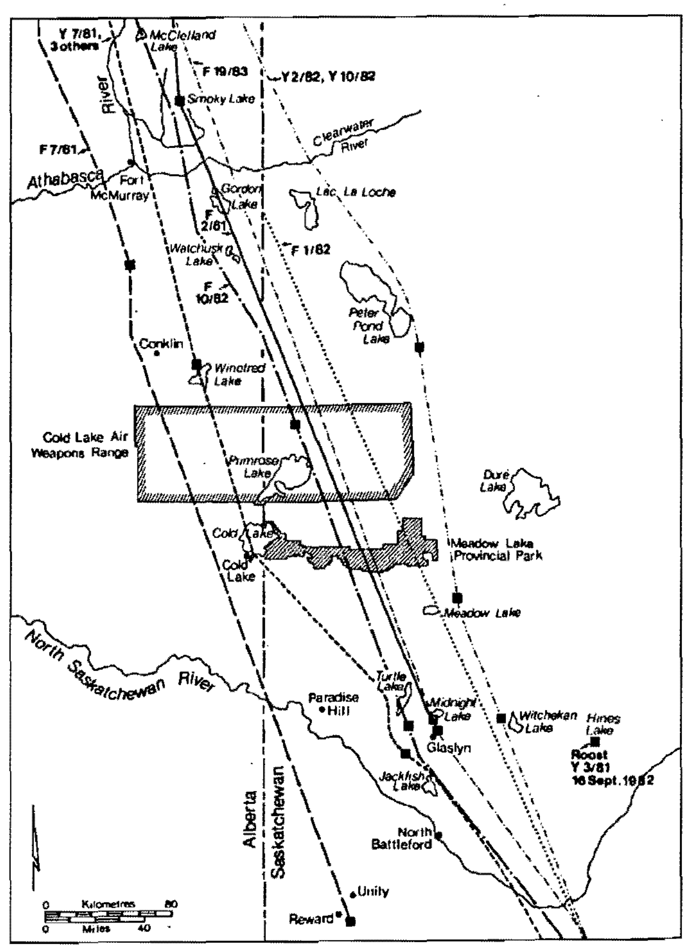
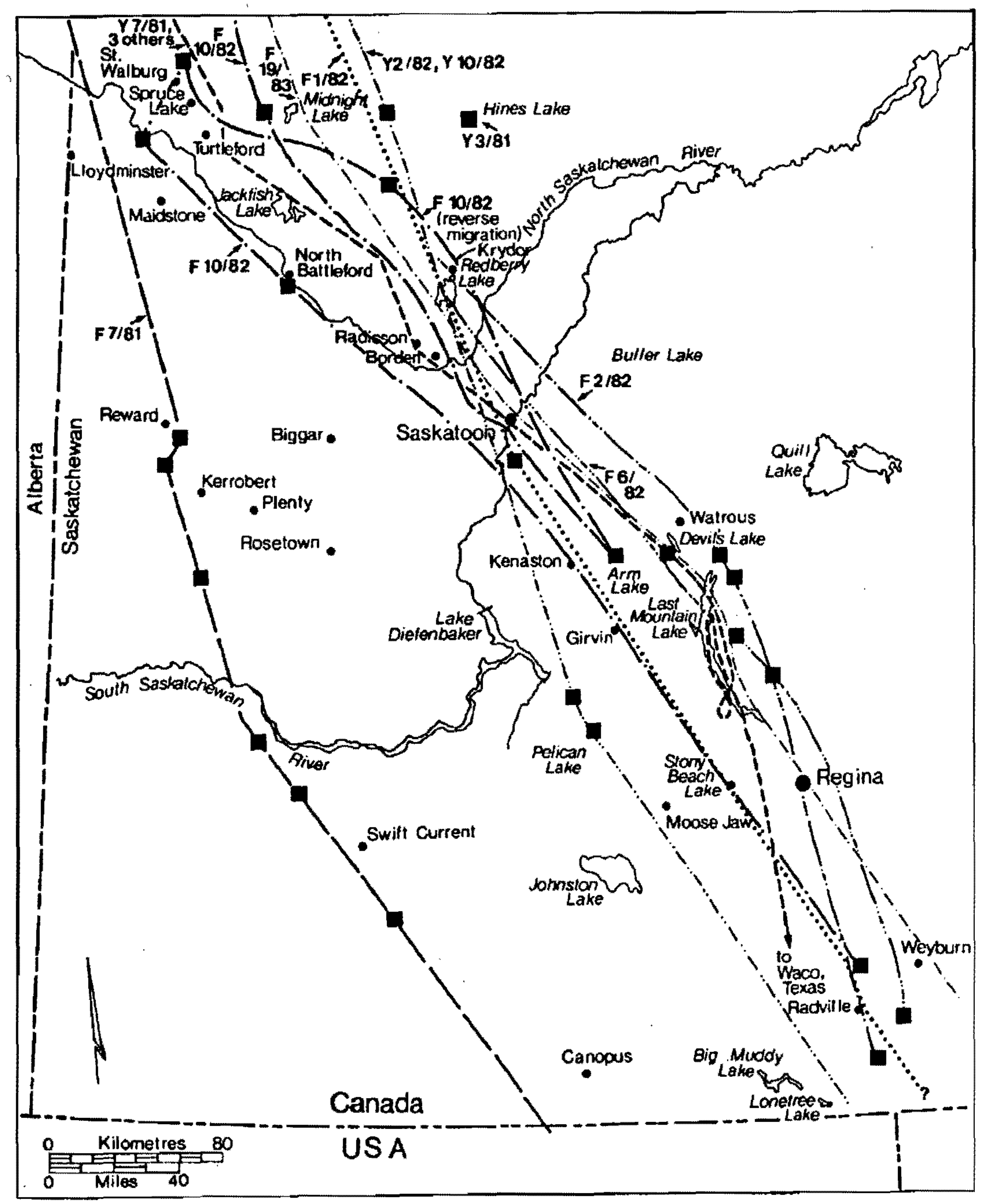


Figure 5
Fall migration routes of radio-tracked Whooping Cranes: Saskatchewan



The Whooping Crane migration route generally remains well east of this contour line but approaches it to within 25 km just west of the Valentine National Wildlife Refuge in Nebraska (Fig. 7).

It seems unlikely that a certain elevation interval indicated by the 1000-m contour line would have an effect on the cranes' flight unless other factors (e.g., deflection of wind) played a role. There would be an effect if the birds were flying low and if the change in ground relief was abrupt. Such was the case after a crossing of the South Saskatchewan River (Fig. 5), when F 7/81, flying at only 20 m agl, made an abrupt 30° course change when approaching a low escarpment (600-m contour) directly in its path.

3.2.4 Spring migration route

The initial segment of the spring route appears only about 15 km wide, because birds tracked in spring originated from a small area on the winter range. The mean width of the spring migration corridor may be narrower (125 km) than that of the fall migration corridor because fewer birds were tracked in spring than in fall.

The spring migration corridor soon widens, primarily as a result of the westward deviation of F 10/82 (Fig. 10). This family veered northeast after leaving Texas (Fig. 11), then, before reaching the Canadian River, assumed a position on the east side of the corridor. The area of crossing to the east side of the corridor occurred near the Fort Cobb Reservoir, in almost the same spot where F 10/82 roosted on 2 November 1982 (Kuyt 1984a); the cranes may have recognized the reservoir and its general location.

Figure 6
Fall migration routes of radio-tracked Whooping Cranes: Saskatchewan to Nebraska

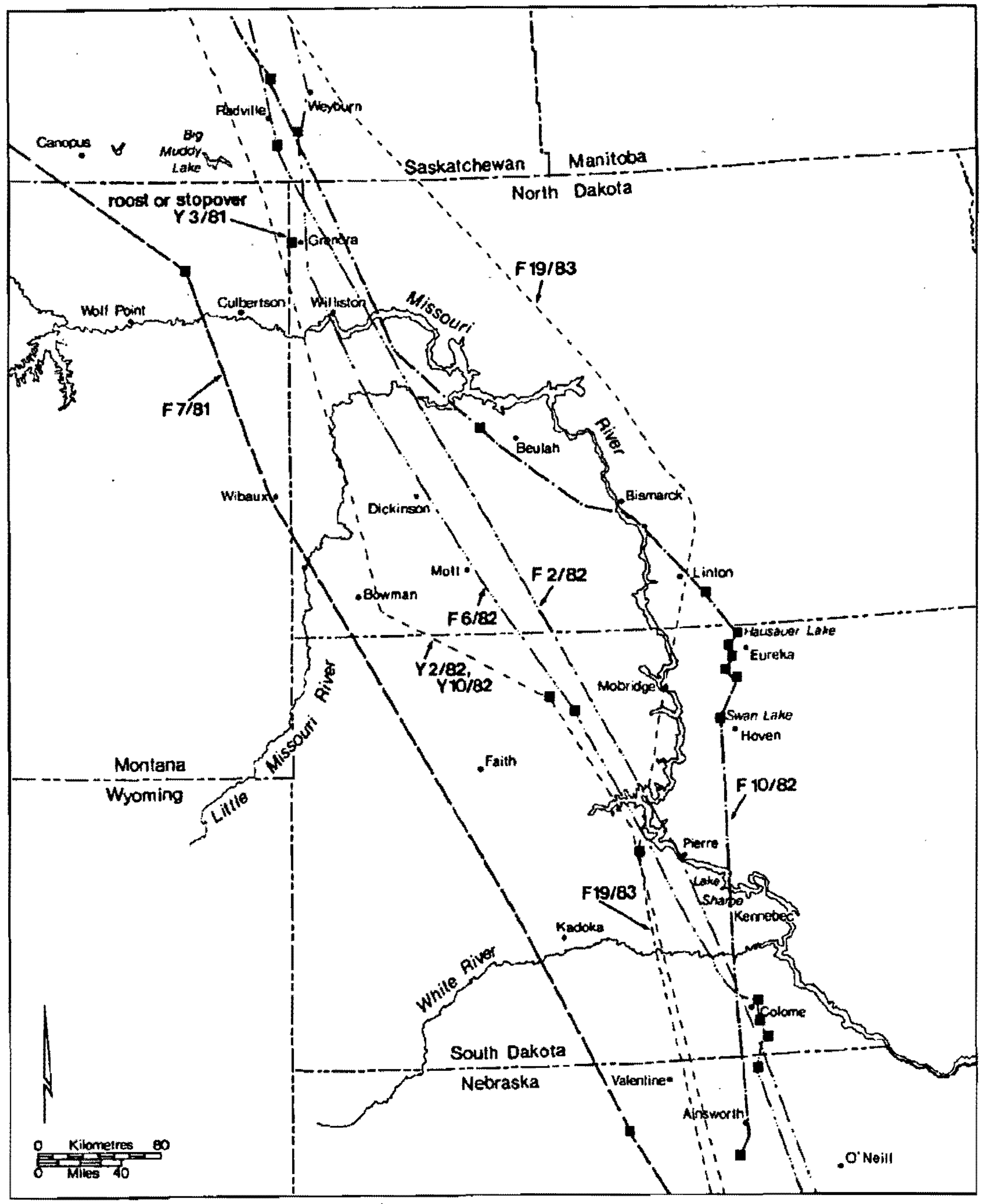


Figure 7
Fall migration routes of radio-tracked Whooping Cranes: Nebraska to Oklahoma

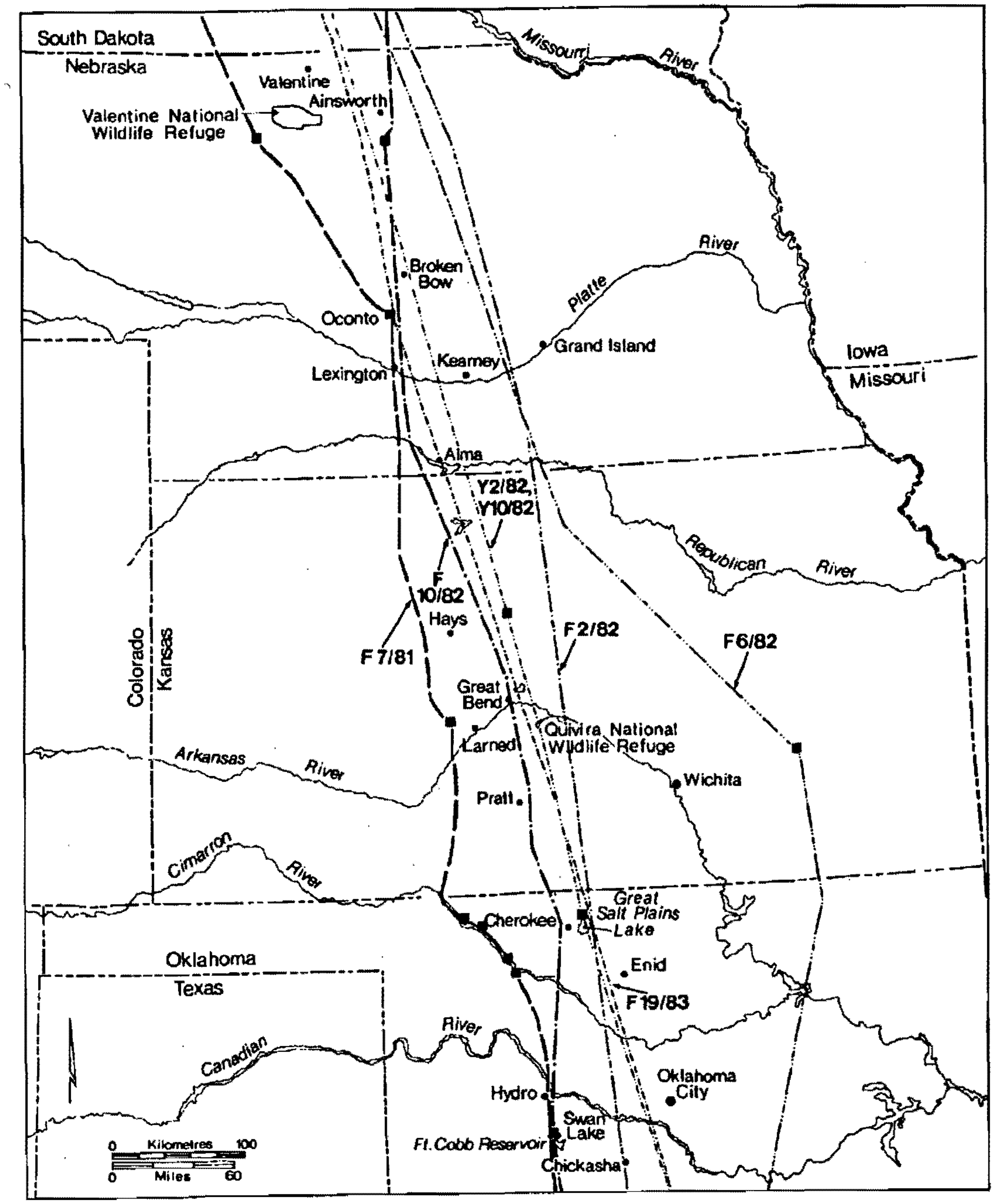


Figure 8
Fall migration routes of radio-tracked Whooping Cranes: Oklahoma to Aransas National Wildlife Refuge

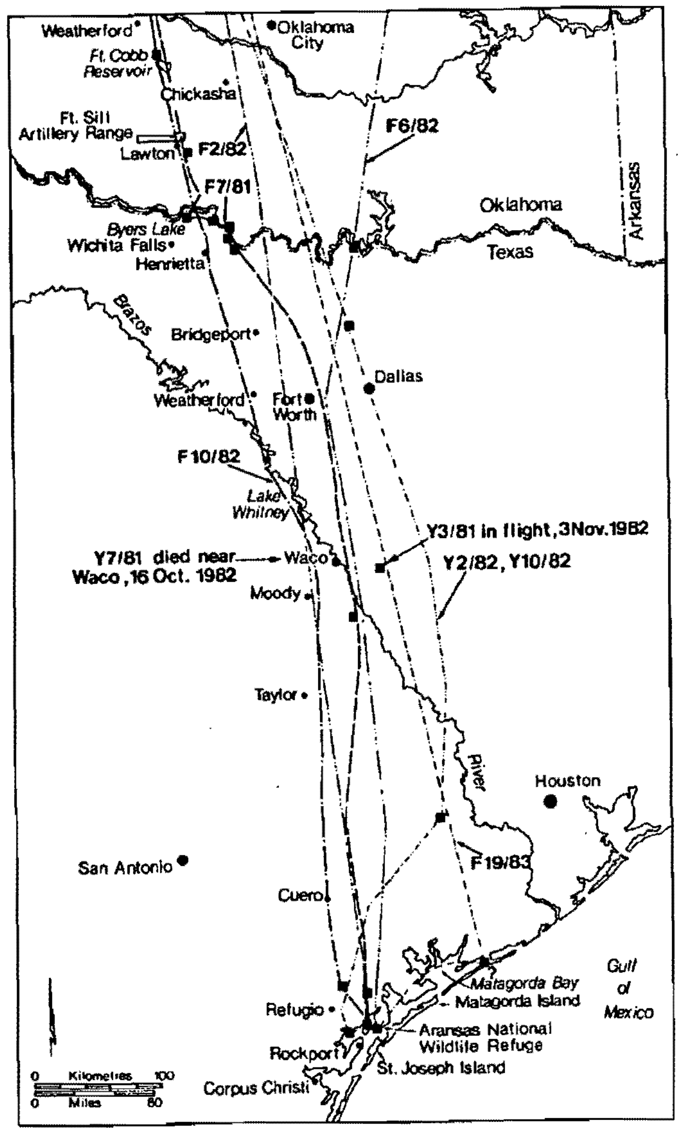


Figure 9
Fall migration corridor of radio-tracked Whooping Cranes, 1981–83

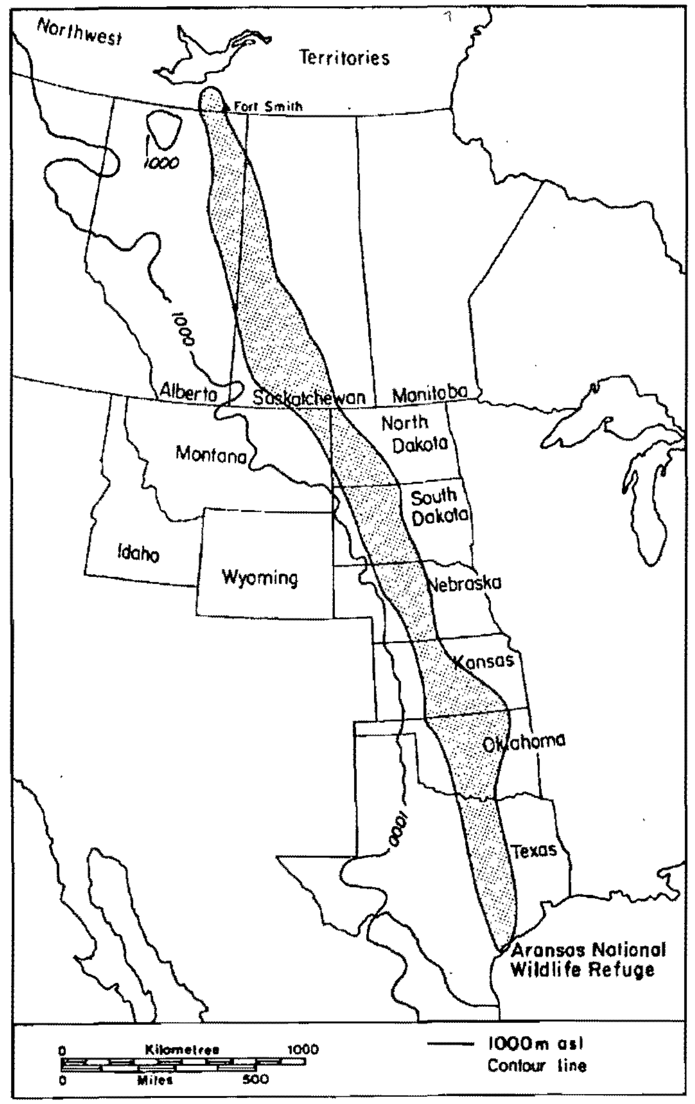


Figure 10
Spring migration routes of radio-tracked Whooping Cranes: Aransas National Wildlife Refuge to Red River

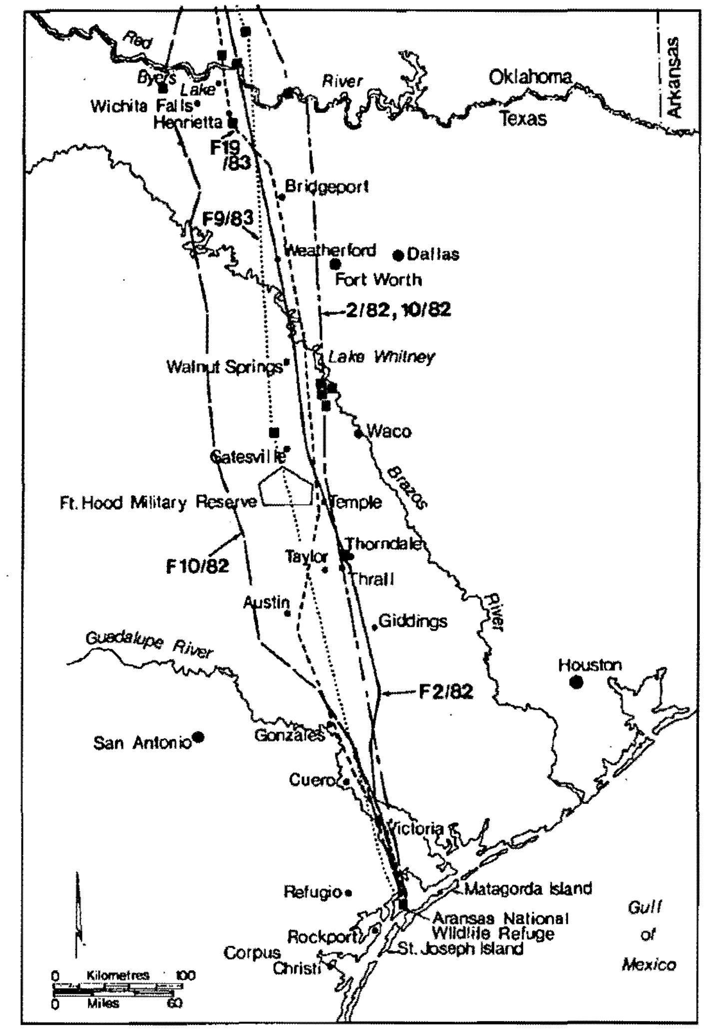


Figure 11
Spring migration routes of radio-tracked Whooping Cranes: Red River to central Kansas

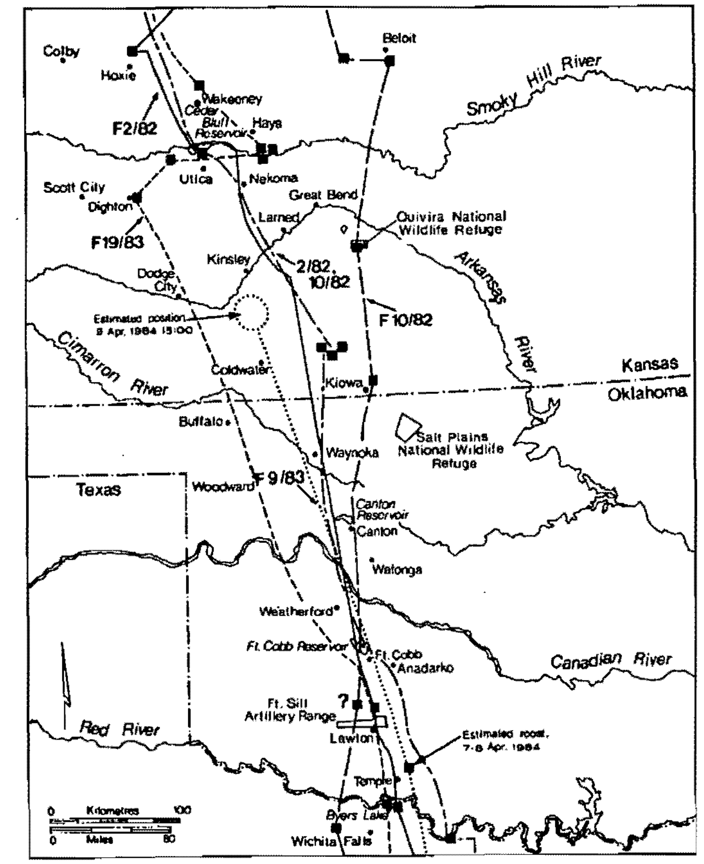
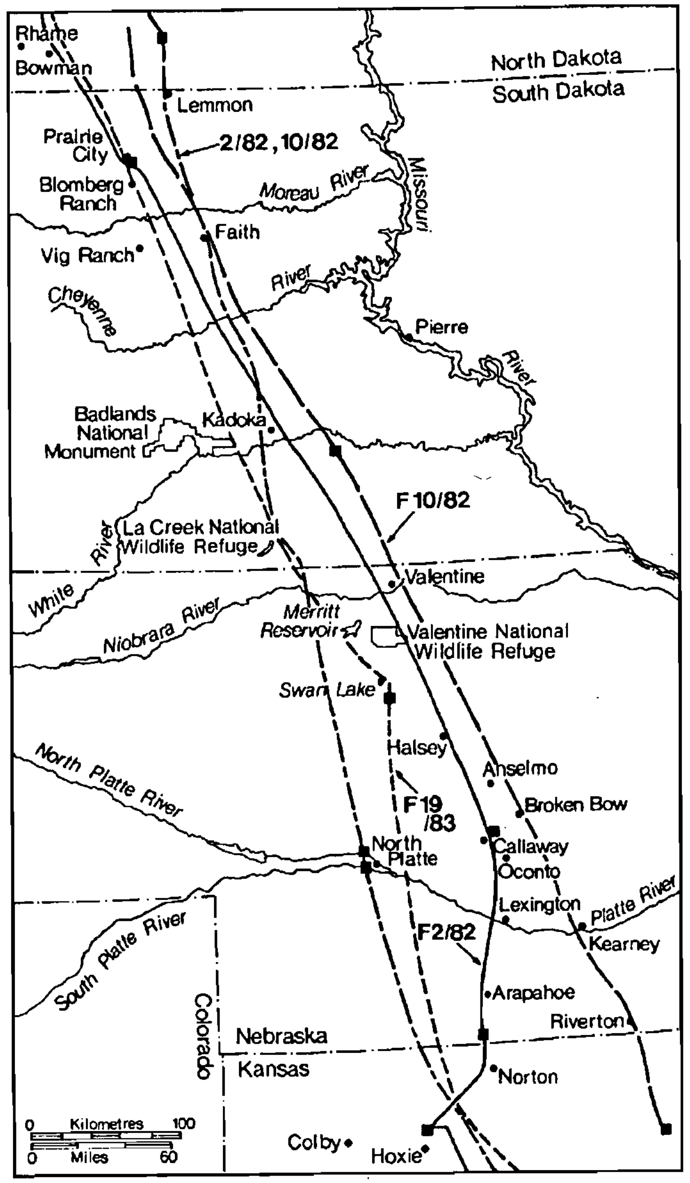


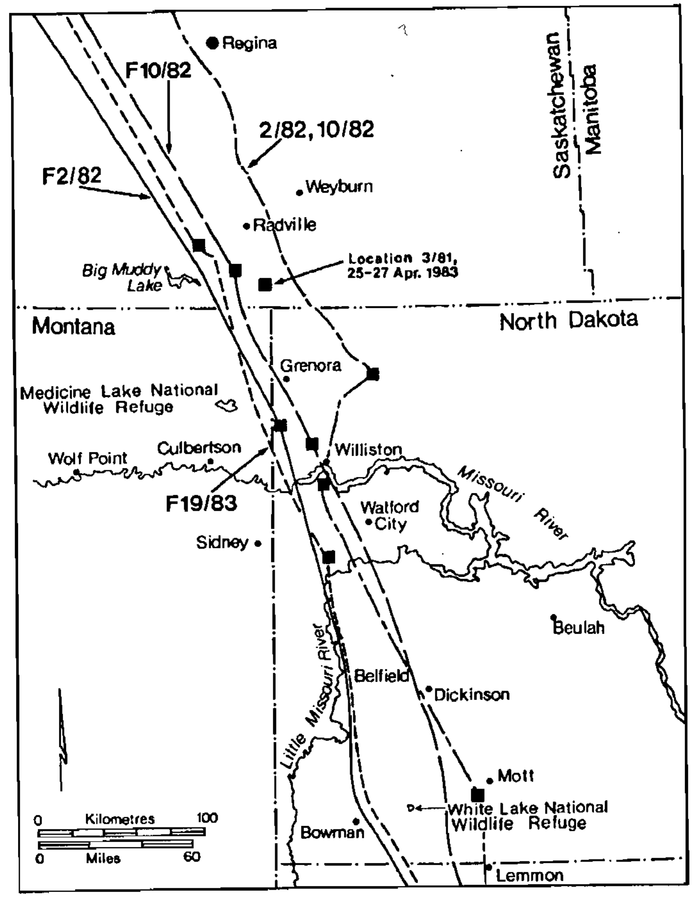
Figure 12
Spring migration routes of radio-tracked Whooping Cranes: Central Kansas to North Dakota



During the spring migration, there were a few indications of the possible influence of geographic features on routes followed. The cranes remained west of the Missouri River (Fig. 12). In North Dakota (Fig. 13), cranes migrating in 1983 and 1984 appeared to be deflected by the Little Missouri River; when they reached the river, the birds abruptly veered north about 20° and began following the valley. Family 2/82 was flying at 1500 m agl in 1983 and F 19/83 and companions were at 370 m agl in 1984 when the direction shifts occurred at about the same location. Visibility was good on both occasions, and the cranes could have been visually guided by the river. Favourable winds or thermal conditions over the rugged terrain along the Little Missouri River may also have influenced the cranes' flight path. I saw other birds, such as Turkey Vultures *Cathartes aura*, American White Pelicans *Pelecanus erythrorhynchos*, and a Golden Eagle *Aquila chrysaetos*, using thermals in the area.

After crossing Saskatchewan (Fig. 14), cranes passed through Meadow Lake Provincial Park and the nearby Cold Lake Air Weapons Range on the Saskatchewan–Alberta

Figure 13
Spring migration routes of radio-tracked Whooping Cranes: North Dakota to Saskatchewan



border (Fig. 15). On 22 April 1983, after having landed on an ice floe in the Athabasca River the previous evening, F 2/82 continued its northward migration (Kuyt 1986a). As the three birds, flying over Calumet Lake at below 450 m above sea level (asl), approached the Birch Mountains (reaching 820 m asl in the area), they detoured north until they had passed the low mountains (Fig. 16), then resumed their original northwesterly course.

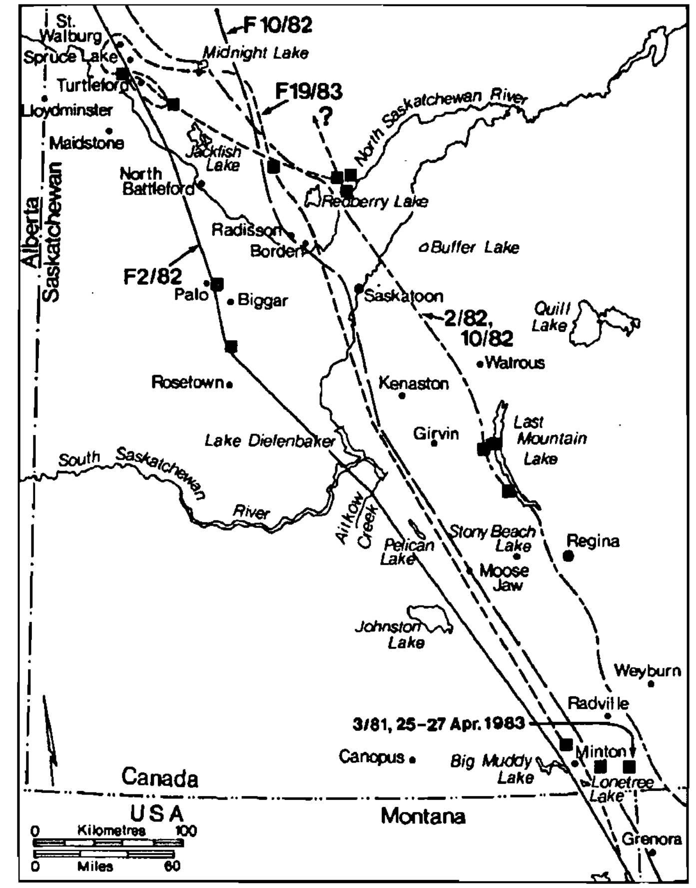
In spring 1984, Goossen (1987c) tracked Y 2/82 and Y 10/82 to a landing site west of Fort McMurray. The following day, the cranes continued their migration, which would have taken them across the Birch Mountains, a climb from 450 to 790 m asl over a distance of about 90 km. Unfortunately, the birds were not under observation during all of this section. The next day, Goossen tracked the two yearlings to a landing west of WBNP (Fig. 16). In that area, the Caribou Mountains, rising to 1020 m asl, may have discouraged the cranes from continuing farther west. For the next two days, the birds displayed apparently erratic flights; on 22 May, Goossen tracked them to a landing only 1.5 km south of the location from where the birds had initiated their migration the previous fall (Kuyt 1984b).

The orientation of the spring migration corridor (340°) is much like that of the fall corridor. It is also similar with respect to the location of the continuous 1000-m contour line that the birds did not cross (Fig. 17).

3.2.5 Extent of migration corridor and reverse migration

The total length of six migrations ranged from 3923 to 4224 km and averaged 4008 km (Table 9). The longest

Figure 14
Spring migration routes of radio-tracked Whooping Cranes: south-central Saskatchewan



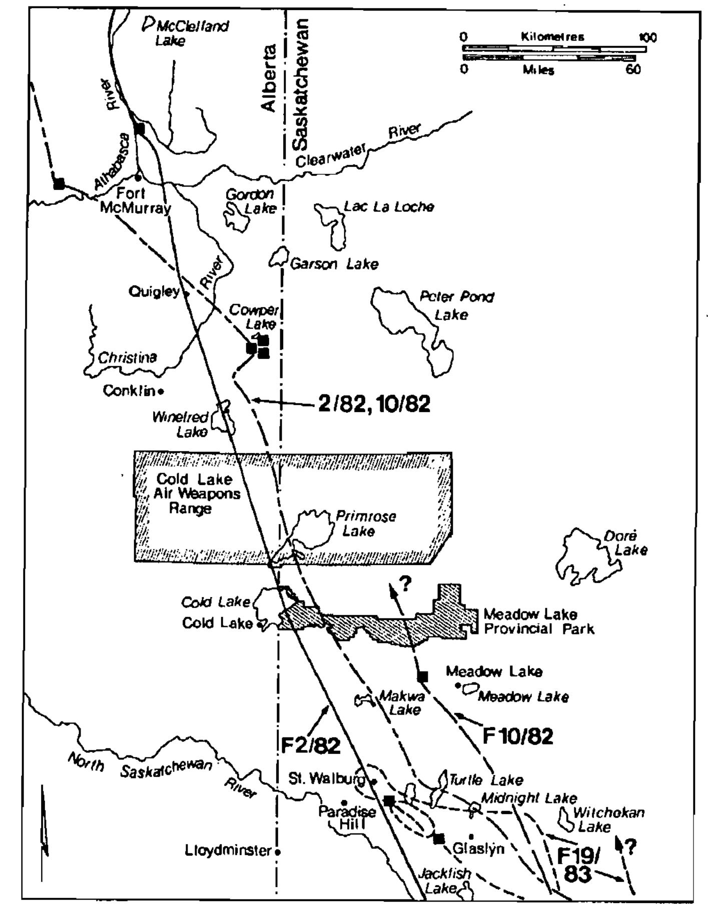
spring migration (in distance and in time) was made by two-year-old cranes 2/82 and 10/82 as a result of repeated deviations from a straight course, particularly during the last few days of their spring migration (Fig. 16).

By far the longest migration was the fall journey of F 10/82. The family flew 4670 km (Kuyt 1984a), but this distance included a highly unusual reverse migration that added about 700 km. On 14 October 1982, pushed by a 30 km/h tail wind from the northwest, F 10/82 flew rapidly from west of Midnight Lake to Arm Lake (Fig. 5). In the late morning of 15 October, a complete reversal in wind direction occurred. When F 10/82 took off at 13:41, the birds continued to fly downwind, which now took them in a northwesterly direction, exactly opposite to the previous day's course.

The birds continued to fly downwind that day and the next until they ran into deteriorating weather near St. Walburg (Fig. 5). In shifting winds, 0°C temperature, and occasional rain and sleet, the cranes began to fly erratically and made several landings alternated by short flights. On 17 October, the cranes resumed flight, now in a southwesterly direction but still in light rain and snow. The cranes were eventually forced down northeast of Lloydminster; they resumed their flight on 18 October (now to the southeast) until they reached the North Battleford area in late afternoon. Here the birds staged until 27 October, when they resumed their southward migration.

On 15 October, when F 10/82 was flying on its northwesterly reverse migration southeast of Saskatoon, I simultaneously heard the radio signal of F 1/82's juvenile,

Figure 15
Spring migration routes of radio-tracked Whooping Cranes: Saskatchewan to northern Alberta



which, with its parents, was labouring into the same wind that was helping F 10/82 to the northwest. At one time, the two families were respectively 15 km southwest and 15 km east of Saskatoon, flying parallel courses but in opposite directions! F 1/82 continued only a short distance, landing 35 km south of Saskatoon. The birds remained there until 27 October (Goossen 1987a), the same day that F 10/82 resumed its normal migration from the North Battleford area.

3.2.6 Staging areas and duration of stopovers

A staging area can be defined as any site where migratory birds prepare themselves physiologically for their next migration flight (Pitelka 1979). This implies that there may be several staging areas during one migration and that staging can occur in both fall and spring. Bellrose (1972) defined a staging area as a site adjacent to breeding areas where ducks in the same state of physiological preparedness gather at the beginning of fall migration.

In 1976, I noted that most, if not all, of the cranes in the Sass and Klewi areas were still present on 14 September, although the birds were concentrated in two or three small areas adjacent to the breeding range. In 1983, I saw a similar concentration of birds south of the Klewi breeding range, in an area from which the birds suddenly disappeared on or about 16 October. Sass family 1/82 spent 24 September–8 October in the area immediately south of the Klewi breeding range, after a highly unusual 17-km movement from its Sass breeding territory (Goossen 1986b), a move that was repeated by the same pair with their 1983

Figure 16
Spring migration routes of radio-tracked Whooping Cranes: northern Alberta to Wood Buffalo National Park

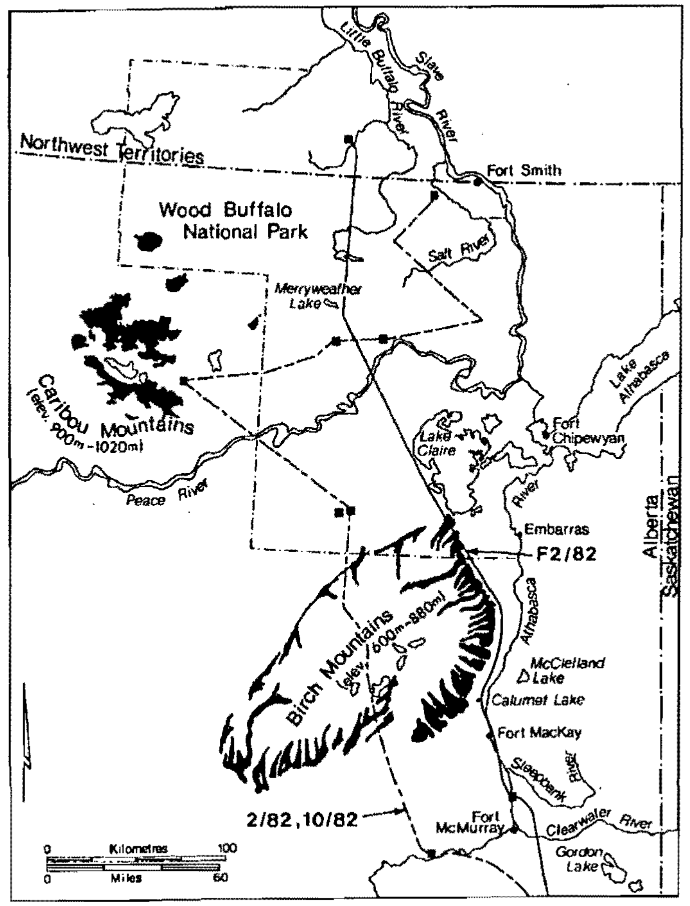
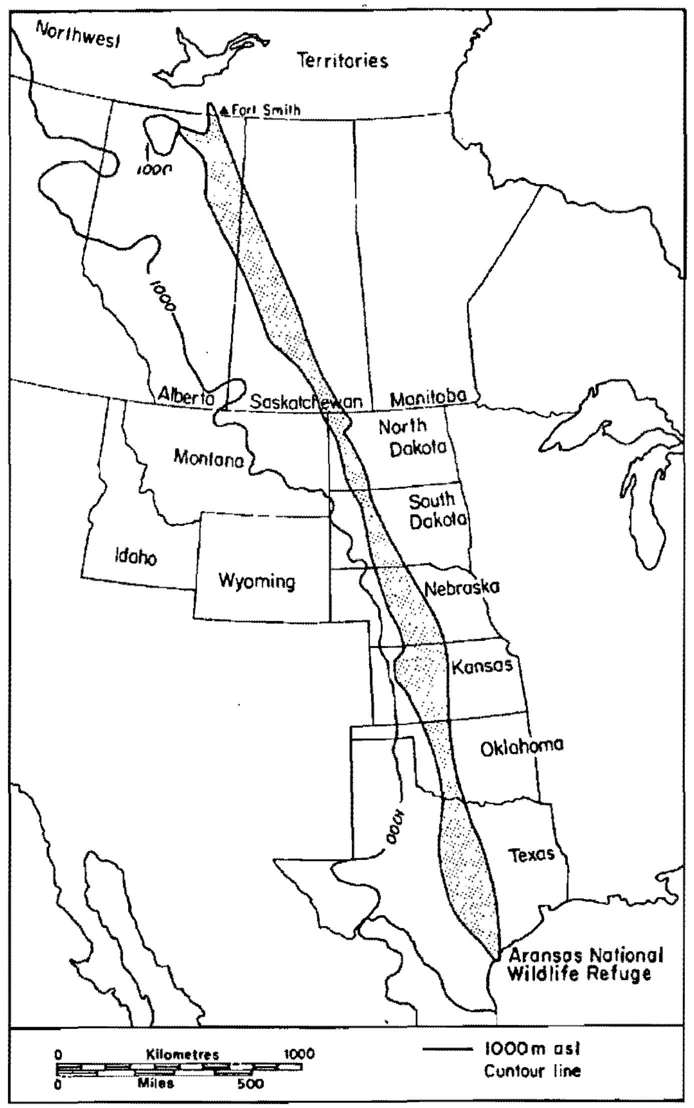


Figure 17
Spring migration corridor of radio-tracked Whooping Cranes, 1983–84



juvenile the following year (Kuyt 1984b). This area, immediately south of the Klewi breeding range, may have a special significance for some Whooping Cranes. In spring 1983, I radio-tracked F 2/82, still accompanied by the 1982 juvenile, to the same site, even though it was not this family's nesting area. The following day, the three birds were observed on the 1982 nest island near the Sass River; 10 days later, when the pair had a new nest nearby, I found the radio-equipped yearling alone in the area south of the Klewi breeding range where it and its parents first landed in spring 1983. Perhaps these areas should be viewed as premigration staging areas *sensu* Bellrose (1972).

The most important stopover during the Whooping Crane's fall migration is located in Saskatchewan, and I will refer to the south-central portion of Saskatchewan as the Whooping Crane staging area. It encompasses about 95 000 km² enclosed by a line connecting Lloydminster, Meadow Lake, Quill Lake, Regina, Moose Jaw, Swift Current, and Kerrobert (Figs. 4 and 5). Most staging Whooping Cranes will be found in this area, but some birds may be found staging in other parts of Saskatchewan or even in the northern United States. While searching for Y 7/81 and its companions on 18 September 1982, I picked up signals of Y 3/81 near Muddy Lake just north of the Canada–United States border (Kuyt 1984a). On 12 October, I located Y 3/81 in the company of several Sandhill Cranes on the ground near Grenora, North Dakota (Fig. 6). Sixteen days later, Goossen (1987a) and I independently heard the yearling's radio signal immediately south of Grenora, and it is likely that the bird had been in the vicinity from about 18 September to 28 October, an unusually long staging period.

3.2.6.1 Fall staging in Saskatchewan

Staging periods of four birds at Devil's Lake and four other birds at Buffer Lake in Saskatchewan in fall 1981 were 24 and 30 days, respectively. The same fall, F 2/81 spent 18 days in Saskatchewan until the death of the chick, as a result of collision with a power line (Kuyt 1982). Family 7/81 spent 11 days near Luseland, Saskatchewan, in fall 1981.

Staging periods of families are generally shorter than those of subadult birds, which arrive on the staging area earlier and depart earlier. Most Whooping Cranes on fall migration will spend two to three weeks on the staging area, a pair or family sometimes occupying only a half-section (Kuyt 1982). Dates of occupancy of fall staging areas by various groups of birds are shown in Table 10.

During surveys of cranes in Saskatchewan, particularly in fall, we often located Whooping Cranes other than those equipped with radio transmitters. Whether in pairs, families, or flocks of up to four birds, most kept to themselves; on several occasions, however, birds joined to form flocks of up to 10. Most of these were colour-banded subadults. I have also observed the same birds staging on the same wetland in successive years, which suggests that, in addition to having breeding and winter territories, Whooping Cranes may also have staging territories to which they traditionally return (Kuyt 1984b). The Lobstick family (F 10/82), which has been seen on or near a small lake near Radisson, Saskatchewan (Fig. 5), during most years since 1982 (spring and fall), best exemplifies staging territoriality (B. Johns, pers. commun.).

The staging area also contains the last recorded (1922) Saskatchewan breeding site in the Kiyiu Lake area southwest of the village of Plenty (Bradshaw 1956; Fig. 5), as well as other historical nest sites (Allen 1952).

Staging periods of seven families averaged at least 13 days, whereas two pairs and a flock of four subadults staged for an average of 25 days (Table 10).

3.2.6.2 Fall stopovers

Fall stopovers, excluding the major staging period referred to in Section 3.2.6.1, are infrequent and probably result from unfavourable flying weather. In 1981, F 2/81 remained grounded northeast of Fort McMurray (Fig. 3) from 18 to 23 September because of dense smoke from forest fires in WBNP (Kuyt 1982). Similarly, F 7/81 remained on the ground in the Birch Mountains northwest of Fort McMurray from 5 to 7 October 1981 as a result of unfavourable weather, including adverse winds (Goossen 1982).

After leaving the fall staging area in Saskatchewan, cranes migrate rapidly. Southward migration through the United States averaged 10.6 days for seven families and 9.7 days for three groupings of subadults (Table 10). There is considerable evidence that F 19/83 travelled from Saskatchewan to the Texas coast in only four days, a journey that involved nocturnal flight assisted by strong tail winds (Goossen 1987b).

From 27 to 31 October 1981, unfavourable southerly winds kept F 2/81 at Byers Lake, Texas (Fig. 8). Early termination of daily flights and stops were also recorded in 1981 (Larned, Kansas), 1982 (Beulah, North Dakota, and O'Neill, Nebraska), and 1983 (Pierre, South Dakota). Stops were always brief, and flights resumed when the weather improved.

The longest fall stopover was recorded by Young (1984), when Y 2/82 and Y 10/82 remained in the vicinity of Great Salt Plains Lake, Oklahoma (Fig. 7), from 13 to 22 October 1983, a period characterized by southerly winds, a low ceiling, and heavy rain. Whooping Crane family F 24/83 (with unbanded chick) and several thousand Sandhill Cranes were also seen in the same area. The cranes resumed their migration when rain ceased and winds again became northerly.

3.2.6.3 Spring stopovers

Although spring stopovers, like fall stopovers, appeared to be largely caused by weather, the limited data indicate that unfavourable weather was not always a sufficient reason to keep birds on the ground.

On 11 April 1983, F 2/82 was forced down near Hoxie, Kansas, by a severe lightning storm accompanied by hail, snow, rain, and gusty winds (Fig. 11). Unfavourable conditions continued for the next two days; on 14 April, under still-unsuitable weather conditions, the cranes resumed migration and took over five hours to fly only 85 km. On 12 and 13 April, "dancing" behaviour was noted for the first time during this spring. The dancing may have indicated changing hormonal levels in the adults associated with the impending breeding season, which stimulated them to resume migration even though weather conditions were below optimum. The adults in that family traditionally nest early.

Family F 2/82 reached the Callaway, Nebraska, area on 15 April 1983 (Fig. 12), progressing at only 21.8 km/h while flying under marginal weather conditions. For the next two days, the birds foraged intensively in cornfields as

Table 9
Duration and length of migration flights

Season	Total distance WBNP to ANWR (km)	No. of normal flying days	Mean daily flight: Distance (km)	Mean daily flight: Duration (Hrs:Min)	Mean ground speed	Remarks	Source
Fall							
1981	3957	9[a]	319[a]	6:42[a]	45.5[a]	–	Kuyt 1982
1981	–	1	306	–	35.0	Data for northern Alberta only	Goossen 1982
1982	3970	13	341	6:31	55.1	–	Kuyt 1984a
1982	–	7	402	6:35	17.1–91.8	Partial data for F6/82 only	Goossen 1987a
1983	–	5[a]	349[a,b]	6:24[a,b]	54.5[a,b]	–	Goossen 1987b
1983	3923	10	389	7:39	50.7	Flights made by two yearlings	Young 1984
Mean	3950		357	6:46	52.7		
Spring							
1983	3931	8	464	8:02	57.9	Maximum speed 104 km/h	Kuyt 1986a
1983	–	5	538	8:55	60.5	ANWR to central Saskatchewan only	Labuda 1983
1984	4042	5	560	9:43	57.6	Maximum speed 98.7 km/h	Kuyt 1986b
1984	4224	10	375	7:12	51.9	Subadults	Goossen 1987c
Mean	4066		463	8:28	54.7		
Overall mean	4008		397	7:31	52.9		

[a] Data pertain to flights from central Saskatchewan to ANWR.
[b] Median values used.

Table 10
Departures, arrivals, and stopover periods of Whooping Cranes migrating in fall, 1981–83

Identification of birds	Date of departure from WBNP	Date of arrival in Sask.	Date of departure from Sask.	Staging period (d)	Arrival date ANWR	Length of migration Sask. to ANWR (d)	Total migration period (d)	Remarks
F 7/81	4 Oct. 1981	10 Oct.	20 Oct.	10	1–3 Nov.	13–15	28–30	Weather delay S of WBNP, 5–8 Oct.
F 2/81	17 Sept. 1981	25 Sept.	–	>18	–	–	–	Weather delay N of Alberta, 18–25 Sept.
F 3/81	16 Oct. 1981	18 Oct.	After 19 Oct.	?	7 Nov.	≤18	23	
F 10/82	8 Oct. 1982	11 Oct.	27 Oct.	16	4 Nov.	8	27	Weather delay N of Alberta; reverse migration Saskatchewan
Y 3/81 and five-year-old	15 Sept. 1981	16 Sept.	16 Sept.	36	<3 Nov.	≤8	47–50	Y 3/81 staged North Dakota 18 Sept.–27 Oct.
Y 7/81 and three others	15 Sept. 1981	16 Sept.	11 Oct.	24	–	≥7	≥33	Y 7/81 found dead Waco, Texas, 16 Oct. 1982
F 1/82	13 Oct. 1982	15 Oct.	27 Oct.	12	11–12 Nov.	16–17	29–30	–
F 2/82	18 Oct. 1982[a]	20 Oct.	27 Oct.	7	2–3 Nov.	7–8	16–17[a]	–
F 6/82	20 Oct. 1982[a]	21 Oct.	28 Oct.	7	3 Nov.	7	15[a]	–
F 19/83	16 Oct. 1983[a]	17 Oct.	7 Nov.	21	10 Nov.	4	25[a]	–
Y 2/82, Y 10/82	24 Sept. 1983	26 Sept.	11 Oct.	15	25 Oct.	14	31	–
F 7/82	16 Oct. 1983[b]	–	–	–	8–12 Nov.	–	25	10 Nov. est. arrival date at ANWR
F 15/83	16 Oct. 1983[b]	–	–	–	8–12 Nov.	–	25	10 Nov. est. arrival date at ANWR
F 20/83	16 Oct. 1983[b]	–	–	–	7 Nov.	–	22	–
F 9/83	18 Oct. 1983 or later	–	–	–	27 Nov.	–	<38	F 9/83 departed WBNP after 18 Oct. (Kuyt 1984b)

[a] Estimate based on Saskatchewan sightings (Kuyt 1984a, 1984b).
[b] Estimate (Kuyt 1984b).

though to replenish energy resources lost during the tiring flights of the previous two days.

From 19 April to 8 May 1984, subadults 2/82 and 10/82 remained in the North Platte, Nebraska, area (Fig. 12), forced down by rainy, windy weather. Even though there were at least five days during that period when weather was suitable for migration (Goossen 1987c), the two cranes stayed on the ground. Flight behaviour of these subadults during the last week of their spring migration (Fig. 16) showed course deviations unlike those of migrating adult cranes, again suggesting the different roles that age and physiology may play in the migratory behaviour (including duration of stopovers) of adult and subadult cranes.

On 18 April 1984, F 19/83, accompanied by an unbanded Whooping Crane, landed northwest of Redberry Lake after a 647-km migration day (Fig. 14). The following morning, the cranes resumed their migration as expected but made several unusual course changes and landed near Spruce Lake (Fig. 14) after having flown only 144 km. Gusty northwesterly winds from 22 to 25 April probably kept the Whooping Cranes on the ground, although several small flocks of Sandhill Cranes were observed nearby in northward flight.

On 26 April, the four Whooping Cranes, watched by the ground crew, took flight. When the tracking aircraft arrived, only the radio-carrying yearling was located. The following day, the yearling flew in an apparently aimless fashion, finally ending up northeast of Redberry Lake. The bird is believed to have left the area on 9 or 10 May (B. Johns, pers. commun.). The stopover may have been weather-induced (for the adults), but it is clear that the migratory urge and orientation of the yearling differed from those of the older birds.

On 20 April 1983, F 10/82 and F 2/82 took off from the Williston, North Dakota, area at about 09:40 in favourable weather (Fig. 13), and the trackers expected excellent progress. Shortly after crossing the Canada–United States border, F 10/82 unexpectedly landed at mid-day near Minton (Fig. 14), where the birds remained until 30 April, even though several favourable flight days had passed. The ground crew also located radio-equipped subadult 3/81 14 km southeast of F 10/82, but that bird departed early on 27 April. In contrast, F 2/82 continued its migration and landed near Rosetown (Fig. 14) after a normal migration day, covering almost 500 km at 72 km/h (Kuyt 1986a). Why F 10/82 (and subadult 3/81) interrupted their migration and F 2/82 continued is not clear. The adults in F 10/82 had been a breeding pair only since 1982 (the male hatched in 1978) and were much younger than the adults in F 2/82, which have nested in the Sass area for many years. It should be remembered that F 10/82 also made the reverse migration the previous fall.

Three of the families tracked in spring averaged 11.3 days in crossing the United States (Table 11), a period similar to that of the fall migration. Subadults took eight and 34 days to cross the United States, the latter figure due to the long weather delays in Kansas and Nebraska. Again, older and more experienced cranes appear to exhibit a greater urgency to reach the breeding range than younger cranes.

Spring staging, comparable with that in fall, does not occur. Family 2/82 and two two-year-old birds did not linger at all in Saskatchewan en route to the summer range (the family contains a traditionally early-nesting pair, and the subadults had already experienced long delays in the United States). On several occasions, separation between adults and their young of the previous year has been witnessed in central Saskatchewan (Bard 1956). Whenever this separation occurs, some migration delays for the yearling can be expected. Yearling 19/83 separated from its parents on 26 April, and the young bird did not resume its flight north until 9–10 May.

Accurate information on the duration of the flight from Saskatchewan to WBNP by family groups is available for F 2/82 only, and that family took two days to make the flight, which was similar to the fall journey over the same segment. Families 10/82 and 19/83 took a maximum of seven or eight days, but they were not observed in WBNP until early May; consequently, they could have completed the journey in two days. Two two-year-old birds flew from central Saskatchewan to WBNP in eight days, but their flight was not direct (Goossen 1987c). The final portion of Y 19/83's migration is of interest, because it took this bird less than seven days (Table 11) to fly from Saskatchewan to WBNP over a section it had covered only once before (the previous fall, guided by its parents).

The minimum recorded duration of the spring migration is 14 days for fast-moving F 2/82 (Table 11), a figure comparable with several fall flights (Table 10), including that of 16–17 days for the same family.

3.2.6.4 Duration of migration

The average fall migration of 10 families lasted 23.5 days. Three fall migrations involving one or two subadults averaged 37 days.

Although the average spring migration for four families was a maximum of 24.3 days (Table 11), this migration can be made in much less time: in 1980 and 1982, I documented spring migrations of 10–17 days. Two subadults completed spring migration in 43 days, and two other immature birds (a yearling and a two-year-old) took less than 41 days to complete the spring flight.

Whereas most birds covered the northern leg of their journey between WBNP and the Saskatchewan grain belt in two days (fall or spring), the subadults took longer in spring. Similarly, the fall passage across the United States by family groups was completed in only 10–11 days, whereas subadults in spring took considerably longer to fly from ANWR to Saskatchewan.

A comparison of the three distinct portions of the fall migration (flight between WBNP and Saskatchewan, staging, and flight between Saskatchewan and ANWR) with the spring migration shows that the flights are similar in duration for all fall migrants (adults and subadults) and for families in spring. The difference in duration between the entire fall and spring migrations can be attributed solely to the periods spent by Whooping Cranes on the Saskatchewan fall staging area. This observation underlines the great importance of that area to Whooping Cranes.

3.2.7 Flight behaviour

3.2.7.1 Methods of flight

Several factors (weather, proficiency of radio-tracker, habitat, aircraft fuel requirements) determined the length of time that migrating Whooping Cranes were observed by air crews. I saw F 10/82 for almost 50% of the distance the birds flew in fall from Saskatchewan to ANWR; comparable figures for spring tracking were 49% (F 2/82) in 1983 (Kuyt 1986a) and 44% (F 19/83) in 1984 (Kuyt 1986b).

Table 11
Departures, arrivals, and stopover periods of Whooping Cranes migrating in spring, 1983–84

Identification of birds	Date of departure from ANWR	Date of arrival in Sask.	Date of departure from Sask.	Staging period (d)	Date of arrival in WBNP	Length of migration ANWR to Sask.	Total migration period (d)	Remarks
F 11/82	17–18 Apr. 1983	<14 May	-	-	-	<27	-	Unbanded yearling found dead, Saskatchewan, 14 May 1983
F 2/82	9 Apr. 1983	20 Apr.	21 Apr.	0	22 Apr.	12	14	Traditionally early-nesting pair
F 10/82	11 Apr. 1983	20 Apr.	30 Apr.	10	≤8 May[a]	10	27	Young breeding pair
Two-year-old 3/81	18 Apr. 1983	25 Apr.	27 Apr. (?)	2 (?)	<28 May	8	<40	Bird first found WBNP, 28 May
F 19/83	6 Apr. 1984	18 Apr.	26 Apr.	8	≤4 May	12	<28	Weather delay, Saskatchewan; young breeders
F 9/83	6 Apr. 1984	-	-	-	≤4 May	-	<28	-
Two-year-olds 2/82, 10/82	9 Apr. 1984	13 May	14 May	0	22 May	34	43	Delays near Pratt, Kansas (12–17 Apr.) and North Platte, (19 Apr.–8 May)
Y 19/83	6 Apr. 1984	18 Apr.	9–10 May	21	≤17 May	12	<41	Y 19/83 separated from parents 26 Apr.

[a] Estimate based on nest initiation (Kuyt 1986a).

During the first year of radio-tracking, it became abundantly clear that the most common type of migration was by means of sustained, high-altitude flights that combined thermal spiralling and downwind gliding. The glide phase resulted in a gradual loss of altitude until the cranes encountered a new thermal updraft, resulting in the next series of spirals, followed again by gliding flight. This pattern was most common during periods of favourable weather and probably required relatively little expenditure of energy. This seemingly effortless method of flight resembles that of a sailplane.

Pennycuick et al. (1979) described the same method of flight for the Common Crane *Grus grus* but stated that powered flight (i.e., not spiralling and gliding) was the primary mode of migration.

Young (1984) observed two subadult Whooping Cranes during fall migration spiralling 47%, gliding 41%, flap-flying 9%, and flapping-enhanced gliding 3% of the time.

Spiral climbing was accomplished by the birds turning with extended wings into a thermal updraft, gaining altitude, turning again and gaining ground speed, then turning once more to gain altitude. From the aircraft above, I viewed the spiralling and gliding movements as a series of overlapping circles and partial ellipses separated by straight lines (glides).

The frequency of alternation between spiralling and gliding and the length of glides, numbers of spirals, height of spiralling column, slope of glide path, elevation at which spiralling was resumed, and other factors of flight could not be determined in most instances. Nevertheless, during the last segment of the 1983 spring tracking, I was able to obtain detailed information on these particular aspects of the cranes' migration.

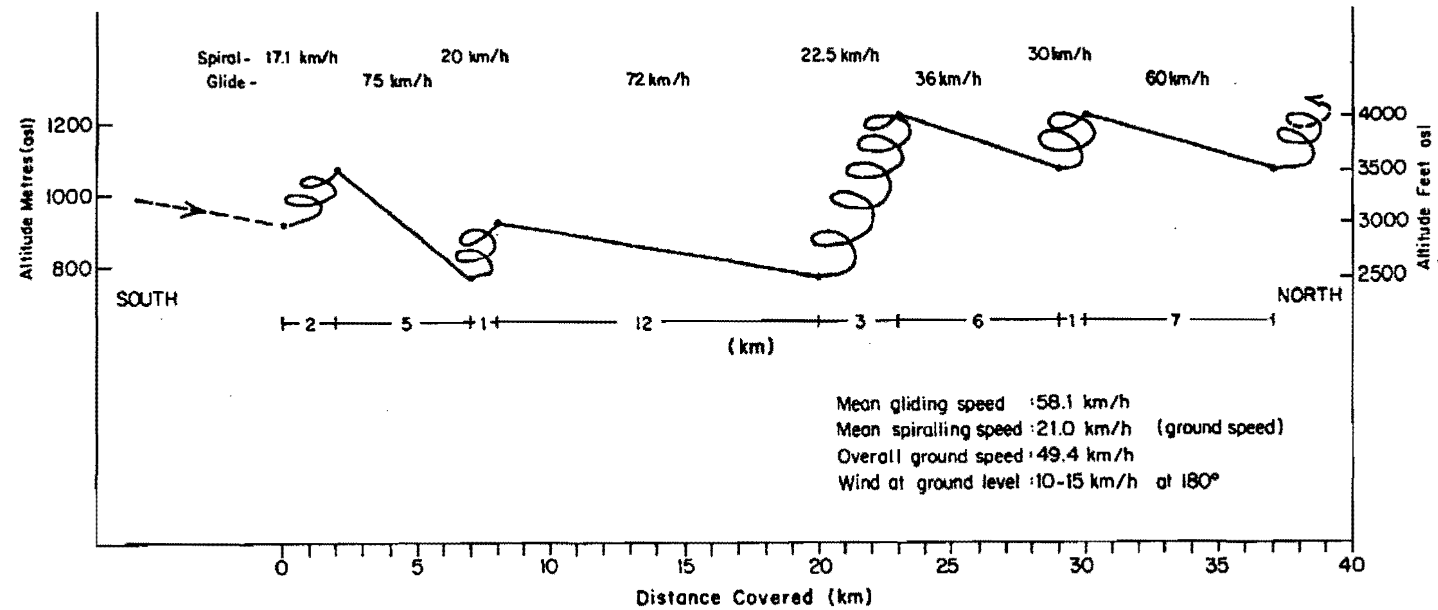
From Merryweather Lake in WBNP (Fig. 16) to the Northwest Territories–Alberta border, there is an almost continuous series of small lakes and other reference points that enabled me to locate the position of the northward-migrating cranes accurately. At 16:48 on 22 April 1983, F 2/82 was flying due north at 80 km/h at an elevation of 900 m asl about 25 km northeast of Merryweather Lake. During the next seven minutes (16:48–16:55), the cranes circled, gaining only 2 km in forward direction, aided by a light tail wind. A 5-km glide at 75 km/h then followed, which lasted four minutes (16:55–16:59), followed by a brief spiralling session (16:59–17:02), which lifted the birds to 900 m asl and resulted in a gain of about 1 km in forward direction (Fig. 18). By 17:12, the birds had crossed the Little Buffalo River and began spiralling again. Their 10-minute glide (17:02–17:12) had covered 12 km at 72 km/h. The birds then spiralled for eight minutes (17:12–17:20) to 1200 m asl and gained 3 km in forward direction. A 6-km glide (17:20–17:30) at 36 km/h was followed by a brief spiralling session (17:30–17:32) over the next 1 km, which took the birds back up to 1200 m asl, where they began a 7-km glide (17:32–17:39) at 60 km/h.

The irregularity of alternation between spirals and glides seemed to indicate that the cranes were opportunistic in utilizing thermals. Thermals were probably spaced unequally and of unequal lifting force, as the birds did not glide set distances separated by equal periods of spiralling.

One of the advantages of the spiralling behaviour of migrating cranes is that the birds have the opportunity to test for favourable air currents or wind direction. On 5 April 1984, F 9/83 left ANWR at about 10:00, and our tracking aircraft caught up to the birds 30 km north of ANWR. As we circled the spiralling cranes at 820 m agl, we noted that winds at this elevation were northerly, unlike the easterly surface winds. The cranes were flying at only 10 km/h, and they soon turned abruptly and flew back to ANWR. The following day, with southeasterly winds aloft, the cranes resumed their migration in earnest. Although cranes occasionally will migrate into head winds, the birds were perhaps reluctant to start their journey under less than optimum conditions.

The number of consecutive spirals made by migrating cranes ranged from two to 12 but most often were between four and six. I observed F 10/82 during about half of a 11:15–13:15 period of "good-weather" flying near Beulah, North Dakota (Fig. 6). In that time, the cranes spiralled for 32 minutes (total of 56 clockwise spirals) and glided for 32 minutes. Spiralling "bouts" consisted of 2–10 spirals and averaged 5.1. Thermal activity was probably not at optimum levels, because recent rains in the area had flooded fields (Kuyt 1984a). During a one-hour period in

Figure 18
Alternate gliding and spiralling by F 2/82 between Merryweather Lake and Northwest Territories-Alberta border, 22 April 1983



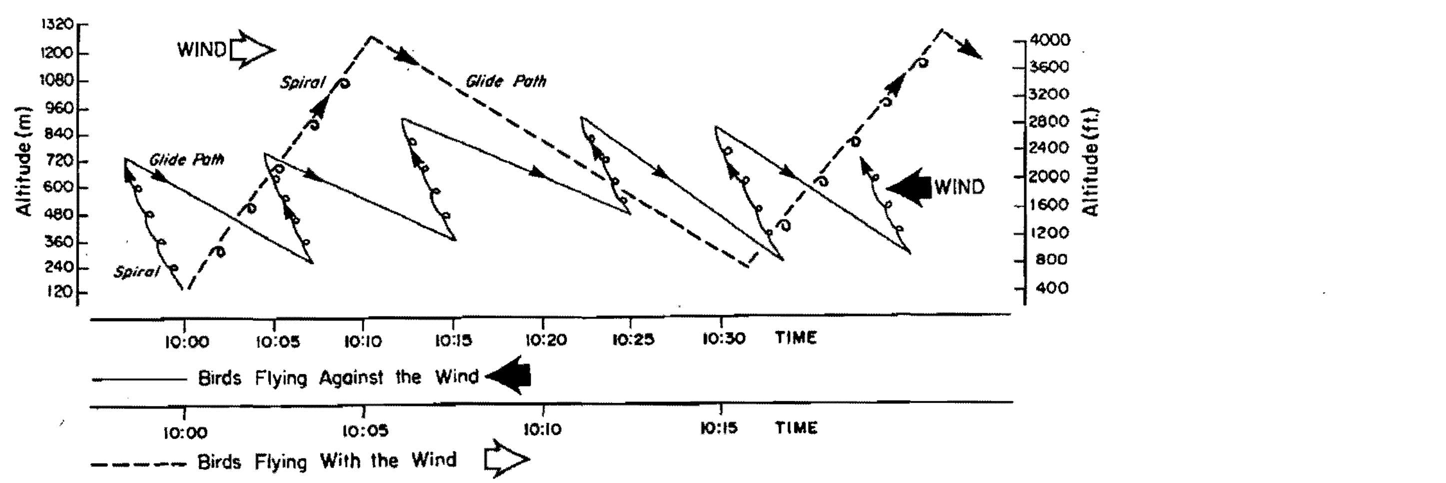
fall 1981, F 7/81 spiralled 13 times (1–12 spirals per climb, mean number of spirals 5.0) in 26 minutes (Kuyt 1982). The rest of the hour was made up of 13 gliding periods totalling 39 minutes. Later that day, with improved thermal conditions and strengthening tail winds, the cranes increased the mean number of spirals to 5.4 per climbing period and lengthened glide periods from 3 to 4.4 minutes. The largest number of consecutive spirals was recorded during the warmest part of the day, when spiralling activity was most intense. Relatively few spirals were noted during tail-wind-assisted flight at medium to high altitudes. A few spirals were all that were required to keep the birds at the desired altitude in a layer of air with favourable flow.

The amount of lift produced by spirals possibly depended on the intensity of thermal uplifts. Goossen (1987c) recorded a rate of climb of 87 m/min during 1984 spring tracking. On 16 April 1984, the flock of seven Whooping Cranes I was tracking began spiralling at 13:15, 20 km southwest of Norton, Kansas (Fig. 12). The birds began a series of seven clockwise spirals, which in two minutes took the cranes to 1500 m asl (730 m agl). The cranes had gained 600–670 vertical metres in two minutes (90 m per spiral) and easily outclimbed our aircraft, which climbed at an estimated 150 m/min (Kuyt 1986b).

The longest daily migration flights of Whooping Cranes occurred on days with good thermal activity and favourable winds. During those days, spiralling cranes gained not only altitude but also forward distance as a result of tail winds. Whooping Cranes will spiral into head winds, but there is also a prerequisite of satisfactory thermal updrafts. Under these conditions, spiralling cranes will be blown back along their route, the glide path between spiralling events is steeper than during tail-wind-assisted migration, and the entire migration is much slower than those assisted by a tail wind (Fig. 19). It nevertheless allows cranes to migrate under less than optimum conditions with less expenditure of energy than flap-flying into the wind.

During head winds and with a crane flock made up of several elements, migration is much more varied and

Figure 19
Schematic pattern of spiralling and gliding by migrating Whooping Cranes as influenced by head or tail winds



laboured than the high-speed movement of a single family flying under optimum migration conditions. On 16 April 1984, a flock of seven cranes (F 19/83 and two pairs) flying into a head wind was blown back almost 2.5 km during a spiralling session. At 13:27, the cranes had completed their northward glide and were less than 300 m agl. During the next five minutes (13:29–13:34), I observed the following manoeuvres: at 13:29, the birds were flap-flying low in V-formation; at 13:30, the cranes made two clockwise spirals, then proceeded by flap-flying; at 13:32, the birds made four counterclockwise spirals, followed by flap-flying; at 13:33, the flock, in three elements, carried out six clockwise spirals with the family leading, the spiralling followed by gliding and flapping, during which the two pairs joined and caught up to the family to form a V-formation. During these five minutes of frantic activity, the Whooping Crane flock gained a meagre 3 km. This method of progress was maintained for much of the day, with both clockwise and counterclockwise spirals observed, sometimes in the same thermal (Kuyt 1986b).

During the tracking work, we observed clockwise and counterclockwise spirals; naturally, curiosity was aroused about the two different directions of spiralling. Goossen (1987a) determined that counterclockwise spiralling by F 2/82, F 10/82, and F 6/82 during separate migrations was significantly more common than spiralling in the opposite direction, but highly imbalanced sample sizes may have made the relationship applicable to only one of the three families and hence subject to individual preference. The following year, Goossen (1987b) found that 84% of F 19/83's circling was clockwise, again a significant difference being indicated. In 1984, Goossen (1987c) found that 109 of 192 observations of two two-year-old cranes indicated mainly counterclockwise spiralling, although the difference was not statistically significant. There was no indication that favourable or unfavourable winds influenced the direction of spiralling. Much larger sample sizes are needed to pursue the analysis of this aspect of migration behaviour.

Flapping flight was also observed frequently but generally at lower altitudes than the flights generated by thermal activity. Young (1984) estimated that 75% of flapping flight occurred between 30 and 150 m agl, and altitudes recorded during flapping flight ranged from 15 to 300 m and averaged 100 m. Particularly in the morning before complete development of thermals, spiralling birds occasionally used wing flapping. Flapping flight was most frequently used by low-flying birds in the morning, during unfavourable weather, or late in the day, when updrafts had ceased and birds began to search for a night roost. Flapping flight enables the birds to maintain a relatively constant distance above ground, but, because it consumes energy, cranes normally do not keep it up for long. Young (1984) recorded 33% flapping within 76 minutes of take-off and 67% within 66 minutes of landing.

I observed shallow or intermittent wing flapping during low-, medium-, and occasionally high-altitude gliding with a strong tail wind. The frequency of wing flapping appears to decline with increasing altitude, and the occasional flaps by birds at high altitudes may have been used only to maintain altitude or an individual's position in the formation. In these situations, cranes sometimes flew in single file, with occasional wing flapping and pushed by strong tail winds. It was this wind-assisted high-altitude flight that was the most rapid of all.

Young (1984) referred to this relatively rare type of flight as flapping-enhanced gliding and records 83% of this behaviour as occurring within 63 minutes of take-off (17%) or within 46 minutes of landing (66%). This type of flight occurred from 90 to 380 m at an average altitude of 196 m agl.

3.2.7.2 Flight altitude

Because of existing variables (effect of weather, individual or age preference, time of day, extent and intensity of thermal activity), it is not realistic to designate an average migration altitude. Labuda (1983) recorded 600 m agl as the approximate average altitude, but it is not clear how that figure was obtained. Young (1984) reported that the Whooping Cranes he tracked flew between 15 m and a maximum altitude of 1100 m agl. Among 64 estimated altitudes of subadult cranes radio-tracked in 1984 (Goossen 1987c), 34% were under 510 m agl, in contrast to 1982 and 1983, when 68% of flight altitudes were below 510 m agl. However, I found that family groups migrated at a lower altitude in 1984 than in 1983 (Kuyt 1986b).

Sandhill Cranes migrating through the Central Flyway flew at between 60 and 1600 m agl, and nearly 75% of the flights were between 150 and 760 m agl (Melvin and Temple 1980). The highest elevation of migrating Sandhill Cranes (accompanied by a juvenile foster-parent-raised Whooping Crane) was recorded by Drewien and Bizeau (1981) when the birds crossed Cochetopa Pass (elev. 3093 m asl) in northwestern Colorado, at an altitude of 3630 m asl, or about 530 m agl. Migration altitudes of other bird species are summarized by Van Tyne and Berger (1959). Whooping Cranes of the WBNP–ANWR population are capable of flying at great height; although they do not encounter mountain ranges as do Sandhill Cranes in Colorado, they migrate at much greater height above ground. On 22 October 1981, F 7/81 made a 9.5-hour nonstop migration of 742 km from northeastern Montana to Valentine, Nebraska (Table 12). Much of the flight was in the form of high-altitude spiralling and gliding, assisted by a strong tail wind. At 14:53, I located the three birds flying at 1700 m asl near Bowman, North Dakota (Fig. 6). For the next 45 minutes, visual contact was maintained with the birds as they climbed as high as 2750 m asl (1950 m agl). At 15:35, when flying over western South Dakota, we lost the birds from view; for the next 2.5 hours, we followed the radio signal without getting a glimpse of the high-flying birds (Kuyt 1982).

The next day, the same family was observed flying at 1800 m asl (1000 m agl) near Oconto, Nebraska (Fig. 7). Other high-altitude observations (1800 m agl) were recorded by Goossen (1987c) during spring tracking of two subadults in 1984; by Kuyt (1984a) over Saskatoon (2000 m asl, or 1500 m agl) during fall tracking; by Labuda (1983) during spring tracking of F 10/82 in Kansas (1800 m agl) and over central Saskatchewan (1800 m agl); and by Kuyt (1986a) over the Cold Lake Air Weapons Range (2400 m asl, or 1800 m agl) and over Valentine (1400 m agl). All these remarkable altitudes were observed in the afternoon when thermal activity was strongest.

Goossen (1987a) found that 68% of 57 estimated altitudes of F 6/82 were under 500 m. A linear regression equation for the relationship between flight altitude and time of day showed that only 28% of the variance was explained by this relationship. No doubt the variation in flight altitudes (because of factors alluded to above) is responsible for this weak relationship.

3.2.7.3 Duration and length of daily flights, and flight speed

Lengths of daily flights varied widely and were, no doubt, related to weather conditions and perhaps to age of birds. Days considered to be unaffected by weather disturbances are referred to as normal flying days. The mean daily flight distance (and duration) and ground speed during normal flying days were 397 km (7.5 hours) and 52.9 km/h (Table 9). Spring migration flights were generally longer in distance and time than fall flights. The mean ground speeds during the two migrations were quite similar. It is likely that the greater period of daylight (Whooping Cranes almost exclusively migrate during daylight hours) in spring allowed the cranes to cover greater daily distances than in fall. To what degree changes in reproductive condition of Whooping Cranes affect spring migration is not known, but gonadal development and increasing length of daylight are correlated (Van Tyne and Berger 1959).

Whooping Cranes are capable of sustained nonstop migration, and examples of the longest nonstop migration flights are summarized in Table 12. Wind-assisted ground speeds of over 100 km/h were recorded by all four aerial trackers. The record speed of 107.5 km/h was timed during a 10-minute period in southern Saskatchewan, when the passage of a front created strong, gusty northerly winds (Young 1984).

On 9 November 1983, Goossen (1987b) tracked a flock of six Whooping Cranes (F 19/83 and three additional birds) to the area 51 km south–southwest of Enid, Oklahoma (Fig. 7). Surveillance of the rapidly southward-migrating cranes was terminated at 17:22 because of fatigue of the flight crew. The following morning, radio signals could not be picked up in the area of previous contact, and the air crew continued southward in the expectation of relocating the birds.

It was not until the aircraft began to descend into Rockport, Texas (Fig. 9), that the signal was detected. An hour later, the six cranes were observed flying at 30 m altitude about 93 km northeast of ANWR. The birds followed the north shore of Matagorda Bay and, facing into head winds, slowly approached ANWR, where they landed at 16:35.

Goossen travelled across Texas at about 2100 m asl, and this should have enabled maximum radio signal detection distances if the birds had been flying in the morning of 10 November. Goossen hypothesized that the six cranes made an 830-km nonstop journey from the Enid area to the east side of Matagorda Bay, where they landed at 01:12 on 10 November.

It is possible that the eastward deviation of the cranes' flight over Texas was due to the northwesterly wind and a decrease or loss of visual orientation when the birds continued to fly after sunset. From radar studies along the southern coast of the Baltic Sea, Alerstam (1975) found that variation of track directions of Common Cranes flying over the sea was due to incomplete compensation for wind drift. No such drift took place over land, and the author concluded that landmarks are important for exact orientation.

During the 1981 radio-tracking, I calculated the migrating cranes' air speed by subtracting from the ground speed (in the case of a tail wind) or adding to the ground speed (in the case of a head wind) that component of the wind in the same direction as the cranes' travel (Allen 1939). A difficulty was that accurate wind direction and strength could not be determined from the aircraft, and I had to depend on information from the nearest Flight Services office. In contrast to ground speed (an indication of the speed with which the cranes moved along a known distance), the air speed should be an indication of the birds' progress in still air (a condition that rarely occurs). Calculated air speeds ranged from 23.4 to 70.4 km/h (Kuyt 1982). The six highest values (46–70.4 km/h) occurred in the same afternoon, high over the western parts of North and South Dakota, when the cranes were in a spiralling and gliding mode, aided considerably by a tail wind. The winds were likely stronger than we estimated, so that air speeds may have been less than calculated. If these six high values are excluded, all but one of the remaining 24 air speed values fall between 25 and 45 km/h. On 23 October 1981, near Valentine, Nebraska, I measured the cranes' speed (spiralling, gliding, and some flapping) under windless conditions over 48 km and found the air speed (equal to ground speed under those conditions) to be 33.5 km/h.

Table 12
Examples of long-distance, nonstop migration flights, 1981–84

Date	Location	Length (km)	Duration (hr:min)	Mean ground speed (km/h)	Maximum ground speed (km/h)	Tail wind (km/h)	Source
22 Oct. 1981	Bredette, Montana to Valentine, Nebraska	742	9:38	77.0	89.2	20–30	Kuyt
28 Oct. 1982	Southern Saskatchewan to South Dakota	550[a]	–	–	101.7	48–56	Goossen
2 Nov. 1982	Northern Nebraska to Fort Cobb Reservoir, Oklahoma	818	10:48	75.7	90.6	24–40	Kuyt
3 Nov. 1982	Fort Cobb Reservoir to Southern Texas	770	9:42	79.4	103.9	35–37	Kuyt
11 Oct. 1983	Southern Saskatchewan to South Dakota	676	8:18	81.4	107.5[b]	"strong"	Young
12 Oct. 1983	South Dakota to central Kansas	779	11:42	66.6	96.0	?	Young
9 Nov. 1983	Pierre, South Dakota to Matagorda Bay, Texas	1809[c]	17:38[c]	–	105.9	37–56	Goossen
11 Apr. 1983	Northern Texas to central Kansas	666	9:52	67.5	104.0	10–40	Kuyt
11 Apr. 1983	ANWR to Wichita Falls, Texas	656	8:45	75.0	105.0	35–50	Labuda
6 Apr. 1984	ANWR to northern Texas	655	9:10	71.5	94.3	16–24	Kuyt
18 Apr. 1984	North Dakota to central Saskatchewan	647	8:00	80.9	98.7	16–30	Kuyt

[a] Estimate.
[b] Times for 10 minutes only.
[c] Hypothetical.

3.2.7.4 Flight formations

Although flight formations are easily observed, it is still unclear why birds fly in formation. Lissaman and Schollenberger (1970) suggested that the V-formation in Canada Geese *Branta canadensis* evolved to minimize the energy costs of flying by recapturing upward-rising components of the wing tip vortexes generated by the wings of nearby birds in the same formation. Gould and Heppner (1974) indicated that the V-formation may have important behavioural components as well. A high degree of visual communication within a group of three or more close-flying and highly manoeuvrable Whooping Cranes would be essential.

Whooping Cranes almost always fly in pairs, as a family, or in small flocks when migrating, so it was relatively easy to describe the usually well-developed regularity in spacing and alignment. Whooping Cranes usually flew in a triangle (V), in a line (echelon), or in modifications of these two formations. The triangular formation (Fig. 20) was the most common configuration of a Whooping Crane family, particularly during soaring and gliding. In almost all situations, one of the adult birds would be in the lead of V- and echelon formations, and the second bird in the V would normally be about 3 m behind the leader, with the third bird on the other side of the V. On many occasions, I noted the juvenile bird was a little closer to a parent than the distance between parents or other cranes in both V- and echelon formations.

A modification of the V-formation was the J-formation or reverse J (Fig. 21a, e), which occurred when a pair of Whooping Cranes joined a family group flying in a triangle. The pair would always be on the same side of the V.

The front-line formation (Fig. 21b), with all birds in a line abreast and at the same altitude, was observed rarely. In all situations, this formation was temporary, leading almost immediately to a V-, echelon, or spiralling formation. Another formation, seen only twice, was the single file (Fig. 21d). The first time it was observed, the formation dissolved almost at once, when the five cranes began a clockwise spiral (Fig. 21c). In both of these transitory formations, the yearling was flying next to one of the adults not its parents—a rare event, because in practically all other circumstances the yearling (or juvenile in fall migrations) would be between its parents when flying in a mixed flock.

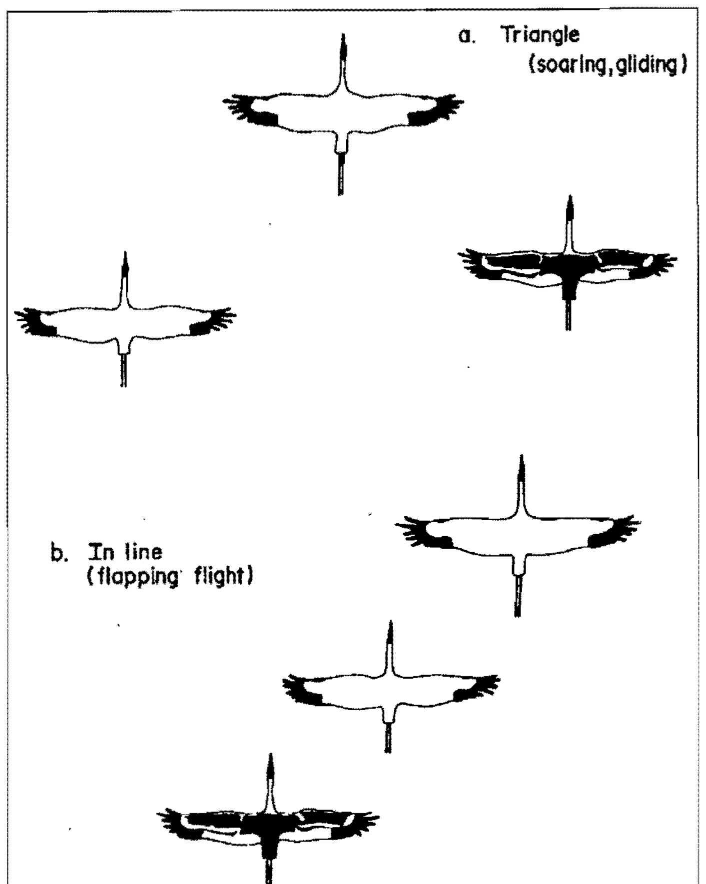
When a family group began spiralling, invariably one of the parents would begin the spiralling activity from the V-formation. In 1981, with the adults in F 7/81 of noticeably different sizes, the larger adult always initiated spiralling. I could not determine if the cranes flew on one level, because spiralling Whooping Cranes are not as tolerant of close-flying aircraft as gliding birds. I suspect that not all (perhaps none) of the three cranes in F 7/81 were at the same level, as sometimes during spiralling the smaller adult and the juvenile would exchange positions by simply "sliding" across the formation without wing flapping or other evasive action. Such movements in a rather confined space would be possible only if the three birds were flying in staggered positions.

During spiralling, whether clockwise or counter clock wise, the juvenile bird was almost always in the rear and on the outside of the spiral, and the three birds would maintain this formation in each spiral (Fig. 22c,d). Rarely did we see cranes "follow the leader" in spiralling (Fig. 21c). After the last spiral had been completed, the lead bird would often yaw slightly several times (as if adjusting its course?) before beginning the glide. Then each bird would shorten its wingspan by drawing the carpal joint closer to the midline of the body. When viewed from the front, the wings of the gliding birds would display a deeply bowed appearance. This wing configuration undoubtedly contributed to the rapid flight of gliding cranes.

Several interesting manoeuvres occurred when Whooping Cranes flew in small flocks made up of multiple elements (Kuyt 1986a). When the flock consisted of seven birds (a family and two pairs), I was able to record the sequence of flock formation upon completion of spiralling. Usually the family would be in the lead, with the two pairs, separated by gaps, following in a loose J-formation (Fig. 21f). Soon the two pairs would close up (Fig. 21g), and sometimes the rearmost pair would shift to the shorter leg of the J- formation (Fig. 21h), resulting in a symmetric V (Fig. 21i). In that situation, the yearling would be flying next to a bird other than its parent. Sometimes the formation remained in the shape of a reverse J (Fig. 21j). Differences were noted later in the 1984 spring migration, when the flock consisted of six birds. Apparently, a pair had left the formation and a new single bird had joined. The "lone" bird, although part of the flock, never assumed a lead position and usually flew some distance from its neighbour, leaving a distinct gap in the formation.

Several of these formations were photographed, from which Figure 22c–i was derived. Only in Figure 22i, as the six cranes flew in echelon flight, did the single adult crane fly next to another bird (adult of F 19/83), but a gap still persisted ahead of the single adult.

Figure 20
Configurations of flying Whooping Crane family



With a relatively narrow migration corridor used by highly conspicuous birds, it was not surprising that encounters occurred between migrating Whooping Cranes. The first of these was recorded south of Valentine National Wildlife Refuge, when two Whooping Cranes briefly joined migrating F 7/81 (Kuyt 1982). Although the five cranes flew as a unit for short distances, when the two units became separated (invariably during spiralling), the two nonfamily members would, by wing flapping, eventually catch up, only to be separated again during the next series of spirals. These two birds did not display a close mutual relationship during flight and even separated from each other during brief periods.

On 31 October 1982, as we approached F 10/82, which had just landed on Swan Lake east of Mobridge (Fig. 6), we observed a pair of Whooping Cranes, hitherto unseen among a large flock of Lesser Snow Geese *Chen caerulescens caerulescens*. When the family landed, the two cranes left the feeding geese and joined F 10/82. We were later advised by a South Dakota State Game Agent that the pair had arrived on Swan Lake the previous day. The five cranes took off the following morning; although they, too, occasionally separated during spiralling, the two groups were much more cohesive than F 7/81 and its companion pair. Family 10/82 and the associated pair remained together at least until about 18:18 on 3 November, when darkness forced us to leave the flying birds just north of ANWR. The following morning, we located F 10/82 in a small pond 24 km north of AWNR; the pair may have continued its flight to the refuge the previous night.

On 15 October 1982, F 1/82 was observed migrating south about 30 km east of Midnight Lake (Fig. 5) in the company of a pair of adult Whooping Cranes (Goossen 1987a). The five cranes landed 20 km south of Saskatoon, where they remained until 27 October, when F 1/82 and a single adult resumed migration. This family was not one of the primary tracking targets, and no further information is available on this group's flight behaviour.

In fall 1982, when tracking Y 7/81 and three older subadults, I found flight formations and behaviour of these four birds to be similar to those of family groups. On 16 September, the four cranes passed directly over our tracking aircraft refuelling in Cold Lake, Alberta. The birds were only 150 m above us when they began spiralling. I could distinguish the yearling by the radio package on its leg. That bird was last in line and on the outside of the spiral, the same position typically occupied by the juvenile in a family group.

On 18 April 1983, while tracking F 2/82 near Faith, South Dakota (Fig. 12), I noted two Whooping Cranes in steady flapping flight several hundred metres behind F 2/82. The family had been flying with 23 Sandhill Cranes in early evening. At about 18:15, the Sandhill Cranes separated from F 2/82; shortly thereafter, the two Whooping Cranes joined the family. Half an hour later, the five birds deviated to the northwest; the flock then separated into its two components, with F 2/82 briefly reversing its course, then resuming its northwesterly flight and rejoining the pair. At 19:08, the five birds landed on a large lake, where the pair chased the family away. The two groups remained 100 m apart (Kuyt 1986a). The following morning, F 2/82 took off, unaccompanied by the pair; in early evening, however, we again sighted a pair of Whooping Cranes now following 20 km behind the family.

Figure 21
Whooping Crane flight formations of five or seven birds, April 1984

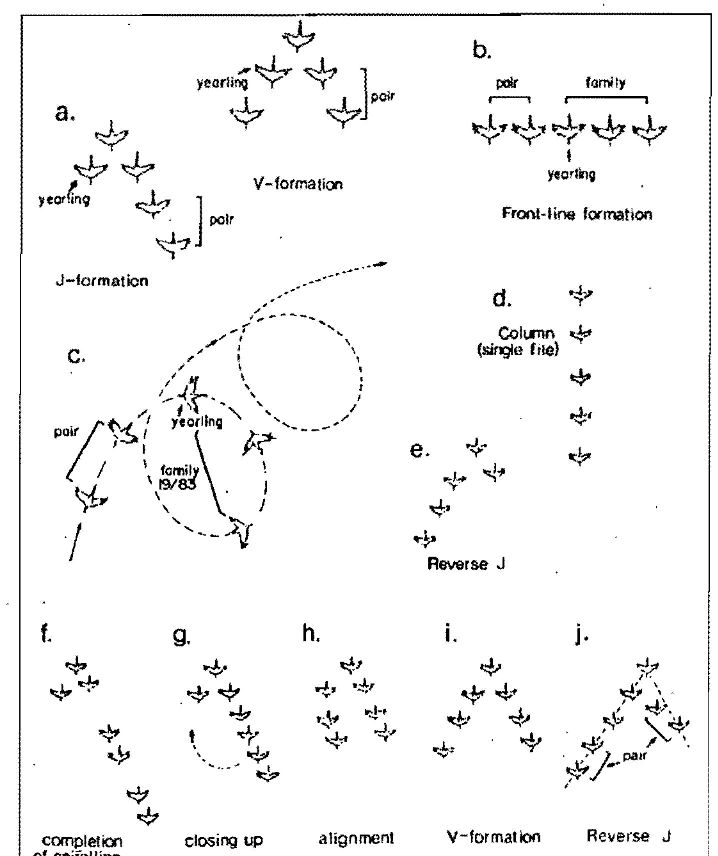
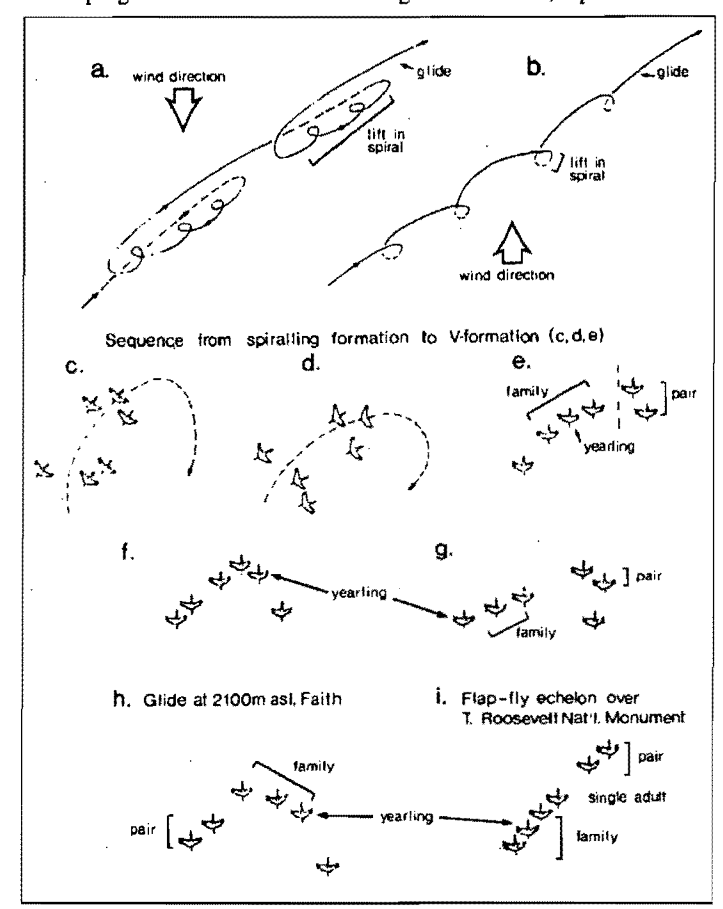


Figure 22
Whooping Crane manoeuvres and flight formations, April 1984



On 6 April 1984, when I tracked F 19/83 with two colour-banded adult Whooping Cranes from ANWR, the five birds did not at first fly in an orderly fashion. This was particularly evident during spiralling, when the two units (family and pair) could be seen flying a few metres apart, with both components describing similar spirals. After completion of spiralling, the flock sometimes formed a J but usually would assume the normal gliding V-formation, with the family forming one leg of the V and the pair on the other side, so that the formation was symmetric (Fig. 21a). As the day progressed, the five cranes improved their formation flying and spiralling manoeuvres and covered 655 km nonstop (Kuyt 1986b), practically crossing Texas on their first migration day.

The five cranes continued flying as a flock on 8 and 9 April (poor weather had prevented the birds from flying far on 7 April). After being grounded by unfavourable weather from 10 to 12 April, near Dighton, Kansas (Fig. 11), the five cranes resumed migration as one flock and, making slow progress against head winds, landed south of Arapahoe, Nebraska (Fig. 12), in early afternoon. Two other Whooping Cranes (radio-equipped crane 3/81 and an unbanded bird) were on the ground 200 m away, and it is likely that these two birds decoyed the five low-flying cranes. Although all seven cranes remained in a small wet meadow, the three component groups fed separately.

On 16 April, the seven cranes took off together. The formation during spiralling was loose, with the three components spiralling almost independently within the same thermal. After completing a series of spirals, the three elements would gradually close ranks and eventually glide in a compact V-formation (Fig. 21f–i). Later in the day, with improved thermal activity, spiralling and formation flying were noticeably improved.

On 17 April, I observed F 19/83 flying with three other birds. The radio-equipped subadult 3/81 and another bird (presumably its mate) had left the flock, and a new single adult had joined. The remaining pair was the same banded pair that initially flew with F 19/83. The three components of the flock were again much in evidence during spiralling; when gliding, gaps showed in the formation, reflecting perhaps individual differences or social organization. The family almost invariably assumed the lead position, with the paired adults in the lead a few times. The single adult was almost always the last bird in the formation (Fig. 22c–h).

3.2.7.5 Interactions of flying Whooping Cranes with other birds or aircraft

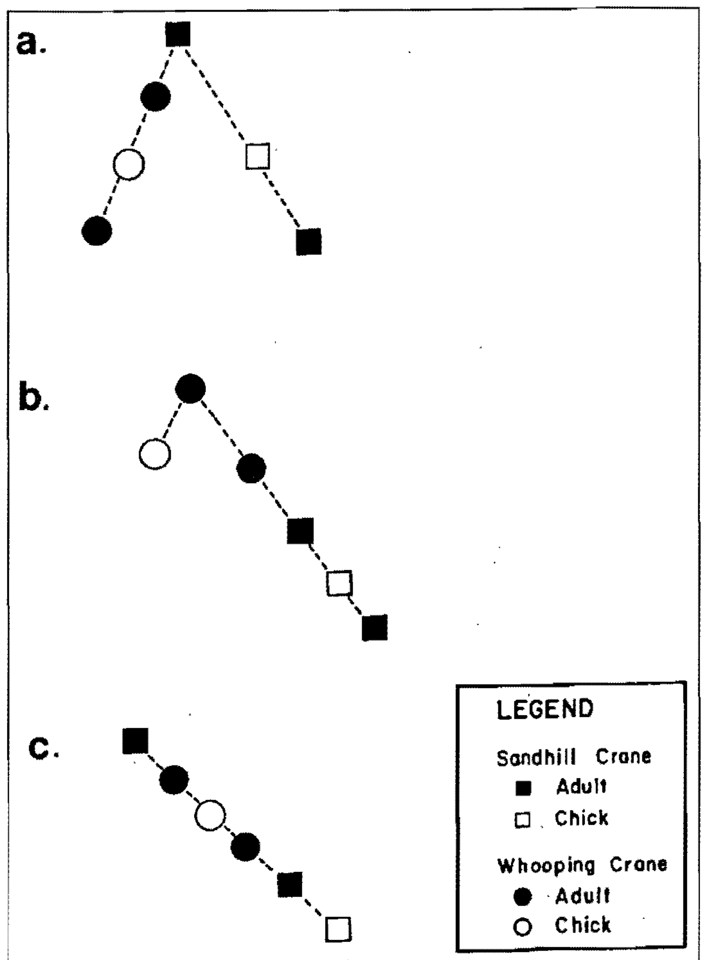
3.2.7.5.1 Sandhill Cranes — Sandhill Cranes shared airspace with Whooping Cranes on numerous occasions and often flew in the same formation. This association frequently occurred in fall from Nebraska to Texas, when migrating flocks of Sandhill Cranes were often encountered. Sandhill Cranes begin migration earlier in the spring than Whooping Cranes, and therefore mixed flocks were rarely seen then.

Flocks of Sandhill Cranes numbering up to 200 birds often used the same thermals as the Whooping Cranes, but both species flying in one formation (with one exception) occurred only when Sandhill Crane flocks contained fewer than about 15 birds. The first observation of the two species uniting in one flock was made on 25 October 1981, when F 7/81 was joined by two grey Sandhill Cranes and a light-brown smaller crane (likely a juvenile) several minutes after the Whooping Cranes had departed from a 30-minute stopover. Individual spiralling of all six birds occurred, followed by flap-flying in a loose flock and flying in echelon. Finally, an unequal V-formation was assumed, with a Sandhill Crane at the apex, the other two Sandhill Cranes on the right leg of the V, and F 7/81 behind the leader on the left side. Sometimes the birds were in a J-shaped flock with F 7/81 leading, or the six cranes flew in echelon (Fig. 23). At no time did the juvenile of either species fly directly ahead of or behind a bird of the other species. Adult birds of both species led the flock at intervals; when the six birds had been flying for 55 minutes, the Whooping Cranes separated. The two families of congeners flew in greater unison than some flocks made up entirely of different groups of Whooping Cranes.

On 26 October 1981, F 7/81 was joined by 17 Sandhill Cranes, and the 20 birds continued to fly as a unit until they entered the Fort Sill Artillery Range near Lawton, Oklahoma (Fig. 8), where military exercises, complete with aircraft traffic and artillery explosions, were under way. Separation of the two species occurred sometime during the birds' passage through the artillery range, because the cranes emerged from the south side of the range in separate flocks.

In fall 1982, F 10/82 was joined by a pair of Whooping Cranes and, later, by Sandhill Cranes. The five white cranes flew in a variety of formations with the Sandhill Cranes. Sometimes all birds (including as many as seven Sandhill Cranes) would be in one flock; then the two Whooping Crane units would become separated (sometimes by as much as 1 km), each with its own group of Sandhill Cranes, before reuniting into one flock. Many different combinations occurred—echelons, V- and J-formations, and loose flocks—but at no time was the juvenile Whooping Crane observed flying directly behind or in front of a bird not its parent.

Figure 23
Configurations of flying Whooping Crane and Sandhill Crane families



On 4 November 1982, F 10/82's last fall migration day, the birds were joined by a single Sandhill Crane and later by five more. The nine birds occupied various positions for about 12 minutes; just before reaching ANWR, the two species separated.

A few times during the last two days of fall migration, we noted the juvenile Whooping Crane occupying the penultimate position in the formation and even, during brief spiralling sessions, the lead position. During the last migration day, when the Whooping Cranes were flying with Sandhill Cranes, I also noted the juvenile flying behind or in front of a Sandhill Crane. Perhaps these new positions indicated that the juvenile Whooping Crane had begun assuming a greater degree of independence.

During the fall migration in 1983, two subadult Whooping Cranes flew with 2–80 Sandhill Cranes in frequently changing formations, sometimes separated by Sandhill Cranes in the same flock and occasionally leading (Young 1984). The same two Whooping Cranes did not associate with Sandhill Cranes on their spring migration in 1984 until they had reached WBNP on 20 May, when they were observed flying with seven Sandhill Cranes for about an hour. The following day, the Whooping Cranes, now alone, resumed their migration (Goossen 1987c).

I do not believe that Whooping Crane families actively sought out the Sandhill Cranes in an attempt to join forces. Rather, the Sandhill Cranes seemed intent in joining their larger congeners, even to the extent of increasing their flap-flying speed to catch up. Migrating subadult Whooping Cranes appeared to compromise their flight behaviour to maintain contact with the Sandhill Crane flock (Young 1984), using flapping flight to regain contact with the Sandhill Cranes. In this situation, subadult Whooping Cranes may have benefitted from flying with more experienced birds.

3.2.7.5.2 Other birds — During our studies, we noted American White Pelican, Black Vulture *Coragyps atratus*, Turkey Vulture, Golden Eagle, Bald Eagle *Haliaeetus leucocephalus*, Red-tailed Hawk *Buteo jamaicensis*, and other birds occasionally near migrating Whooping Cranes. A circling Bald Eagle observed near F 2/82 over Cold Lake, Alberta, obviously caused concern to the cranes, because the spiralling birds kept slipping out of formation when the eagle approached (Kuyt 1986a). Near Lake Diefenbaker (Fig. 14), a Red-tailed Hawk flew through the crane formation, briefly disturbing the spiralling birds.

Young (1984) observed two Black Vultures 50–350 m from two spiralling Whooping Cranes, with all four birds flying in the same direction and utilizing the same thermals. In April 1983, I saw 12 Turkey Vultures soaring over rugged terrain near the Little Missouri River (Fig. 13), using the same air currents as nearby flying F 2/82, a Golden Eagle, and a flock of 50 American White Pelicans. Although all birds appeared to use the same thermals, at no time was there a joining of different species.

3.2.7.5.3 Aircraft — Even though Whooping Cranes are accustomed to a certain amount of aircraft traffic on breeding and winter ranges, there was concern that tracking aircraft would disturb migrating Whooping Cranes. All flight crews approached flying cranes cautiously, particularly during the early phase of the radio-tracking, but it was soon discovered that migrating Whooping Cranes could be approached close enough (an estimated 300 m) for observation without unduly disturbing the birds. None of the flight crews felt that the nearness of the aircraft influenced the birds' flight.

After tracking the cranes visually and returning to the migrating cranes after refuelling, flight crews often found that the cranes were still flying the same course. The aircraft's presence or absence had no obvious influence on the cranes' migration course. After the direction of the migration had been established on normal migration days, that course would generally be maintained throughout the day, with major deviations mainly the result of weather disturbances.

Whooping Cranes in a spiralling mode are less tolerant of nearby aircraft than when gliding or flap-flying with the aircraft at the same distance. An aircraft flying parallel but at a distance from gliding cranes can be seen by the birds almost continuously; when spiralling, however, cranes would have to turn their heads constantly to keep the circling aircraft in view, and at close distances this could disturb them. We generally kept a much greater distance from spiralling birds than from gliding ones.

Aircraft that suddenly appeared had an immediate and gravely disturbing effect on migrating cranes. On 2 November 1982, when we followed five Whooping Cranes (F 10/82 and a pair) spiralling at over 1500 m agl near Pratt, Kansas (Fig. 7), the spiralling flock suddenly separated into its two components, which veered in opposite directions. At the same time, we noted two military jet fighters at low altitude crossing beneath the survey aircraft. It took several minutes before the five birds were reunited.

Similarly, two military jets suddenly passing below our aircraft near Lake Diefenbaker (Fig. 14) on 20 April 1983 obviously disturbed the cranes. The three Whooping Cranes veered away before we noted the jets, and we could not relocate the cranes for 10 minutes.

On a few occasions, survey aircraft accidentally approached the cranes too closely. Labuda (1983) described two incidents in which aircraft and cranes flared in opposite directions after having approached each other as close as 90–180 m.

On 20 October 1981, F 7/81 began to climb into a cloud layer extending to 2100 m asl. Our aircraft remained below the 1200-m asl ceiling because of icing conditions, and we radio-tracked the birds for 43 minutes. Near Swift Current, Saskatchewan, with the aircraft in level flight, the signals rapidly became stronger; four minutes later, as we watched carefully, the three cranes suddenly became visible as they descended from the overcast, a few hundred metres from the aircraft. The birds were in gliding mode and apparently not disturbed by the aircraft. They continued to glide to a landing near Russell Creek Reservoir (Kuyt 1982).

3.2.7.6 Nocturnal migration

Melvin and Temple (1980) quoted several authors who suspected that Sandhill Cranes migrated by night and day. Anderson et al. (1980) and Melvin and Temple (1980) reported Sandhill Cranes landing in Florida and Texas several hours after sunset, but Melvin and Temple (1981) concluded that Sandhill Cranes are primarily diurnal migrants and that nocturnal flights, when they do occur, are made under favourable wind conditions and more likely when cranes approach a predetermined destination.

That was the situation on 9 November 1983, when F 19/83, tracked to the Enid, Oklahoma, area (Fig. 7) and flying at over 100 km/h, apparently continued after sunset, aided by 31–57 km/h tail winds (Goossen 1987b).

Four subadults, including Y 7/81, tracked in fall 1982 to the Last Mountain Lake area (Fig. 5), displayed erratic movements in late afternoon and evening on 11 October 1982 (Kuyt 1984a). The birds continued to fly after sunset, and they could not be located by air or ground crews the following morning. Five days later, Y 7/81 was found dead below a power line 30 km west of Waco, Texas (Fig. 8). Winds were easterly in the afternoon of 11 October but had swung to the west the following day. Both 11 and 12 October were warm and clear, excellent days for migration.

Young (1984), in his study of migrating subadults, reported that 11 of 13 migration flights began in the morning, one began in late afternoon (17:10), and one began just before sunset (18:51). Two of the flights ended after dark: one at 23:02, the other (a 779-km flight) at 21:24. The latter flight covered 128.5 km after dark in an estimated 1.9 hours, flown under favourable wind conditions. Young (1984) estimated that the two subadults travelled 290 km (7% of the distance between WBNP and ANWR) at night.

On 1 November 1982, Goossen tracked F 6/82 to the Beloit area, 160 km south of Grand Island, Nebraska (Fig. 7). At 18:03, it became too dark to see the flying birds, but the signal was followed until 21:00, when the birds were believed to have landed 100 km east of Wichita, Kansas. The cranes had flown 242 km after sunset, aided by a full moon and northerly winds of 9–19 km/h. The rather abrupt southeasterly shift of the cranes' migration (Fig. 7) may have been due to loss of visual orientation during this night flight (Goossen 1987a).

The flock of seven cranes I tracked on 16 April 1984 had begun to use higher airspace in later afternoon, most likely because of better thermals produced by the deeply dissected country between the Kansas border and the Platte River (Fig. 12). After the high-flying cranes had crossed the Platte River, the wind decreased and the birds began to flap-fly. An hour later, the cranes were over the Nebraska Sandhills, southwest of Halsey (Fig. 12); at 19:35, impending darkness forced the air crew to return to North Platte. The terrain being crossed by the cranes in darkness offered few suitable wetlands as roosting sites; from the radio signals, I knew that the cranes continued flying until at least 19:52, when we landed. From the cranes' 17 April early-morning location in extensive wetlands near Swan Lake (Fig. 12) and from their ground speed the previous evening, I calculated that the cranes had flown 69 km after dark, from 19:35 until about 21:25 (Kuyt 1986b).

Just after sunset on 22 October 1981, we noted F 7/81 circling and flying low over the land, apparently searching for a suitable roost. This search may have caused the cranes to extend their flight 6 km (10 minutes) after dark. The birds landed safely near the Valentine National Wildlife Refuge after a 742-km nonstop flight (Table 12). In this situation and the previous one, it is likely that the nocturnal flights were necessitated because of the unavailability of suitable roosts.

On 3 November 1982, with F 10/82 approaching ANWR after a 770-km nonstop flight, we had to leave the flap-flying cranes because of darkness. The cranes flew for about 22 minutes after dark (Kuyt 1984a), but that night they did not succeed in reaching the refuge, still 40 km away. Here it appears that the cranes were attempting to reach a predetermined destination (Melvin and Temple 1981).

3.2.7.7 *Visual recognition of landscape features*

Melvin and Temple (1980), in studying migration ecology of Sandhill Cranes, reported the phenomenon of course changes shortly before the cranes landed.

On 9 April 1983, when F 2/82 approached Thorndale, Texas (Fig. 10), near the end of its first day of spring migration, the birds suddenly veered to the northwest, continued on this course for 10 minutes, then landed. There were no weather conditions to account for this course change. The following day, as we watched F 2/82 approach the town of Byers, Texas, the birds abruptly swung west and, after flying on this course for 6 km, landed in a marshy extension of Byers Lake (Fig. 10). Again, there were no weather conditions to account for the sudden change. During the last half-hour of the cranes' migration that day, the birds had made 10°–30° course shifts on four occasions, most likely searching for a suitable landing site (Kuyt 1986a).

On the evening of 18 April near Prairie City, South Dakota (Fig. 12), the tracked cranes again made a sudden 20° course change to the west, about 45 minutes before landing. The same cranes may have made a course shift on 20 April near Biggar, Saskatchewan (Fig. 14). The following evening, we observed F 2/82 veer 40° west when about 6.5 km from their eventual roost on a shore-fast ice floe north of Fort McMurray, Alberta (Fig. 16).

Labuda (1983), while tracking F 10/82, reported that the birds made a sharp course change 45 minutes before landing at the Quivira National Wildlife Refuge in Kansas (Fig. 11). Goossen (1987c) reported a sudden shift in the course flown by two subadult Whooping Cranes 30 km before they landed within 1.5 km of where they had initiated their migration the previous fall (Kuyt 1984b). Here, the drastic change in course was probably in response to recognition of familiar landmarks.

In April 1984, after four radio-tracked cranes crossed Birch Lake, east of Midnight Lake, Saskatchewan (Fig. 15), they abruptly turned westward on a new course that took them directly over the same 0.5-ha pond south of Midnight Lake where F 3/81 had roosted in fall 1981 (Kuyt 1982). When the four birds reached a point 40 km west of Midnight Lake, they suddenly shifted 45° to the northwest, then, 10 minutes later, 15° to the west. The ground crew reported several other course changes, and the cranes then landed near Spruce Lake (Fig. 14). Again, there were no weather conditions to account for these course changes. This flock included F 19/83, which spent the period of 18 October–5 November 1983 in the area 8 km southeast of Midnight Lake. It is likely that the birds recognized landscape features from 1983 and perhaps from other previous visits.

When Y 19/83 separated from three other birds (including its parents) on 20 April 1984, the older birds resumed their northward migration (Kuyt 1986b). We followed Y 19/83 as it leisurely flew southeast, finally landing 17 km east of Turtleford (Fig. 14). The following day, the ground crew accidentally flushed the yearling, and the air crew then followed the bird to the west. At 10:00, we observed the crane struggling into a head wind (the only time we saw the bird flying into a head wind in that area) until it reached the same stubble field where it had spent the previous week with its parents! It had relocated the field from 33 km away. As the yearling had succeeded in finding the family's feeding area on the stubble field after making the journey only once before (with its parents), it is probable the yearling found its way back by visual cues. After reaching the area, the bird circled a few times, perhaps checking for the presence of its parents or other cranes, then flew 167 km southeast to Redberry Lake (Fig. 14), an important staging area for Whooping Cranes. The previous year, F 19/83 had flown over the southwest corner of Redberry Lake in its fall migration, so the yearling was probably familiar with the area.

Most of the large rivers encountered by migrating Whooping Cranes generally flow east or southeast. Major exceptions are portions of the Missouri and Athabasca rivers. There was some indication (see Sections 3.2.3 and 3.2.4) that portions of the "oriented" rivers provided landmarks for the cranes.

Visual recognition of a different geographic feature was manifest on 22 April 1983, when F 2/82, flying below 150 m agl, approached the Birch Mountains (Fig. 16), which locally rise to 820 m asl. The 6°C temperature aloft (Kuyt 1986a) precluded the development of thermals, and the cranes, unable or "unwilling" to cross the mountain directly in their path, abruptly deviated 30° east. The cranes skirted the mountains and, once past them, resumed their original northwesterly course.

3.2.8 Disturbance to cranes on the ground

On 16 and 17 April 1983, F 2/82 remained near Callaway, Nebraska (Fig. 12), and I had the opportunity to accompany the ground crew and observe the birds from the ground. The comings and goings of the tracking and film crew vehicles attracted the attention of the rural residents. In the evening of 17 April, two people drove to the roost pond and walked towards the cranes. The birds called several times and began walking away. We blew our vehicle's horn, and the interlopers retreated. A truck arrived half an hour later, and several people walked to the pond where the cranes were roosting. The cranes called in alarm and in darkness flew to another roost pond about 1 km north. There were a number of power lines in the area, and the unnecessary flushing of the birds could have had disastrous results.

Goossen (1987a) was advised by his ground crew on 31 October 1982 that the Whooping Cranes being monitored near O'Neill, Nebraska, had been flushed from a corn stubble field by hunters. Although there were other incidents of this type of disturbance, ground crews did not detect gunfire in the vicinity of the birds (Howe 1989).

On 20 October 1982, F 2/82 landed in Saskatchewan near an active gravel pit and railway line. The cranes had moved by the following day, possibly as a result of disturbance near the gravel pit (Goossen 1987a). Five or six Whooping Cranes remained in the Indi Lake area south of Saskatoon for 12 days; although local bird-watchers observed the birds on numerous occasions, the cranes remained relatively undisturbed and resumed their fall migration in a normal manner.

The various observers during the radio-tracking work reported several other incidents in which birds on the ground may have been disturbed by local residents or even by tracking crews, but these disturbances were usually accidental and at no time resulted in long-distance moves by the cranes.

3.2.9 Time of juvenile independence

Alonso et al. (1984), in studying Common Cranes on the Iberian peninsula, found that the family group's cohesion declined steadily as spring approached. Increasing feeding experience and efficiency enabled juveniles (then almost yearlings) to become self-sufficient. The authors indicated that the family breakup is a gradual process, and the existence of a wintering area with large numbers of birds facilitated the separation. Young birds had the opportunity to form small "bachelor" flocks, similar to flocks seen on the breeding range that consisted of yearlings and other nonbreeding cranes. Alonso et al. (1984) also indicated that the juvenile Common Cranes usually departed for the breeding range after the adults had already left.

There is considerable evidence that many Whooping Crane families remain intact throughout the spring migration until their arrival in WBNP. In April 1980 and 1981, I saw intact family groups on the breeding range before nesting activities had started. Four banded yearlings were observed on 9 May 1979 in the vicinity of their parents' nesting territories. Laying had just begun, and it is likely that all four families had arrived with their offspring at about the same time (Kuyt 1986a). All of these birds had left ANWR on 7–8 April 1979 (F. Johnson, pers. commun.).

In 1983, we tracked F 2/82 from ANWR to WBNP, and the juvenile did not separate until after the birds had reached the previous year's nest area (Kuyt 1986a).

Labuda's (1983) and my subsequent observations of the behaviour and movements of F 10/82 (this pair nested for the first time in 1982) between its landing just north of the Canada–United States border and its arrival on the breeding range are different than observations I made of F 2/82 (an experienced pair). Pair 10/82 and the juvenile apparently arrived at the breeding range separately. Anderson et al. (1980) reported a juvenile Sandhill Crane returning to the natal marsh in Wisconsin unassisted by its parents.

On 14 May 1983, a local resident found a recently dead yearling Whooping Crane near Edam, 25 km southeast of Turtleford, Saskatchewan. A pair of unbanded adult birds had also been seen nearby as early as 2 May, when the yearling was first reported by various residents. Only one juvenile remained unbanded in fall 1982, undoubtedly the bird found dead near Edam. The bird and its parents had begun spring migration from ANWR on 17 or 18 April, and they could easily have reached Edam by 2 May. This may have been another example of parent–juvenile separation in central Saskatchewan.

Bard (1956) observed apparent separation between adult Whooping Cranes and their two juveniles on 23 April 1956, when the adults spiralled out of sight, leaving the juveniles on a Saskatchewan stubble field.

In spring 1984, yearling Y 19/83 separated from its parents in the Spruce Lake area, and the young bird remained in south-central Saskatchewan for two weeks before continuing to WBNP (Kuyt 1986b). If competition between birds of similar age exists, separation of yearlings from young breeding adults (pairs 10/82, 19/83) before reaching the breeding range is more likely than when parents are older, more experienced birds (Kuyt 1986a).

The 1981–84 radio-tracking project has provided information showing that separation between adults and yearlings may occur in south-central Saskatchewan or when the nesting territory has been reached. In recent years (1988, 1989), separation has been observed on the winter range (T. Stehn, pers. commun.) when yearlings began their spring migration with birds other than their parents. It remains to be seen if this behaviour is detrimental to the survival of juvenile Whooping Cranes or whether it is a development associated with increasing densities of cranes on the winter range.

3.2.10 Mortality

3.2.10.1 Breeding range

Of 135 juvenile Whooping Cranes colour-banded between 1977 and 1988, two birds died shortly after banding. One crane, banded on 30 July 1977, later that day was found in a shallow pond with a wing caught in a dead tree; the bird was extricated and appeared normal upon release but was found drowned in a shallow pond the next day. The second bird died in 1987 as a result of a serious leg fracture sustained during the capture attempt. Only three juvenile Whooping Cranes survived the extremely dry conditions in WBNP in 1981. The three birds were captured and equipped with radios and colour bands, and all three successfully left WBNP with their parents. Of six juveniles equipped with radios in 1982, two were found dead several days later, presumably killed by wolves. The other four birds fledged and eventually left WBNP. In 1983, the last of the three years that cranes were captured to be equipped with radios, six received radios, but remains of four birds (with functioning radios) were found in September (Table 1). The remaining two juveniles left WBNP with their parents in fall 1983.

Of the 15 birds equipped with radios, nine fledged and six died on the breeding range, probably before fledging. Wolf predation on prefledged Whooping Cranes was first identified as a mortality factor in 1979 (Kuyt 1981b). Kuyt and Goossen (1987) determined that radio-equipped birds suffered significantly greater mortality than cranes equipped with colour bands only, although sample sizes and differences in ages of young cranes banded might have biased these results. Younger cranes would naturally be expected to suffer greater mortality than older birds because the former would be exposed to predation by wolves for a longer period. In recent years, colour-banding of cranes was done late in the season when some juveniles were already capable of short flights. This made capture more difficult but reduced the time of vulnerability to mammalian predators. Howe (1989) compared survival of radio-marked birds with an estimate of annual survival in the entire WBNP–ANWR population and found that the radio-marking affected the survival of postfledging Whooping Cranes only marginally.

There are only two records of adult Whooping Crane mortality on the breeding range, a nine-year-old male found dead of heart disease near its nest in 1986 and an unbanded adult-plumaged bird found dead from unknown causes in 1991. I have seen no other disruption of nesting pairs or losses of adults. Therefore, most mortality among adults occurs during migration or on the winter range. Losses of subadults not associated with definite summer territories would be more difficult to document in WBNP. In the absence of such known mortality, it is possible that most losses of subadults also occur during migration or in winter.

3.2.10.2 During migration

Two of the nine radio-equipped fledged birds died during the present study as a result of power line collisions, a third of the total (six) postfledging losses. Radio-equipped juvenile 2/81 and its parents spent the period of 25 September–12 October 1981 on a half-section of land near Midnight Lake. On 12 October, the juvenile bird collided with a 10-m-high single-strand electric power line servicing a nearby farmstead; it died a week later from its injuries.

Subadult 7/81, during its second fall migration, was found dead under a power line near Waco, Texas, on 16 October 1982 (Fig. 8). The radio-equipped bird and three older companions had resumed fall migration from the Last Mountain Lake area on 11 October 1982 at an unusually late time in the day and apparently continued flying after sunset. The subadult was last seen in North Dakota two days before it was found dead (Faanes 1987).

Tracking crews noted a number of instances when Whooping Cranes passed just over power lines or even underneath them (Kuyt 1984a). In the week before juvenile 2/81's collision with the power line in Saskatchewan, I noted several times that the bird barely cleared the wire as it flew with its parents from the roost to a feeding area.

As of 1989, power lines had been implicated as the cause of death or crippling of at least 17 Whooping Cranes in North America, all but five birds from the experimental Grays Lake population (Fjetland 1987; J. Lewis, pers. commun.). Most accidents occur during periods of inclement weather and low visibility (Brown et al. 1984).

In late October 1982, ground observers noted an injured Whooping Crane near Saskatoon. The bird, one of the adults of F 1/82 staging at Indi Lake, was believed to have been injured by one of several nearby Golden Eagles, although no attack was witnessed. On 27 October, I saw chick 1/81 with three adult Whooping Cranes on an apparently normal migration flight 200 km southeast of Indi Lake, and the birds reached ANWR about 11 November.

Windingstad et al. (1981) reported a Golden Eagle attacking a healthy juvenile Whooping Crane in Colorado. The bird, in flight with its two foster-parent Sandhill Cranes, died as a result of the attack.

3.2.10.3 Winter range

Four of nine fledged radio-equipped Whooping Cranes died or disappeared at ANWR, two during their first winter, one during its second winter, and one during its third winter (Table 1). Suspected causes of death included predation (perhaps by a Great Horned Owl, *Bubo virginianus*) and avian tuberculosis or a similar disease (T. Stehn, pers. commun.).

On 3 January 1989, a colour-banded adult female Whooping Crane was shot and killed by a waterfowl hunter near St. Joseph Island, Texas (Fig. 9), the first known shooting of a Whooping Crane from the WBNP–ANWR flock since 4 January 1968, when an adult female crane was shot under similar circumstances immediately north of the ANWR border. On 15 April 1991 a female Whooping Crane in breeding condition was shot and killed about 100 km west of Temple, Texas (Fig. 10).

Waterfowl hunting occurs in the vicinity of the ANWR, and this activity, as well as associated boat traffic near and through the refuge, contributes to disturbance of Whooping Cranes. The above examples indicate minimal losses directly attributable to hunting, but disturbance to Whooping Cranes remains a source of concern.

4.0 Conclusion

This paper describes the Whooping Crane migration corridor—its location and use period in spring and fall, as determined by studies of birds equipped with radio transmitters. Prior to this study, little was known about the ecology of migrating Whooping Cranes, including behaviour, mortality, and habitat use. The migration studies concentrated mainly on the transmitter-equipped cranes, but considerable information was obtained from observations of Whooping Cranes encountered incidentally within the migration corridor. Our observations that, with some exceptions, Whooping Cranes usually landed on or near small wetlands for overnight roosting and feeding agree with the more detailed studies of habitat use by ground crews (Howe 1989). Our aerial observations showed that there was an abundance of small wetlands throughout most of the crane migration corridor. It has been pointed out by Howe (1989) that, in the absence of quantitative data on habitat availability, it could not be determined if the infrequent use of large wetlands possibly reflected their scarcity.

The use by Whooping Cranes of small wetlands near grainfields for overnight roosting and feeding may account for the relative paucity of sighting reports by the public from agricultural areas. On several occasions, farmers were surprised when tracking crews pointed out to them that Whooping Cranes were using their land. This use of small wetlands makes it difficult to develop an effective management strategy (Howe 1989). In view of the recent shooting of two Whooping Cranes (Saskatchewan, April 1990; Texas, April 1991) in rural areas, education of the public must be a continuing part of any management strategy.

The present study provides important information about mortality of Whooping Cranes. Many of the deaths occurred before cranes had fledged in WBNP, most likely as a result of wolf predation. Management of mortality would be difficult, as wolf predation is related to drought in this national park, where wildlife, including the wolf, is protected. Of greater concern appears to be mortality of cranes at ANWR, where serious losses of unknown cause have occurred during the 1989–90 and 1990–91 winters. The present study indicated that the most serious losses of migrating Whooping Cranes were due to collisions with power lines. Brown et al. (1984) provided management recommendations; consultation with utility companies to discuss power line modifications prior to construction of new lines should be mandatory.

The radio-tracking studies in spring 1983 and 1984 contributed only little information on the separation of adult breeding birds from their young of the previous year. More data on time and location of separation might provide a more complete explanation for this interesting behaviour.

The 1981–84 radio-tracking studies resulted in the accumulation of detailed information about the Whooping Crane migration corridor, flight behaviour, use and location of stopover areas, and crane mortality. The study should prove to be useful as a guideline for future telemetry work involving cranes or other long-distance diurnal migratory birds.

Literature cited

Alerstam, T. 1975. Crane (*Grus grus*) migration over sea and land. Ibis 117:489–495.

Allen, F.H. 1939. Effect of wind on flight speeds. Auk 56:291–303.

Allen, R.P. 1952. The Whooping Crane. Natl. Audubon Soc. Res. Rep. 3. 246 pp.

Alonso, J.C.; Veiga, J.P.; Alonso, J.A. 1984. Familienauflösung und Abzug aus dem Winterquartier beim Kranich *Grus grus*. J. Ornithol. 125(1):69–74.

Anderson, R.K.; Jansen, D.K.; Cogger, T. 1980. Fall and spring migration route and behavior of eastern Greater Sandhill cranes: 1978–1979. Unpublished report. U.S. Fish Wildl. Serv., Twin Cities, Minnesota. 21 pp.

Bagg, A.M.; Gunn, W.W.H.; Miller, D.S.; Nichols, J.T.; Smith, W.; Wolfarth, F.P. 1950. Barometric pressure–patterns and spring bird migration. Wilson Bull. 62(1):5–19.

Bard, F.G. 1956. Whooping Cranes in migration, 1956. Blue Jay 14(2):39–42.

Bellrose, F.C. 1972. Mallard migration corridors as revealed by population distribution, banding and radar. Pages 3–26 *in* Population ecology of migratory birds. U.S. Fish Wildl. Serv. Rep. 2.

Bradshaw, F. 1956. The home of the Whooping Crane. Blue Jay 14(3):76–78.

Brown, W.M.; Drewien, R.C.; Walker, D.L. 1984. Crane flight behavior and mortality associated with power lines in the San Luis Valley, Colorado. For., Wildl. and Range Exp. Stn., Univ. of Idaho, Moscow, Idaho. 16 pp., figures, appendices.

Crete, R.A.; Toepfer, J.E. 1978. Migration of radio-tagged eastern Greater Sandhill Cranes. Unpublished report. U.S. Fish Wildl. Serv., Twin Cities, Minnesota. 42 pp.

Drewien, R.C.; Bizeau, E.G. 1981. Use of radio telemetry to study the movements of juvenile Whooping Cranes. Pages 130–134 *in* Lewis, J.C.; Masatomi, H. (eds.), Crane research around the world: Proc. Int. Crane Symp., Sapporo, Japan. Int. Crane Found., Baraboo, Wisconsin.

Drewien, R.C.; Kuyt, E. 1979. Teamwork helps the Whooping Crane. Natl. Geogr. 155(5):680–693.

Faanes, C.A. 1987. Bird behavior and mortality in relation to power lines in prairie habitats. U.S. Fish Wildl. Serv. Tech. Rep. 7. 24 pp.

Fjetland, C.A. 1987. Comments on Whooping Crane recovery activities. Pages 312–314 *in* Lewis, J.C. (ed.), Proc. 1985 Crane Workshop, Grand Island, Nebraska.

Gilmer, D.S.; Cowardin, L.M.; Duval, R.L.; Mechlin, L.M.; Shaiffer, C.W.; Kuechle, V.B. 1981. Procedures for the use of aircraft in wildlife biotelemetry studies. U.S. Fish Wildl. Serv. Resour. Publ. 140, Washington, D.C. 19 pp.

Goossen, J.P. 1982. A report on the radio-tracking of a Whooping Crane family from Wood Buffalo National Park to Luseland, Saskatchewan. Unpublished report. Can. Wildl. Serv., Edmonton. 49 pp.

Goossen, J.P. 1986a. A report on the 1981 premigration abundance, distribution and movements of Whooping Cranes in and near Wood Buffalo National Park, Alberta – Northwest Territories. Unpublished report. Can. Wildl. Serv., Edmonton. 18 pp.

Goossen, J.P. 1986b. A report on the 1982 premigration abundance, distribution and movements of Whooping Cranes in and near Wood Buffalo National Park, Alberta – Northwest Territories. Unpublished report. Can. Wildl. Serv., Edmonton. 22 pp.

Goossen, J.P. 1987a. A report on the 1982 radio-tracking of migrating Whooping Cranes from Wood Buffalo National Park to Aransas National Wildlife Refuge, Texas. Unpublished report. Can. Wildl. Serv., Edmonton. 57 pp.

Goossen, J.P. 1987b. A report on the 1983 radio-tracking of migrating Whooping Cranes from Saskatchewan to Aransas National Wildlife Refuge, Texas. Unpublished report. Can. Wildl. Serv., Edmonton. 26 pp.

Goossen, J.P. 1987c. A report on the 1984 radio-tracking of migrating Whooping Cranes from Aransas National Wildlife Refuge, Texas to Wood Buffalo National Park, Alberta. Unpublished report. Can. Wildl. Serv., Edmonton. 33 pp.

Gould, L.L.; Heppner, F. 1974. The Vee formation of Canada Geese. Auk 91:494–506.

Heppner, F.H. 1974. Avian flight formations. Bird-Banding 45:160–169.

Howe, M.A. 1987. Habitat use by migrating Whooping Cranes in the Aransas–Wood Buffalo corridor. Pages 303–311 *in* Lewis, J.C. (ed.), Proc. 1985 Crane Workshop, Grand Island, Nebraska.

Howe, M.A. 1989. Migration of radio-marked Whooping Cranes from the Aransas–Wood Buffalo population: patterns of habitat use, behavior, and survival. U.S. Fish Wildl. Serv. Tech. Rep. 21. 33 pp.

Johns, B.W. 1987. Whooping Crane sightings—Prairie provinces 1979–1985. Unpublished report. Can. Wildl. Serv. 10 pp.

Kuyt, E. 1979. Banding of juvenile Whooping Cranes and discovery of the summer habitat used by nonbreeders. Pages 109–111 *in* Lewis, J.C. (ed.), Proc. 1978 Crane Workshop, Rockport, Texas.

Kuyt, E. 1981a. Population status, nest site fidelity, and breeding habitat of Whooping Cranes. Pages 119–125 *in* Lewis, J.C.; Masatomi, H. (eds.), Crane research around the world: Proc. Int. Crane Symp., Sapporo, Japan. Int. Crane Found., Baraboo, Wisconsin.

Kuyt, E. 1981b. Clutch size, hatching success, and survival of Whooping Crane chicks, Wood Buffalo National Park, Canada. Pages 126–129 *in* Lewis, J.C.; Masatomi, H. (eds.), Crane research around the world: Proc. Int. Crane Symp., Sapporo, Japan. Int. Crane Found., Baraboo, Wisconsin.

Kuyt, E. 1982. Whooping Crane tracking report, segments 1–8. NWT to Aransas National Wildlife Refuge. Unpublished report. Can. Wildl. Serv., Edmonton. 49 pp.
Kuyt, E. 1984a. Radio-tracking of Whooping Cranes during fall migration from Wood Buffalo National Park to Aransas National Wildlife Refuge, August–November, 1982. Unpublished report. Can. Wildl. Serv., Edmonton. 93 pp.
Kuyt, E. 1984b. Radiotelemetry-assisted studies of Whooping Cranes in Wood Buffalo National Park prior to migration, autumn 1983. Unpublished report. Can. Wildl. Serv., Edmonton. 39 pp.
Kuyt, E. 1986a. Northward radio-tracking of a Whooping Crane family migrating from the Aransas National Wildlife Refuge to Wood Buffalo National Park, April 1983. Unpublished report. Can. Wildl. Serv., Edmonton. 82 pp.
Kuyt, E. 1986b. Northward radio-tracking of a Whooping Crane family migrating from the Aransas National Wildlife Refuge to west-central Saskatchewan, April–May 1984. Unpublished report. Can. Wildl. Serv., Edmonton. 78 pp.
Kuyt, E.; Goossen, J.P. 1987. Survival, age composition, sex ratio, and age at first breeding of Whooping Cranes in Wood Buffalo National Park, Canada. Pages 230–244 *in* Lewis, J.C. (ed.), Proc. 1985 Crane Workshop, Grand Island, Nebraska.
Labuda, S.E. Jr. 1983. Whooping Crane migration: a radiotelemetry study, spring 1983. Unpublished report. U.S. Fish. Wildl. Serv., Austwell, Texas. 16 pp., maps.
Lingle, G.R. 1985. Status of Whooping Crane migration habitat within the Great Plains of North America. Pages 331–340 *in* Lewis, J.C. (ed.), Proc. 1985 Crane Workshop, Grand Island, Nebraska.
Lissaman, P.B.S.; Schollenberger, C.A. 1970. Formation flight in birds. Science 168:1003.
Melvin, S.M. 1980. Migration ecology and wintering grounds of Sandhill Cranes from the Interlake region of Manitoba. Ph.D. thesis, Univ. of Wisconsin–Madison. Univ. Microfilms Int., Ann Arbor, Michigan. 263 pp.
Melvin, S.M.; Temple, S.A. 1980. Migration ecology and wintering grounds of Sandhill Cranes from the Interlake region of Manitoba. Unpublished report. U.S. Fish Wildl. Serv., Washington, D.C. 60 pp.
Melvin, S.M.; Temple, S.A. 1981. Migration ecology of Sandhill Cranes: a review. Pages 73–87 *in* Lewis, J.C. (ed.), Proc. 1981 Crane Workshop, Tavernier, Florida.
Melvin, S.M.; Drewien, R.C.; Temple, S.A.; Bizeau, E.G. 1983. Leg-band attachment of radio-transmitters for large birds. Wildl. Soc. Bull. 11(3):282–285.
Nesbitt, S.A. 1975. Spring migration of Sandhill Cranes from Florida. Wilson Bull. 87(3):424–426.
Nesbitt, S.A. 1976. Use of radio-telemetry techniques on Florida Sandhill Cranes. Pages 299–303 *in* Lewis, J.C. (ed.), Proc. Int. Crane Workshop, Oklahoma State Univ. Publ. Print., Stillwater, Oklahoma.
Pennycuick, C.J.; Alerstam, T.; Larsson, B. 1979. Soaring migration of the Common Crane *Grus grus* observed by radar and from an aircraft. Ornis Scand. 10:241–251.
Pitelka, F.A. 1979. Introduction: the Pacific coast shorebird scene. Pages 1–11 *in* Pitelka, F.A. (ed.), Shorebirds in marine environments. Studies in Avian Biology No. 2. Cooper Ornithol. Soc. 261 pp.
Salyer, J.W. 1982. Summary cooperative Whooping Crane tracking project, fall 1975 – spring 1982. Unpublished report. U.S. Fish Wildl. Serv., Pierre, South Dakota. 6 pp.
Shields, R.H.; Benham, E.L. 1968. Migratory behavior of Whooping Cranes. Auk 85(2):318.
Stephen, W.J.D. 1979. Whooping Crane sightings Prairie Provinces 1977 and 1978. Blue Jay 37(3):163–168.
Toepfer, J.E.; Crete, R.A. 1979. Migration of radio-tagged Greater Sandhill Cranes from Minnesota and Wisconsin. Pages 159–173 *in* Lewis, J.C. (ed.), Proc. 1978 Crane Workshop, Colorado State Univ. Print. Serv., Fort Collins, Colorado.
U.S. Fish and Wildlife Service. 1986. Whooping Crane Recovery Plan. U.S. Fish and Wildlife Service, Albuquerque, New Mexico. vi + 283 pp.
Van Tyne, J.; Berger, A.J. 1959. Fundamentals of ornithology. John Wiley & Sons, New York. 808 pp.
Ward, J.P.; Anderson, S.H. 1987. Roost site use versus preference by two migrating Whooping Cranes. Pages 285–288 *in* Lewis, J.C. (ed.), Proc. 1985 Crane Workshop, Grand Island, Nebraska.
Windingstad, R.M.; Stiles, E.H.; Drewien, R.C. 1981. Whooping Crane preyed upon by Golden Eagle. Auk 98(2):393–394.
Young, L.S. 1984. Autumn migration of subadult Whooping Cranes. Unpublished report. Montana Coop. Wildl. Res. Unit, U.S. Fish Wildl. Serv. 13 pp., field notes, maps, appendices.

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