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LESLIE J. RISSLER, *Dept. of Biology, Univ. of Virginia, Charlottesville, Virginia 22903 (to whom correspondence should be addressed)*; DAVID N. KAROWE, *Dept. of Biology, Virginia Commonwealth Univ., Richmond, Virginia 23284-2012*; FRANCESCA CUTHBERT, *Dept. of Fisheries and Wildlife, Hodson Hall, Univ. of Minnesota, St. Paul, Minnesota 55108*; AND BRIAN SCHOLTENS, *Dept. of Biology, College of Charleston, Charleston, South Carolina 29424.* *Received 10 Feb. 1995, accepted 1 May 1995.*

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Diurnal activity budgets of pre-nesting Sandhill Cranes in arctic Canada.—Lack (1968) contended that waterfowl clutch size evolved in relation to female food consumption during egg formation. Ryder (1970) modified this hypothesis noting that several arctic-breeding geese did not feed during egg-laying. Those geese probably used nutrients accumulated on wintering and staging areas to lay and incubate clutches (Ankney and MacInnes 1978, Raveling 1979). More recent studies of endogenous reserves and the amount of time spent feeding when at, or near to, the ultimate breeding areas before clutch initiation have suggested that this simple model does not apply to all populations (e.g., Greater White-fronted Geese [*Anser albifrons*], Fox and Madsen 1981, Budeau et al. 1991; Canada Geese [*Branta canadensis*], Bromley and Jarvis 1993), even geese breeding in the high arctic (e.g., Snow Geese [*Anser caerulescens*], Gauthier and Tardif 1991).

Sandhill Cranes (*Grus canadensis*) allocate less nutrients to clutch formation in relation to body size than northern nesting geese (ca 7% vs 17%, Bromley, unpubl. data), and generally are believed to acquire necessary nutrients for migration and reproduction at spring staging areas (Krapu et al. 1985). This enables arriving cranes to cope with highly variable weather conditions encountered on arctic breeding areas and initiate clutches with minimal local exogenous supplement to their nutrient reserves.

Both Sandhill Crane sexes share incubation. As female cranes contribute comparatively less nutrient investment to the clutch and to incubation than geese, we hypothesise that there is less male investment in vigilance and female protection, more time spent in maintenance or improvement of condition by the male and less time feeding by females than in arctic nesting geese. During a study of pre-nesting waterfowl in the central Canadian Arctic, we tested the predictions that: (1) male cranes feed less and spend more time alert than females, but that the differences would be less marked than among arctic nesting geese, and (2) the nesting phenology of cranes precede that of locally breeding Greater White-fronted and Canada geese because: (1) most of the cranes' reproductive material is endogenously de-

rived, and (2) first egg-date of cranes is more dependent on snow melt (i.e., nest site availability) than on female acquisition of nutrient reserves.

Study area and methods.—Pre-nesting behavioral observations were made in 8 km^2 of tundra at the Walker Bay Field Station (WBFS) of the Northwest Territories Department of Renewable Resources on the Kent Peninsula, NWT, Canada (68°20′N, 108°05′W). This area has been used for the long-term study of Canada and Greater White-fronted geese since 1990, and goose observations from other seasons are presented here where appropriate. We sampled paired Sandhill Crane activity from 28 May to 5 June 1992 by scan sampling a segment of 110° from WBFS, scoring each individual according to its sex (males distinguished by their larger size and longer bills than females, Tacha et al. 1992), locomotory status (sit, stand, walk, run, fly) and activity/posture (alert, head low, sleep, feed, social activity, sexual behavior, comfort activity etc). In the analysis, these categories were combined as far as possible to be comparable with the behaviors described by Tacha et al. (1987), namely searching, feeding, locomotion, resting, comfort and social. We distinguished "alert" behavior, recorded when a bird was standing with its head up, from "social" as defined by Tacha et al. (1987). Scans were carried out every 15 min, scoring male and female activity separately from between four and 12 pairs present in the study area, recording 144 scans evenly spread throughout the 24-h period. The data base comprised 1723 individual observations up until the discovery of the first egg on 5 June.

Snow cover on the study area declined from 98% on 24 May to 75% by 5 June (based on regularly walked transects); snow melt was the latest during 1992 of the five studied seasons 1990–1994 inclusive, mainly as a result of prolonged sub-zero temperatures during 29 May–2 June inclusive. Sandhill Cranes were not much in evidence in the study area during 24–27 May, with only single pairs observed intermittently. From 28 May, four pairs were regularly present in the study area and observations commenced at 14:00 h that day. Date of clutch initiation was determined by direct observation. Greater White-fronted and Canada geese nests were found by active search, direct observation and flushing females in the course of other activities. First egg dates for cranes and geese were established on the basis of an average laying interval of 33 h.

Results.—Cranes were paired on arrival; no larger groups were seen until after nest initiation. There were few territorial clashes, pairs were consistent in their use of the study area, foraging in snow-free patches close to their ultimate nest sites. The overall activity budget, summarized by two-h periods (Fig. 1) indicated cranes fed for 33.5% of the 24-h daylight period, rested (slept) for 37.8%, spent 15.4% of the time in locomotion and were alert 13.0% of the time. Courtship, comfort and other minor activities combined comprised less than 1% of the remainder. Resting behavior was inversely correlated with alertness ($r = -0.694$, $P < 0.05$), locomotion ($r = -0.919$, $P < 0.01$), feeding ($r = -0.795$, $P < 0.01$) and searching ($r = -0.635$, $P < 0.05$); alert behavior was positively correlated with locomotion ($r = 0.551$, $P < 0.05$) and feeding ($r = 0.552$, $P < 0.05$); locomotion was positively correlated with feeding ($r = 0.645$, $P < 0.05$) and searching ($r = 0.670$, $P < 0.05$). Hence, cranes showed marked changes between the active and resting phases of their daily behavior.

Male cranes spent more time alert (16.3% vs 9.6%, t-test, $P < 0.001$) and fed less (26.8% vs 40.2%, t-test, $P < 0.001$) than females. Male and female time budgets were not significantly different for all other major activities (locomotion 14.5% vs 12.6%, rest 39.8% vs 35.8, search 2.1% vs 1.4%, other activities 0.5% vs 2.4%, t-tests, $P > 0.05$ for all activities). Male cranes spent proportionally less time alert and more time feeding than females compared with studied goose species, while female cranes were more alert and fed less than female geese (Table 1). Nesting was highly synchronous in all species (Table 2). Although Crane nesting densities were extremely low in this tundra habitat, all seven nests were initiated between 5 and 10 June ($\bar{x}$ = 6 June). Most Canada Goose clutches were initiated

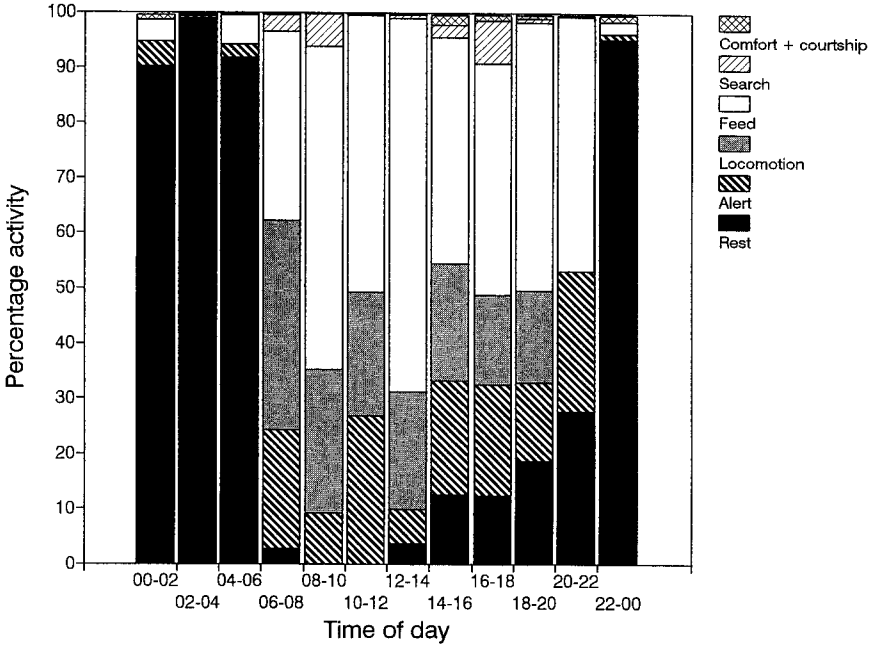

FIG. 1. Diurnal patterns of activity of Sandhill Cranes from Walker Bay Field Station, Northwest Territories, spring 1992.

TABLE 1

COMPARISON OF THE RATIO BETWEEN FEEDING AND ALERT BIRD BUDGETS[a] FROM PUBLISHED ACCOUNTS OF PRE-NESTING FEEDING IN ARCTIC-NESTING GEESE WITH DATA FOR SANDHILL CRANES FROM WALKER BAY FIELD STATION, NWT

Study	Species	Alert ratio of female to male allocation	Feeding ratio of female to male allocation
Budeau et al. (1991)	Greater White-fronted Goose	0.15	1.98
Fox and Madsen (1981)	Greater White-fronted Goose	0.23	1.91
Gauthier and Tardif (1991)	Snow Goose	0.20	1.72
This study	Crane	0.59	1.50
This study[b]	Greater White-fronted Goose	0.15	1.53
This study[b]	Canada Goose	0.12	1.60
Mean values WBFS 1990–1993[b]	Greater White-fronted Goose	0.19	1.59
Mean values WBFS 1990–1993[b]	Canada Goose	0.15	1.72

[a] Values indicate the ratio of the percentage of time spent by females to that spent by males from each of the studies.
[b] Unpubl. data.

TABLE 2

FREQUENCY DISTRIBUTIONS OF FIRST EGG DATES OF GREATER WHITE-FRONTED GEESE, CANADA GEESE, AND SANDHILL CRANES FROM WALKER BAY FIELD STATION, SPRING 1992

Date	Greater White-fronted Goose	Canada Goose	Crane
5–6 June	0	0	4
7–8 June	0	0	3
9–10 June	3	3	0
11–12 June	3	7	0
13–14 June	1	10	0
15–16 June	8	1	0
17–18 June	2	2	0

on 13 June and eight out of the 17 Greater White-fronted Goose clutches were initiated during 15–16 June.

Discussion.—At WBFS, time devoted to feeding by pre-nesting female Cranes (40%) was less than geese during the same year (59% in Greater White-fronted Geese in 1992, range 55–65% from four seasons 1990–1993 and 66% in Canada Geese, range 57–73% for three seasons 1991–1993 Bromley, unpubl. data), and from other studies (e.g., 68% in Greenland White-fronted Geese [*A. a. flavirostris*], Fox and Madsen 1981, 76% in Snow Geese, Gauthier and Tardif 1991). Early arriving cranes probed for below-ground plant storage organs as well as lemmings (abundant during early spring 1992), and scavenged caribou (*Rangifer tarandus*) carcasses. Such food items offered a more profitable feeding resource per unit dry weight, but require more search and handling time than the intensive grazing and probing which formed the basis for goose foraging.

Female cranes fed more than males before nesting, an observation which fits the model of pair-bond investment in long-lived monogamous birds such as the geese and cranes, in which a female maximizes energy intake in preparation for reproduction, while the attendant male sacrifices feeding time to protect her from other males and potential predators. The major differences between crane and goose behavior were the reduced male crane investment in vigilance, plus the smaller proportion of time spent feeding and the larger proportion of time spent alert by the female. Since cranes share the burden of incubation (in contrast to geese), these observed patterns fit with the model of a trade-off between investment in female protection through male vigilance and a need to maximise reserves to improve fitness in the face of the incubation burden placed upon the male. The male benefits by spending proportionally more time feeding, enabling an increased role in incubation which in turn gives the female greater flexibility not to feed early after arrival to accumulate reserves to see her through incubation.

It is likely that the late 1992 season had a considerable impact upon the behavior and possibly on the timing of crane breeding at WBFS. However, in other years, there appeared little correlation between nest initiation dates and snow melt (unpubl. anecdotal information). The presence of persistent snow cover may have greatly influenced food availability for both cranes and their predators. There is a need for further study of Sandhill Crane feeding behavior prior to clutch initiation before we can be confident that this species relies to a greater extent on endogenous reserves accumulated on staging areas for reproduction than do the geese nesting in the same area. However, the results presented here support the assertion that Sandhill Cranes can commence laying eggs earlier than geese in an abnormally

late season. Our observations also support the hypothesis that male cranes spend proportionally less time alert and more time feeding than male arctic nesting geese, presumably as a consequence of the increased physiological demands of shared incubation. Mirroring the different reproductive strategies, female cranes feed less than geese during prelaying because their relative reproductive investment is lower, because male cranes share in incubation.

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ANTHONY D. FOX, *The Wildfowl and Wetlands Trust, Slimbridge, Gloucester, GL2 7BT, United Kingdom (Present address: Dept. of Wildlife Ecology, National Environmental Research Institute, Kalø, Grenåvej 12, DK-8410 Rønde, Denmark.);* HUGH BOYD, *Canadian Wildlife Service, Environment Canada, Ottawa, Ontario KIA 0E7, Canada,* AND, ROBERT G. BROMLEY, *Dept. of Renewable Resources, Government of the Northwest Territories, 600, 5102-50 Avenue, Yellowknife, Northwest Territories X1A 3S8, Canada.* *Received 15 Nov. 1994, accepted 1 May 1995.*