AGE-RELATED DIFFERENCES IN TIME BUDGETS AND PARENTAL CARE IN WINTERING COMMON CRANES

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ABSTRACT.—We compared the behavior and food intake rate of parent, nonparent and juvenile wintering Common Cranes (*Grus grus*) to evaluate possible costs and benefits resulting from parental care. Time devoted to feeding and food intake rates were highest in autumn after arrival from the breeding areas, and decreased throughout the winter in all birds. This decrease was in part determined by a decrease in food availability, but also by satiation, as suggested by the increasing time devoted to resting and other nonforaging activities. Juveniles spent more time feeding and less time alert and preening than birds of both adult classes until February, but had achieved the same time budget as nonparent adults in March, when most juveniles were already independent from their parents. Increased feeding time allowed juveniles to obtain the same daily food intake as nonparent adults during the winter. Juveniles did not change their time budget when the family was in a flock, but the net intake rate of juveniles decreased due to interference from other birds. Parents spent less time feeding and resting, and more time scanning than nonparents. Parental vigilance effort was higher in isolated families than in flocks. However, parents seemed not to suffer from parental care, since their net and absolute intake rates were higher than those of nonparent adults. *Received 3 October 1991, accepted 14 June 1992.*

SEVERAL STUDIES have shown that juveniles and immatures of many bird species have a lower foraging ability than adults (e.g., Greig-Smith 1985, Burger 1987, Draulans 1987, Goss-Custard and Durell 1987a, b), or are excluded by nonparent adults from the better habitats (Gauthreaux 1978, Monaghan 1980, Draulans and Van Vessem 1985, Goss-Custard and Durell 1987a, Catterall et al. 1989). Thus, to increase the offspring's chance of surviving, many vertebrates have extended parental-care periods (Trivers 1972, Clutton-Brock 1991). Among birds, postfledging parental care may extend through several weeks or months, particularly in certain long-lived monogamous species, such as seabirds, geese or cranes, and in cooperative breeders (review in Clutton-Brock 1991). Eventually, the rising cost of parental investment due to increasing offspring demands should lead adults to terminate parental care (Trivers 1974).

In Alonso et al. (1984b), we reported that family breakup in Common Cranes (*Grus grus*) occurred prior to departure on spring migration. In this paper we evaluate some predictions of Trivers' (1974) parent-offspring conflict theory, particularly that there should be differences in time budget between parents and nonparents, changes in time budget with brood size, and a decrease in parental care with increasing offspring age. We test whether parental care results in some measurable cost to the parents in terms of reduced food intake by comparing them with nonparent adults. Since reserves acquired in winter have an influence on breeding success in the subsequent season (Ryder 1970, Ankney and MacInnes 1978, Davies and Cooke 1983, Black and Owen 1989a, b), parents should try to maximize their intake rate, a strategy that could conflict with their parental duties. The gregarious behavior of Common Cranes during winter provided another testable prediction, that members of a family unit would benefit from flocking with other birds, due to the lower individual vigilance time needed in flocks.

The study species and area used were particularly suitable for such a field study. First, Common Cranes feed almost exclusively on cereal seeds taken from stubble and sown fields. This enabled us to measure food intake accurately. The variable, food intake, is more directly related to fitness than feeding time, the variable used in many other studies. In fact, some authors have shown that feeding time and intake rate are not necessarily linearly related (Heinsohn 1987, Swennen et al. 1989). Second, the unobstructed visibility and accessibility of the

area facilitated random sampling of behavioral observations, thereby increasing the statistical reliability of conclusions.

METHODS

The study was carried out at Laguna de Gallocanta in northeastern Spain (40°58'N, 1°30'W) during the winter seasons 1980–1981 to 1985–1986, with the exception of 1983–1984. Most cranes arriving from their breeding areas in northern Europe stage at Gallocanta some days or weeks in November and/or December on their way to southwestern Spain. A variable number remain there throughout the winter. During our study, yearly peak numbers of cranes staging during migration varied between 5,900 (February 1983) and 21,000 (February 1985), and average wintering numbers varied between 3,000 (January 1983) and 10,000 (December 1985–February 1986).

We spent one to two days per week in the field and gathered data continuously from when the cranes left the roost until they returned. Thus, our samples were evenly distributed throughout day and season. Flocks were located opportunistically during regular circuits of the study area by vehicle. We did not repeat the same circuit to avoid the influence of possible relationships of a particular site, habitat, or time of day with activity of the birds. All flocks were plotted on maps scale 1:50,000. We recorded date, time, flock size, percentage of juveniles, and type of ground cover (cereal-sown field, cereal-stubble field, sunflower-stubble field, plowed field, pasture, drinking place, other). In 1984–1986 we measured food availability at stubble fields used by focal birds, after we finished behavioral observations. We took 20 25 × 25 cm random samples of the number of cereal seeds found on the ground.

For each flock we recorded the behavior of 1 to 10 adults and 1 to 5 juveniles; the numbers recorded of each were approximately proportional to the numbers in the flock. Individuals were selected randomly, but at more or less regular distance intervals along the flock's longest diameter to avoid biases due to individual's position in the flock (Inglis and Lazarus 1981). Birds were aged as adults or juveniles (first-winter birds) on the basis of their head and neck color (Cramp and Simmons 1980). We observed adults and juveniles in order to control for possible age differences in our sample due to flock size, food availability, ground type, or other physical or social factor (see Alonso et al. 1987a). Whenever possible, we recorded whether the focal adult was identified as a parent of a family or not. Crane flocks varied in size and age composition from one isolated family (a mated pair with their accompanying one or two juveniles) to large groups composed mainly of adults without offspring (immatures, nonbreeders and/or failed breeders) plus a variable number of families. Frequently, we could identify families even in large flocks by the continual spatial proximity of parents and offspring.

From 1980 to 1983 we observed 882 focal individuals for 3 min through 60–90× telescopes. Times spent in the following activities were recorded to the nearest second: feeding (head down); vigilance (head up with stretched neck); preening; and aggression. All other activities, including flying, also were recorded in the field, but were pooled in the "other" category for analysis. During 1984–1986 we reduced observation time of focal birds to 1 min, and recorded the rate of food intake, easily identified by the characteristic swallowing movement, and the number of paces taken by the bird. The mean dry masses of seeds were significantly different between cereal-stubble fields (0.027 g, $n = 935$ seeds from 50 different fields), cereal-sown fields (0.033 g, $n = 3,000$ seeds from 10 different fields), and sunflower-stubble fields (0.064 g, $n = 836$ seeds from 10 different fields). Therefore, we estimated food intake rate as the product of the number of seeds ingested per minute and the mean dry mass of the corresponding seed sample. We defined net intake rate as the dry mass ingested per minute spent feeding (i.e. engaged in head down), and absolute intake rate as the dry mass ingested per minute of observation. We analyzed the seasonal variation and differences among bird groups (juveniles; parent and nonparent adults) in: percent time devoted to each activity; net and absolute intake rates; and mean duration of activity bouts, taking each observation period as a data point. Additionally, since changes in both photoperiod and moonlight intensity affect the total time spent by the cranes on the foraging grounds (see Alonso et al. 1985), we also calculated monthly averages for total daily time devoted to each activity and total daily food consumption. These were obtained by multiplying time-budget percentages and absolute food-intake rate by the monthly mean time cranes spent on the feeding areas, defined here as total daily activity period. To calculate the time, we determined the difference between the mean roost departure and arrival times on 112 days evenly distributed throughout the six winter seasons. Later we subtracted 15 min to account for the flying time from the roost to the first morning feeding sites, where we began observations, plus 5 min for the flying time between the last evening feeding sites and the roost (estimated from our data on individual radio tracking; for detailed description of roosting-flight counts, see Alonso et al. 1985).

We also studied seasonal trends in net intake rate separately for stubble and sown fields. This allowed us to explore the relative importance of encounter rate and handling time as limiting factors. We assumed that in sown grounds net intake rate was limited mainly by the encounter rate, rather than by handling time, since digging up each cereal seed takes much more time than handling it. The opposite was assumed for stubble fields, where the abundance of superficial grain determined a high encounter rate; and handling each individual seed probably was the
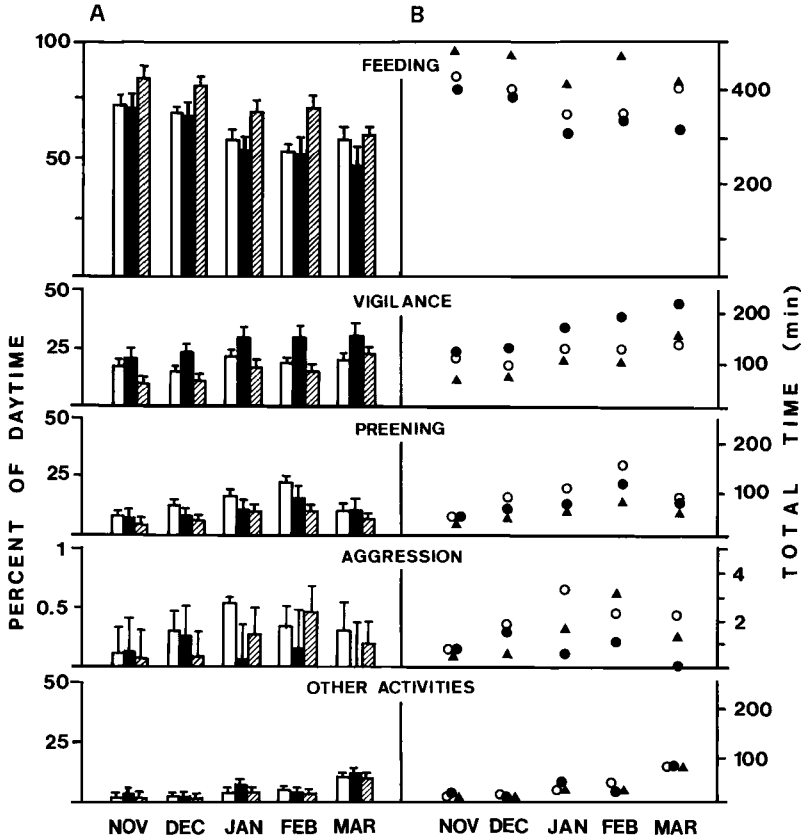
Fig. 1. Seasonal variation in (A) percent time and (B) total daily time spent on different activities by nonparent adults (white bars and dots), parents (black bars and dots), and juveniles (hatched bars and black triangles). The 95% confidence intervals of percent times shown. Note the different scale in aggression. Sample sizes from November to March: 353, 586, 416, 497, and 302 for nonparents; 107, 130, 106, 79, and 63 for parents; and 189, 269, 216, 234, and 219 for juveniles.

limiting factor (for similar approach, see Sutherland et al. 1986).

Sample sizes, respectively, for 1980–1981 through 1985–1986, were 427, 407, 48, 1,659 and 1,297 focal birds. We tested interannual differences in behavior by comparing monthly samples from each year, and found significant differences (Mann-Whitney U-test) only between: December 1984 and 1985 in percent time feeding in nonparent adults; and between January 1985 and 1986 in percent time feeding in juveniles. We also tested possible differences between the 1980–1983 and the 1984–1986 samples. Daily and seasonal trends and age differences were identical in both data groups. Thus, we combined the data from the six winter seasons for analysis resulting in 3,132 min for nonparent adults (2,154 birds), 705 min for parents (485 birds), and 1,765 min for juveniles (1,199 birds).

Since all activities defined were not always performed by focal birds within the observation period, many distributions were skewed or had a relatively large number of zero scores. No suitable transformation was available for distributions like these (see also Goss-Custard and Durell 1987a). Therefore, we analyzed data by nonparametric methods (Mann-Whitney U-test or Kruskal-Wallis test; Siegel 1956). To further assess reliability of our results, subsets of these variables excluding zero scores (which were analyzed separately) also were subjected to equivalent parametric tests (t-test and ANOVA) after logarithmic transformation (bouts and intake rates) or arcsin transformation (percent times). Since feeding time increased with flock size (unpubl. data), we also performed analyses of covariance (Sokal and Rohlf 1969) on all variables including the logarithm of flock size as a covariate. Two-tailed probability values are given for all analyses.

RESULTS

Seasonal trends in time budget.—Percent time feeding decreased throughout the winter in all

birds (Fig. 1A; Kruskal-Wallis test, all $P < 0.001$). Percent time spent on vigilance increased with season in parents and juveniles (Kruskal-Wallis test, $P = 0.026$, and $H = 30.76$, $P < 0.001$, respectively $H = 11.07$), but did not change in nonparent adults ($H = 7.46$, $P = 0.113$). Total daily feeding time also decreased with season, except for small increases in February for parents and juveniles, and in March for nonparent adults (Fig. 1B). Total daily vigilance time still showed an increasing seasonal trend. The time spent preening increased between November and February, and decreased in March in all birds based on percent times (Fig. 1A; $H = 62.79$, $P < 0.001$ in nonparent adults; $H = 9.96$, $P = 0.041$ in parents; and $H = 7.26$, $P = 0.123$ in juveniles) and total times (Fig. 1B). The time spent on aggression showed a peak in midwinter in nonparent adults (Fig. 1A, $H = 22.72$, $P < 0.001$; see also Fig. 1B), did not change in parents ($H = 2.97$, $P = 0.562$), and increased with season in juveniles ($H = 9.86$, $P = 0.043$). The time devoted to other activities increased in all birds ($H = 33.66$, 21.89, and 53.15, respectively, for nonparents, parents and juveniles; all $P < 0.001$).

Cranes interrupted feeding with short vigilance bouts (only a few seconds, see below) or long resting-preening bouts (several minutes to over 1 h). Therefore, our observation periods included many samples with zero feeding, which corresponded mostly to resting time. This resting time increased with season in all birds (Fig. 2A). After eliminating resting time by excluding observation periods with zero feeding, the seasonal decreasing trend in percent feeding time and increasing trend in percent vigilance time remained in parents and juveniles (Fig. 2B; $F_{4,389} = 2.53$, $P = 0.040$ for feeding time in parent adults; $F_{4,1005} = 4.98$, $P < 0.001$ for feeding time in juveniles; $F_{4,389} = 3.05$, $P = 0.017$ for vigilance time in parent adults; $F_{4,1005} = 4.59$, $P = 0.001$ for vigilance time in juveniles). Seasonal trends remained unchanged in nonparent adults. This suggests that the "true" vigilance time (i.e. during feeding) did increase with season in parents and juveniles, but not in nonparent adults.

Seasonal trends in activity bouts.—The length of feeding bouts did not change in parents ($F_{4,166} = 0.68$, $P = 0.608$), decreased in juveniles ($F_{4,236} = 4.70$, $P = 0.001$), and was not clear in nonparent adults (Fig. 3A). The length of vigilance bouts increased with season in all birds ($F_{4,1487}$
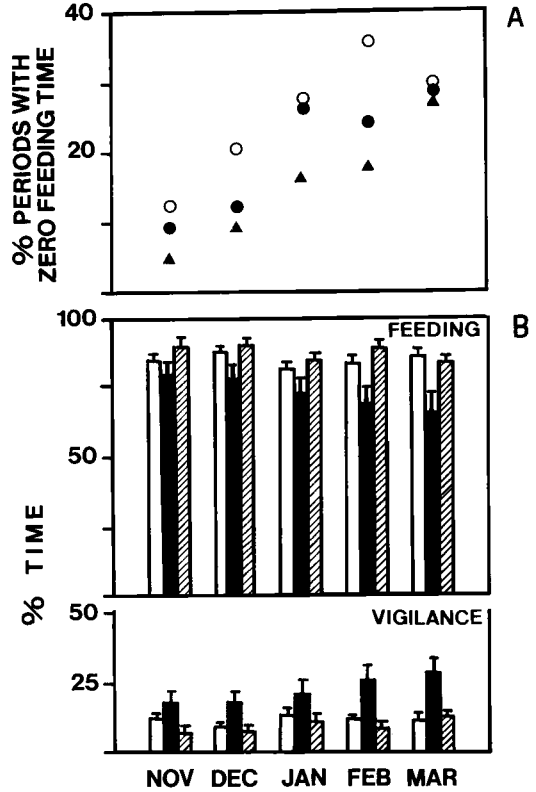

Fig. 2. Seasonal variation in number of observation periods with (A) zero feeding time, and (B) percent time spent feeding and alert, excluding periods with zero feeding time. White dots and bars for nonparent adults; black dots and bars for parent adults; hatched bars and black triangles for juveniles. The 95% confidence intervals of percent times shown. Sample sizes from November to March: 309, 464, 300, 318, and 211 for nonparents; 97, 114, 78, 60, and 45 for parents; and 180, 245, 181, 192, and 212 for juveniles.

$= 2.98$, $P = 0.018$ in nonparents; $F_{4,422} = 7.41$, $P < 0.001$ in parents, and $F_{4,717} = 7.05$, $P < 0.001$ in juveniles), but this increase was due to the seasonal increase of the vigilance bout in the subsample of zero feeding in nonparent adults and juveniles ($F_{4,450} = 3.98$, $P = 0.003$, and $F_{4,150} = 3.51$, $P = 0.009$, respectively). Excluding zero feeding observations, the seasonal increasing trend disappeared in nonparent adults and juveniles ($F_{4,1032} = 1.75$, $P = 0.137$, and $F_{4,562} = 1.94$, $P = 0.102$, respectively). However it remained in parents ($F_{4,344} = 4.14$, $P = 0.003$; Fig. 3B), in which the duration of the vigilance bout in the zero-feeding subsample (i.e. resting and preening) did not change with season ($F_{4,73} = 2.46$, $P > 0.05$). The length of preening bouts did not
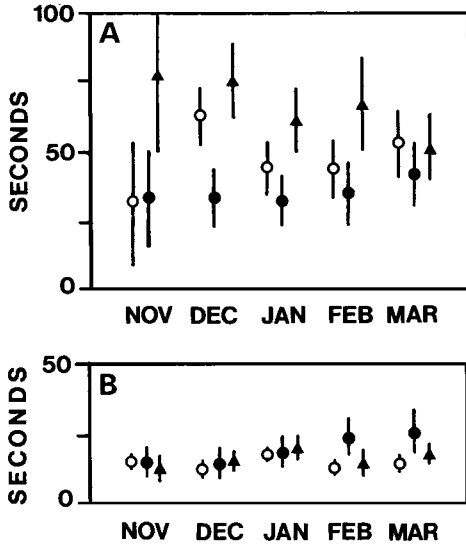
Fig. 3. Seasonal variation in mean duration of (A) feeding bouts and (B) vigilance bouts. White dots for nonparent adults; black dots for parent adults; triangles for juveniles. The 95% confidence intervals shown.

change with season ($F_{4,125} = 1.15$, $P = 0.334$ in nonparents, $F_{4,86} = 1.65$, $P = 0.168$ in parents, and $F_{4,87} = 0.24$, $P = 0.870$ in juveniles).

Age and parent versus nonparent differences.— Cranes devoted most of their daily activity time to feeding, vigilance and preening. Although the percent time devoted to the sum of these activities was similar in parents, nonparents and juveniles (ca. 95% in all), their time budgets clearly differed (Table 1; chi-square test, $P < 0.001$ in all intergroup comparisons). Juveniles spent more time feeding than parents and nonparents in all months, the difference being less marked in March (Fig. 1A; Mann-Whitney test, $P < 0.001$ until February, $P = 0.004$ in March). Parents devoted less time to feeding than nonparents through the whole winter, with monthly differences significant in November, December and January (Fig. 1A, Mann-Whitney test; $P = 0.003$, $P < 0.001$ and $P = 0.039$, respectively). Percent time spent not feeding was highest in nonparents, intermediate in parents, and lowest in juveniles, with all birds converging onto similar values in March (Fig. 2A). Excluding observation periods with zero feeding, each month parents showed the lowest percent time feeding and the highest percent time scanning (Fig. 2B, Student's *t*-test, $P < 0.001$ in all comparisons

with other birds). Juveniles showed the highest feeding and lowest vigilance times, although the latter equalled nonparent values in March ($P < 0.01$ between November and February; in March, $t = 0.73$, $P = 0.466$ for feeding time, and $t = 0.02$, $P = 0.980$ for vigilance time).

Parents did not differ from nonparents and juveniles in monthly percent time spent preening (Fig. 1A; Mann-Whitney test, $P > 0.05$ in all monthly comparisons). Juveniles spent less time preening than nonparents between November and February ($P < 0.01$), but equalled them in March ($P = 0.739$). There were no monthly differences in time devoted to other activities (Fig. 1A, all comparisons $P > 0.05$).

The mean feeding bout was longest in juveniles, intermediate in nonparents, and shortest in parents (Fig. 3A; $P < 0.05$ in all monthly comparisons except parents vs. nonparents in November and February), but the differences disappeared in March ($P > 0.35$ in all March comparisons). There were no monthly differences in the mean durations of vigilance bout and preening bout, except in February and March, when parents showed longer vigilance bouts than nonparents and juveniles (Fig. 3B; $P < 0.01$).

Seasonal trends and age differences in intake rate.— Net intake rate decreased with season in all birds (Fig. 4A, $F_{4,1266} = 64.24$ in nonparent adults, $F_{4,213} = 8.82$ in parents, and $F_{4,750} = 25.05$ in juveniles; all $P < 0.001$). Net intake rate was much higher in stubble fields than in sown fields ($F_{1,1404} = 78.43$, $P < 0.001$). Therefore, we analyzed separately the seasonal trend in stubble fields and sown grounds. The decrease was significant for stubble fields only in adults ($F_{3,768} = 7.10$, $P < 0.001$); for sown grounds, differences were significant for both age groups ($F_{4,633} = 17.46$ in adults, $F_{4,338} = 7.89$ in juveniles; both $P < 0.001$). Net intake rate of parents was higher than that of nonparents (Fig. 4A; Student's *t*-test, $P < 0.001$ in December, February and all-winter sample). Intake rate of nonparents was higher than that of juveniles between November and January ($P < 0.05$), and almost higher in February ($P = 0.066$). In March, there were no age and parent/nonparent differences ($P > 0.25$). Absolute intake rate also decreased with season in all birds (Fig. 4B; Kruskal-Wallis test, $H = 205.53$, 31.91 and 122.13, respectively, for nonparents, parents and juveniles, all $P < 0.001$). Parents had higher intake values than nonparents and juveniles in December and in the all-

TABLE 1. Time budget and mean duration of activity bouts ($\bar{x} \pm$ SE, with n in parentheses) in wintering Common Cranes.

	Parents	Nonparents		Juveniles			Significance of differences[a]		
							Parents/ nonparents	Parents/ juveniles	Non- parents/ juveniles
Percent time									
Feeding	59.76 ± 1.68 (485)	62.47 ± 0.89	2,154	72.60	1.08	1,199	***	***	***
Vigilance	25.50 ± 1.19 (485)	17.90 ± 0.54	2,154	15.15	0.71	1,199	***	***	***
Preening	10.38 ± 1.10 (485)	15.00 ± 0.65	2,154	7.90	0.61	1,199	ns	**	***
Aggression	0.13 ± 0.07 (485)	0.33 ± 0.05	2,154	0.22	0.05	1,199	*	ns	*
Other activities	4.23 ± 0.72 (485)	4.30 ± 0.38	2,154	4.22	0.48	1,199	*	ns	ns
Mean duration of bout (seconds)									
Feeding[b]	35.13 ± 2.51 (171)	49.44 ± 2.62	309	62.90	3.24	241	***	***	***
Vigilance[c]	9.26 ± 0.63 (349)	7.52 ± 0.27	1,037	8.17	0.46	567	***	**	ns
Preening	13.58 ± 1.77 (91)	11.76 ± 1.16	130	11.64	1.92	92	ns	ns	ns

[a] ns, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; Mann-Whitney U-test for differences in percent time; Student's t-test with logarithmic transformation for differences in duration of bouts.

[b] Only observation periods of 3 min.

[c] Observation periods with zero feeding excluded.

winter samples (Mann-Whitney test, $P < 0.001$, also $P < 0.01$ in February with nonparents), but no differences were found for March ($P > 0.50$). Nonparents and juveniles did not differ in absolute intake rate ($P > 0.10$ in all months, $P = 0.857$ in all-winter sample).

Age differences in pacing rate, encounter rate and handling time.—The pacing rate was studied excluding samples with no feeding given that this variable was included to provide an estimate of the feeding costs. Because the pacing rate is greatly influenced by the type of feeding ground, we analyzed it separately for stubble and sown fields. The pacing rate of juveniles was higher than that of adults only in sown fields (Mann-Whitney test, $P = 0.007$), suggesting a lower capability of juveniles in detecting where to dig up the sown grain.

Net intake rate in sown grounds differed with age only considering the all-winter sample ($t = 3.448$, df $= 979$, $P < 0.001$), but not month by month. Assuming that net intake rate is limited in sown grounds by the encounter rate (see Methods), the subtle differences found suggest that the encounter rate was only slightly higher in adults compared to juveniles. In stubble fields, where the limiting factor was assumed to be handling time, age differences were significant between November and January (t-test, all months $P < 0.005$), but disappeared in February ($t = 0.625$, df $= 65$, $P = 0.534$). Thus, the longer

handling times in juveniles could be the major cause of their lower net intake rates between November and January.

Effect of brood size.—There were no significant differences in time budget and intake rate between parents with one and two offspring (Mann-Whitney test, df $= 483$, $P = 0.115$ for feeding time and $P = 0.100$ for vigilance time, and df $= 216$, $P = 0.251$ for net intake rate; Student's t-test, df $= 216$, $P = 0.707$ for absolute intake rate).

Effect of flock size on parent/nonparent differences.—Since the time budget of wintering cranes changes with flock size (in prep.), we performed ANCOVAs on percent times feeding and alert, and on net and absolute food intake rates, including both the factor parent versus nonparent and the logarithm of flock size as a covariate (classes 1–8). The results showed that the differences between parents and nonparents still were highly significant after accounting for flock size ($F_{1,1981} = 32.92$ for feeding time, $F_{1,1981} = 25.80$ for vigilance time, and $F_{1,1486} = 7.22$ for net intake, all $P < 0.001$; $F_{1,1486} = 4.04$, $P < 0.05$ for absolute intake rate).

Comparing the time budgets of parents in isolated families with those in families included in flocks, the former devoted less time to feeding and more time to vigilance (Fig. 5; $t = 3.30$, 392 df, $P = 0.001$, and $t = 3.62$, 392 df, $P < 0.001$, respectively). However, since parents in isolat-
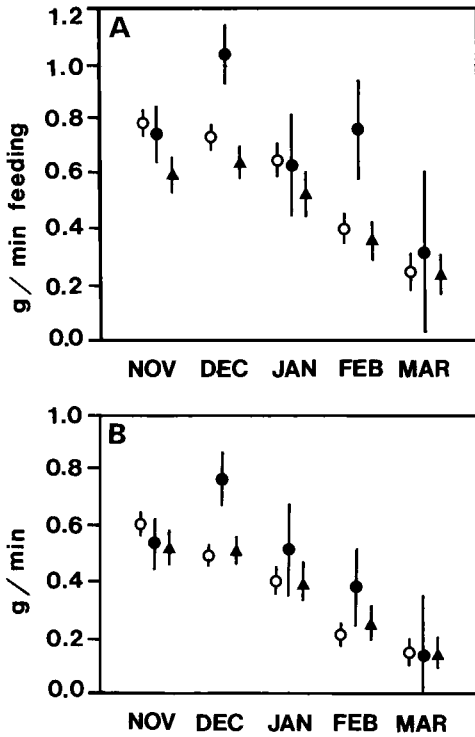
Fig. 4. Seasonal variation in (A) net food intake rates and (B) absolute food intake rates. White dots for nonparent adults; black dots for parents; triangles for juveniles. The 95% confidence intervals shown.

ed families had a higher net intake rate (Fig. 6; $t = 2.29$, df $= 216$, $P = 0.023$), the absolute intake rate did not differ between both groups of parents (Fig. 6; $t = 0.82$, df $= 216$, $P = 0.411$).

Advantages of parental care to offspring.—Only a few juveniles were seen clearly isolated from adult birds at the end of the winter, when their parents depart on migration (Alonso et al.
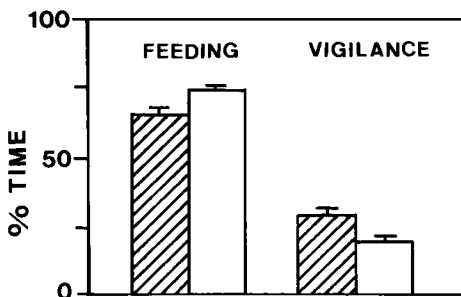

Fig. 5. Comparison between mean percent times spent feeding and alert by parents in isolated families (hatched bars) versus families included in flocks (white bars). Whiskers indicate SE.
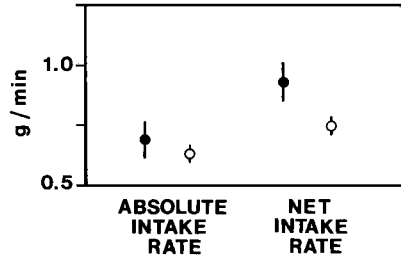

Fig. 6. Comparison between mean absolute and net intake rates (± 1 SE) of parents in isolated families (black dots) vs. families included in flocks (white dots).

1984b). Most independent or nearly independent juveniles remained in flocks of other adults without offspring or with still dependent offspring. This made it difficult to quantify the degree of independence of juveniles seen in flocks and, therefore, to separate the effects of being in a flock from being still dependent on their parents. Thus, to study the advantages of parental care to offspring, we used two different approaches. First, we compared the time budgets of juveniles clearly dependent on their parents, but included in flocks with those in isolated families. The time devoted to feeding was virtually identical ($t = 0.02$, df $= 347$, $P = 0.985$) and that devoted to vigilance did not differ ($t = 0.36$, df $= 347$, $P = 0.720$) between both groups of juveniles (Fig. 7). Juveniles in isolated families had slightly higher net intake rates (Fig. 8; $t = 2.01$, df $= 199$, $P = 0.046$), although the absolute intake rates of both groups did not differ (Fig. 8; $t = 1.55$, df $= 199$, $P = 0.122$). Also, juveniles were involved in more aggressive encounters with increasing flock size (Spearman's $r_s = 0.952$, $n = 8$ log-transformed classes, $P = 0.012$).

Second, we excluded isolated families to eliminate their advantageous effect for juveniles, and compared the intake rate of juveniles clearly identified as still dependent on their parents (i.e. those that followed adults closely) with that of juveniles not clearly attached to adult birds. Both absolute and net intake rates were higher in the former ($F_{1,753} = 15.08$ and $F_{1,753} = 12.64$, both $P < 0.001$, respectively). However, ANCOVA accounting for flock size as a covariate resulted in a nonsignificant effect of degree of dependence from the parents ($F_{1,750} = 2.64$, $P = 0.104$, and $F_{1,750} = 1.86$, $P = 0.174$, respectively). Juveniles clearly dependent on their parents also suffered fewer attacks than those less attached to parents ($X^2 = 95.12$, $P <$
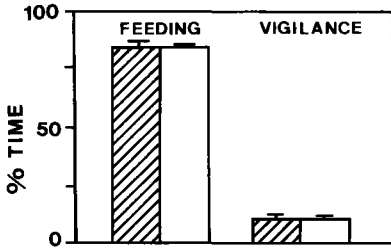
Fig. 7. Comparison between mean percent times spent feeding and alert by juveniles in isolated families (hatched bars) vs. juveniles in families included in flocks (white bars). Whiskers indicate SE.

0.001, $n = 359$ and 221, respectively). In fact, juveniles were seen more frequently on the periphery of flocks than in the center (67% vs. 33% of all juveniles seen in flocks; chi-square test, $P < 0.001$).

DISCUSSION

Seasonal variation of food intake rate.—The simultaneous analyses of both percent and absolute times spent feeding and resting and of both net and absolute intake rates help in understanding to what extent changes in food intake rate are motivational or conditioned by external factors. The proportion of daily activity time that wintering Common Cranes spent feeding versus resting, which is a good indicator of their feeding effort, was highest in autumn, just after arrival by the birds on the study area. At this time, birds probably need to replenish the energy spent on migration from their breeding grounds and spend the maximum possible time feeding, with a minimum time resting. The net intake rate, which represents the relative success of their feeding effort, and the absolute daily intake rate, which indicates their energetic needs, also were highest in autumn. All birds in autumn probably fed at the highest possible rate. The higher intake rates of parents may reflect a higher energy deficit from having reared offspring. The fact that some of the intake of juveniles is still being applied to growth at this time could explain the similarity between their intake rate and that of the heavier nonparent adults. The abundant cereal grain spilled during the previous harvest enables them to reach such high intake rates. Sown cereal in particular is a resource for which effective competitors are scarce, and cranes have achieved a high degree of specialization on such food (Alonso et al. 1984a, Sugden et al. 1988).
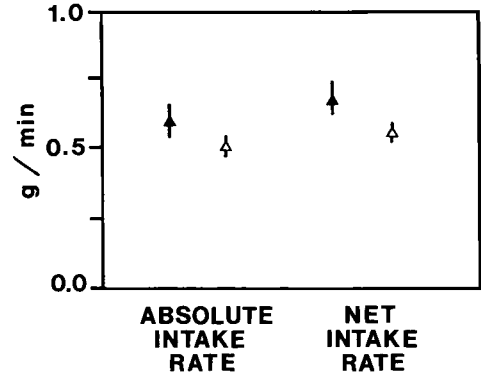

Fig. 8. Comparison between mean absolute and net intake rates (± 1 SE) of juveniles in isolated families (black triangles) versus juveniles in families included in flocks (white triangles).

The marked decreases in both percent and total times spent feeding between December and January, with only a small increase of 9 min in the cranes' daily activity period, together with the increase in percent time spent resting and on other activities, suggest that in midwinter birds were less stressed by food conditions than in autumn. However, the direct benefit from their feeding effort, expressed by the net intake rate, decreased slightly between November–December and January, suggesting that some depletion of food resources also was taking place. Finally, in February and March cranes ingested less food per day with a higher investment in feeding time. This was in part determined by the preponderance during late winter of sown fields in which cranes had to dig up the cereal seeds. Indeed, stubble fields used by the cranes had higher food availability ($\bar{x} = 92.5$ kg/ha, range 0–795) than sown grounds (ca. 5% of the 180 kg sown/ha estimated from maximum food consumption during a crop damage study; see Alonso et al. 1987b). However, an effect of satiation over the winter also may have played an important role, since time devoted to resting and other activities also increased during those months, and the large increase in daily activity time (1.0–1.5 h with respect to January) was not used mostly for feeding. Another fact suggesting that the decreasing net intake rate was not completely determined by lower food availability in late winter was that differences in net intake rate were detected independently in stubble fields and in sown fields (in the latter, food abundance did

not change among different fields, and depletion was usually insignificant).

The "free" time was longer in nonparent birds, which usually gathered during midday hours at secondary roosts where they rested, preened, bathed and drank. Parents fed more regularly throughout the day and spent less time resting. These results suggest that, after December, the photoperiod was not a limiting factor for intake rate. Cereal grain spilled on stubble fields was particularly abundant during the last two years of study, contrasting with other years in the same area, when the limiting effect of food availability on the number of cranes staging and their daily time budget had lasted for a longer time (Alonso et al. 1985).

We conclude that cranes acquire fat reserves as soon as possible over the winter period and later just feed to maintain appropriate intake levels. We think that the relatively long resting time recorded during this study might be reduced in other winter seasons when food conditions could be worse. Our preliminary data on seasonal changes in body mass (lowest during autumn and reaching highest levels already in January, in prep.) also support the conclusion of a voluntary rather than imposed decrease in food intake rate. This submaximal foraging violates a basic assumption of simple optimal-foraging models, and coincides with results from other recent studies (Sih 1982, Kaufman and Collier 1983, Goss-Custard et al. 1984, Erwin 1985, Swennen et al. 1989).

Cost of parental care.—In a previous study we reported that the breakup of most Common Crane families occurred at the end of the winter season, when many parents departed on spring migration leaving their offspring in the winter quarters (Alonso et al. 1984b). This behavior would only be adaptive if juveniles have already learned appropriate skills to ensure their survival. The results of the present study show that this is in fact the case. There was no parental aggression towards their offspring at the end of the dependence period. We do not know if juvenile independence is a gradual process that takes place throughout the winter, or a sudden one with no parent-offspring conflict. When juveniles arrived on our study area in autumn they were still dependent on their parents and followed them closely. The lower food-handling ability of juveniles decreases their net intake rate, but they compensate for it by feeding for longer periods. The result is that, as early

as autumn, the absolute daily intake rate of juveniles does not differ from that of nonparent adults. This measurable benefit to juveniles is possible at an apparent cost to their parents, which devote a substantial effort to vigilance (longer and more frequent vigilance bouts while foraging), and spend less time resting than nonparent adults.

Black and Owen (1989a) observed that parent Barnacle Geese (*Branta leucopsis*) that remained with young for the longest period bred more successfully the next year, and interpreted this as being due to a "contributor" effect of goslings staying in the family. They suggested that offspring staying in the family might assist parents by increasing the offsprings' own vigilance burden and, thus, decreasing their parents' (see also Brown 1982). In our study, however, the increasing vigilance effort with season by juveniles did not result in a decreasing effort by their parents, which in fact increased their vigilance time with season. This suggests that parents did not benefit in any substantial way from their offsprings' vigilance. The other suggestion for how offspring could help parents is by winning more aggressive encounters and so lessening their parents' burden in conflicts with neighbors. The seasonal increase in the frequency of aggressive encounters in which juvenile cranes were involved and the disappearance of parent aggression in March suggest that the increasing offspring experience in aggressive conflicts could help reducing parental investment.

The social context of family groups (presence or absence of additional birds) did not affect the feeding and vigilance efforts of juveniles. Furthermore, feeding and vigilance times of juveniles in flocks did not change with increasing flock size classes. Juveniles, in effect, always maximize their own feeding time, regardless of social conditions. However, since larger flocks are characterized by a higher frequency in both interference competition (Alonso et al. 1987a, b), and aggressive conflicts (this study), juveniles in flocks had lower net intake rates. Furthermore, when included in flocks, juveniles that clearly were dependent on their parents did not have higher intake rate than those less dependent. This suggests that interferences associated with increasing flock sizes outweighed the advantages of being still dependent, so that possible dependence benefits disappeared. Flocking, thus, was clearly disadvantageous for

all juvenile cranes. Coversely, the immediate effect of flocking on parent birds was an increase in feeding time, because vigilance was shared among more flock members. The longer time devoted by parents to vigilance in isolated families indicates that costs of parental care were higher than in families included in flocks.

The results of intake-rate analysis showed that parent cranes did not suffer from the decreased feeding time imposed by the parental care, despite the apparent costs inferred from parent versus nonparent, and from isolated versus included in flocks, differences in time budgets. In fact, parent cranes had higher net and absolute daily intake rates than nonparent adults, and they also had a higher net intake rate and the same absolute intake rate when families were isolated than when they were included in a flock. Since the contributor effect of their offspring seems not to be the main factor determining this parent benefit, we hypothesize that parents were more experienced, including possibly older, individuals than nonparents, and were capable of compensating for the higher vigilance investment when the family was isolated. This agrees with some findings on individual quality and breeding success in other bird species (review in Newton 1989). The results of our study suggest that parental care involved no cost to parent birds in terms of reduced intake rate and, thus, provide little evidence of parent-offspring conflict. Nevertheless, in evolutionary terms, increased vigilance time by parent cranes could probably affect parents' fitness in more critical situations with respect to food availability.

LITERATURE CITED

ALONSO, J. A., J. C. ALONSO, AND J. P. VEIGA. 1984a. Winter feeding ecology of the Crane in cereal farmland at Gallocanta, Spain. Wildfowl 35:119–131.

ALONSO, J. A., J. C. ALONSO, AND J. P. VEIGA. 1985. The influence of moon light on the timing of roosting flights in Common Cranes *Grus grus*. Ornis Scand. 16:314–318.

ALONSO, J. C., J. A. ALONSO, AND J. P. VEIGA. 1987a. Flocking in wintering Common Cranes *Grus grus*: Influence of population size, food abundance and habitat patchiness. Ornis Scand. 18:53–60.

ALONSO, J. C., J. P. VEIGA, AND J. A. ALONSO. 1984b. Famimlienauflösung und Abzug aus dem Winterquartier beim Kranich *Grus grus*. J. Ornithol. 125:69–74.

ALONSO, J. C., J. P. VEIGA, AND J. A. ALONSO. 1987a. Possible effects of recent agricultural development on the wintering and migratory pattern of *Grus grus* in Iberia. Pages 277–299 *in* Proceedings of the III International Crane Workshop (G. Archibald and R. F. Pasquier, Eds.). Intl. Crane Foundation, Baraboo, Wisconsin.

ANKNEY, C. D., AND C. D. MacINNES. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. Auk 95:459–471.

BLACK, J. M., AND M. OWEN. 1989a. Parent–offspring relationships in wintering Barnacle Geese. Anim. Behav. 37:187–198.

BLACK, J. M., AND M. OWEN. 1989b. Agonistic behaviour in Barnacle Goose flocks: Acquisition of social rank in young geese. Behaviour 102:129–146.

BROWN, J. L. 1982. Optimal group size in territorial animals. J. Theor. Biol. 95:793–810.

BURGER, J. 1987. Foraging efficiency in gulls: A comparison of age differences in efficiency and age of maturity. Pages 83–90 *in* Ecology and behaviour of gulls (J. L. Hand, W. E. Southern, and K. Vermeer, Eds.). Stud. Avian Biol. No. 10.

CATTERALL, C. P., J. KIKKAWA, AND C. GRAY. 1989. Inter-related age-dependent patterns of ecology and behaviour in a population of Silvereyes (Aves: Zosteropidae). J. Anim. Ecol. 58:557–570.

CLUTTON-BROCK, T. H. 1991. The evolution of parental care. Princeton Univ. Press, Princeton, New Jersey.

CRAMP, S., AND K. E. L. SIMMONS (Eds.). 1980. The birds of the western Palearctic, vol. 2. Oxford Univ. Press, Oxford.

DAVIES, C. J., AND F. COOKE. 1983. Annual nesting productivity in Snow Geese: Prairie droughts and arctic springs. J. Wildl. Manage. 47:291–296.

DRAULANS, D. 1987. The effect of prey density on foraging behaviour and success of adult and first-year Grey Herons (*Ardea cinerea*). J. Anim. Ecol. 56:479–494.

DRAULANS, D., AND J. VAN VESSEM. 1985. Age-related differences in the use of time and space by radio-tagged Grey Herons (*Ardea cinerea*) in winter. J. Anim. Ecol. 54:771–780.

ERWIN, R. M. 1985. Foraging decisions, patch use,

and seasonality in egrets (Aves: Ciconiiformes). Ecology 66:837–844.

GAUTHREAUX, S. A., JR. 1978. The ecological significance of behavioral dominance. Pages 17–54 in Perspectives in ethology (P. P. G. Bateson and P. H. Klopfer, Eds.). Plenum, New York.

GOSS-CUSTARD, J. D., R. T. CLARKE, AND S. E. A. LE V. DIT DURELL. 1984. Rates of food intake and aggression of Oystercatchers Haematopus ostralegus on the most and least preferred mussel Mytilus edulis beds on the Exe estuary. J. Anim. Ecol. 53: 233–245.

GOSS-CUSTARD, J. D., AND S. E. A. LE V. DIT DURELL. 1987a. Age-related effects in Oystercatchers Haematopus ostralegus, feeding on mussels Mytilus edulis. II. Aggression. J. Anim. Ecol. 56:537–548.

GOSS-CUSTARD, J. D., AND S. E. A. LE V. DIT DURELL. 1987b. Age-related effects in Oystercatchers Haematopus ostralegus, feeding on mussels Mytilus edulis. III. The effect of interference on overall intake rate. J. Anim. Ecol. 56:549–558.

GREIG-SMITH, P. W. 1985. Winter survival, home ranges and feeding of first year and adult Bullfinches. Pages 387–392 in Behavioural ecology (R. M. Sibly and R. H. Smith, Eds.). Blackwell Scientific Publications, Oxford.

HEINSOHN, R. G. 1987. Age-dependent vigilance in winter aggregations of cooperatively breeding White-winged Choughs (Corcorax melanorhamphos). Behav. Ecol. Sociobiol. 20:303–306.

INGLIS, I. R., AND J. LAZARUS. 1981. Vigilance and flock size in Brent Geese. The edge effect. Z. Tierpsychol. 57:1913–200.

KAUFMAN, L., AND G. COLLIER. 1983. Meal-taking by domestic chicks (Gallus gallus). Anim. Behav. 31: 397–403.

MONAGHAN, P. 1980. Dominance and dispersal between feeding sites in the Herring Gull (Larus argentatus). Anim. Behav. 28:521–527.

NEWTON, I. (ED.). 1989. Lifetime reproduction in birds. Academic Press, London.

RYDER, J. P. 1970. A possible factor in the evolution of clutch size in Ross' Geese. Wilson Bull. 82:5–13.

SIEGEL, S. 1956. Nonparametric statistics for the behavioural sciences. McGraw-Hill, New York.

SIH, A. 1982. Optimal patch use: Variation in selective pressure for efficient foraging. Am. Nat. 102: 666–685.

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. W. H. Freeman and Co., San Francisco.

SUGDEN, L. G., R. G. CLARK, E. J. WOODSWORTH, AND H. GREENWOOD. 1988. Use of cereal fields by foraging Sandhill Cranes in Saskatchewan. J. Anim. Ecol. 25:111–124.

SUTHERLAND, W. J., D. W. F. JONES, AND R. W. HADFIELD. 1986. Age differences in the feeding ability of Moorhens Gallinula chloropus. Ibis 128:414–418.

SWENNEN, C., M. F. LEOPOLD, AND L. L. M. DE BRUIJN. 1989. Time-stressed Oystercatchers, Haematopus ostralegus, can increase their intake rate. Anim. Behav. 38:8–22.

TRIVERS, R. L. 1972. Parental investment and sexual selection. Pages 136–179 in Sexual selection and the descent of man (B. Campbell, Ed.). Aldine, Chicago.

TRIVERS, R. L. 1974. Parent–offspring conflict. Am. Zool. 11:249–264.