AGGREGATION SIZE AND FORAGING BEHAVIOUR OF WHITE STORKS *Ciconia cinconia* DURING THE BREEDING SEASON

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ABSTRACT   The foraging behaviour of breeding White Storks *Ciconia ciconia* was studied at a colony in central Spain to test various predictions related to the advantages of flocking. Storks devoted more time to preening and resting with increasing aggregation size. Time spent vigilant by individual Storks decreased significantly as aggregation size increased, mainly due to a reduction of scan duration. Locomotion pattern changed significantly with aggregation size: birds in flocks walked head-up less frequently than solitary individuals. Absolute food intake rate was higher in larger aggregations. This was mainly attributable to lower vigilance intensity as aggregation size increased. Net feeding rates were also higher in larger aggregations. Aggregation size increased with distance to the colony. This was interpreted as a trade-off between travel and vigilance times in order to maximize foraging time. Aggregation of foraging Storks was explained both as a response to predation pressure and as a strategy to improve foraging efficiency through local enhancement.

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INTRODUCTION

Two nonexclusive groups of hypotheses have been advanced to explain the adaptiveness of foraging in flocks: enhanced predator avoidance and increased foraging efficiency (reviewed in Bertram 1978, Morse 1980, Barnard 1983, Krebs & Davies 1987). The first predicts that flocking allows an increase in overall vigilance thus enabling individuals to devote more time to other activities and to achieve a higher feeding rate. Alternatively, the increased foraging efficiency hypothesis predicts that individuals increase their mean food intake rate and reduce its variance through local enhancement around newly discovered food patches. Detailed analysis of scanning behaviour and food intake rates of flock members is necessary in order to assess the relative importance of both hypotheses mentioned. Although many authors have recently investigated the scanning behaviour of birds, relatively few field studies analyse the alternative tactics used by individuals joining a flock to decrease the time spent vigilant, i.e., to reduce the rate of scans or the duration of each scan (but see e.g. McVean & Haddlesley 1980, Studd *et al.* 1983, Glück 1987a). Also, the locomotion patterns of birds while foraging have been only rarely analysed in detail, despite its implications on the efficiency and costs of different food searching strategies. Other testable predictions may be proposed in relation with distance to the feeding site for flock foragers that travel from a central place to feed. For example, according to the reduction-in-vigilance hypothesis, one could predict an increase in flock size as the distance to the feeding site increases: joining a larger flock would enable the individual to devote more time to feeding through a decrease in the time spent vigilant, and so compensate for the longer travel time (see Alonso *et al.* 1987). This relation is not necessarily expected from the local enhancement hypothesis.

White Storks *Ciconia ciconia* are gregarious during the non-breeding season, forming flocks of up to thousands of individuals. During the breeding season, immatures and non- breeders also gather in flocks, while breeding adults nest isolated or in

colonies (Bauer & Glutz 1973, Cramp 1977 Creutz 1985), and forage alone or in aggregations. Stork flocking behaviour may be interpreted as a response both to foraging efficiency and predators, not only at their wintering grounds (Creutz 1985) but also in the breeding areas, where they flee away mainly from dogs, foxes and humans (pers. obs.). The flocking behaviour of Storks and its implications on the foraging success of individuals of this species have not been investigated. In this paper we describe the foraging behaviour of breeding White Storks and discuss the advantages of flocking in relation with the two hypotheses mentioned above. In particular, we analyse the scanning and locomotion patterns of individual Storks and the implications of increased travel time to the feeding site in relation to the size of the aggregation.

STUDY AREA AND METHODS

The study was conducted at the largest White Stork colony of Central Spain (55 breeding pairs in 1988, pers. obs.), near El Escorial (30° 45'N, 04° 05'W), in spring 1988. The area consists of ca. 600 ha of flat wet pasture land used for cattle grazing, with Ash *Fraxinus angustifolia* and Elm *Ulmus campestris*, where the Stork nests are built, and interspersed woodlots of Holm *Quercus rotundifolia* and Pyrenean oaks *Q. pyrenaica*. When flying around the colony (in a radius of approximately 2 km), Storks can see all the foraging area and decide where to go for feeding or which flock to join. The study area is crossed by a motor road and by several tracks, and the pastures are frequently visited by farmers with dogs.

Study dates were restricted to April and first half of May, when most Storks are incubating, and a few pairs brood very small chicks which do not require much food from their parents. The food of adult Storks consist in our study area almost exclusively of earthworms (over 95% in number of items ingested, pers. obs.), which are very abundant in wet or flooded grasslands (mean = 77 earthworms m^{-2} according to own measurements). These circumstances minimized the effects of differences in individual food requirements and various foraging constraints derived from prey selection, such as searching and handling time (Pyke 1984, Stephens & Krebs 1986).

Focal birds were randomly chosen during regular surveys of the study area and their behaviour was tape-recorded during 3-12 minutes (average 5 minutes). Each individual was observed only once daily at any one spot. The number of independent periods recorded was 97, totalizing 444 minutes of continuous observation. For each bird we measured the distance to the centre of the colony and the number of storks forming the aggregation. We considered the following activities: resting, preening, scanning, walking head-up (when the head was raised above the back level) or head-down (head below the back level), and swallowing. The first three activities were expressed as time devoted per minute to each of them and the rest as rates, i.e. respectively as number of paces and items taken per unit time. We distinguished between 'absolute' and 'net' feeding rate (number of food items taken respectively per unit time of observation and per unit time spent strictly feeding, i.e. head-down). Those observation periods in which the bird devoted to resting plus preening more than 10 seconds per minute ($n = 20$) were excluded in the analyses of scanning, walking and feeding, to avoid strong effects non-foraging birds.

Aggregations of Storks varied between 1 and 45 birds. Although 50.5% of all observations were solitary birds, 67% of the foraging individuals were found in aggregations of more than 3 birds. In order to study the variation of aggregation size with distance to the centre of the colony a car transect through the whole study area was repeated nine times along the study period, plotting the location and size of Stork aggregations on maps 1:25000.

Statistical analyses included simple and partial correlations, one-way ANOVA, and residuals analysis. All variables were previously transformed by the square-root function, except aggregation size which was log-transformed (see Nie *et al.* 1975, Sokal & Rohlf 1979).

RESULTS

Storks showed a significant difference in the time spent preening and resting with increasing aggregation size (respectively $r = 0.201$, $P = 0.048$ and $r = 0.227$, $P = 0.025$, $n = 97$). Outside the nest, birds spent most of the time feeding and scanning (Fig. 1).
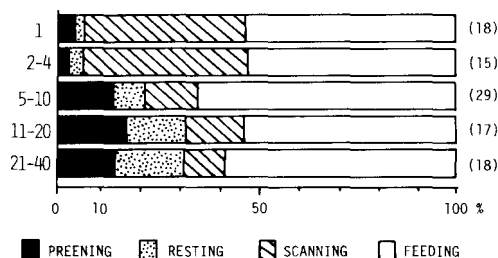

Fig. 1. Percentage of time devoted to each of the four main activities in foraging White Storks during the breeding season. Sample sizes between brackets

Time spent vigilant by actively foraging individual Storks decreased significantly as aggregation size increased (Table 1). This was mainly due to a shorter duration of each vigilance bout with increasing aggregation size (Fig. 2), since the frequency of scans did not change significantly between aggregation sizes.

The frequency of paces head-up decreased with increasing aggregation size, while the frequency

Table 1. Correlation between aggregation size and several parameters in foraging storks.

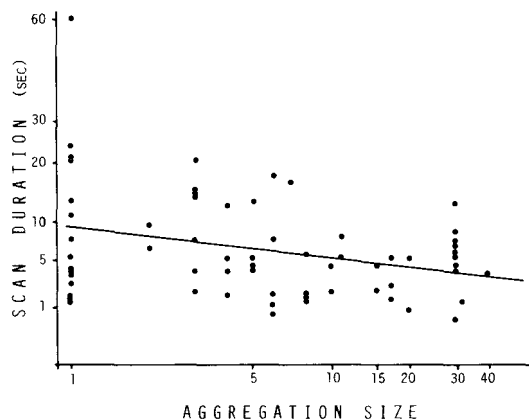| activity parameter	r	P	n
vigilance time (sec/min)	-0.314	0.006	74
scanning rate (no./min)	-0.153	0.194	74
mean scan duration (sec)	-0.325	0.009	64
paces head-up (no./min)	-0.435	0.0001	74
paces head-down (no./min)	-0.052	0.658	74
pecking rate (no./min)	0.347	0.002	74
absolute intake rate (no./min)	0.470	0.00002	74
net intake rate (no./min)	0.297	0.015	67
pecking success (%)	0.255	0.038	67

Fig. 2. Relationship between Stork aggregation size and mean scan duration.

of paces head-down did not change significantly (Table 1).

Pecking and absolute food intake rate (the number of earthworms eaten per minute of observation) increased with increasing aggregation size (Table 1). Also, the net intake rate (the number of earthworms eaten per minute spent feeding) and the pecking success (number of earthworms eaten divided by the number of pecks) increased with aggregation size (Table 1).

Aggregation size increased with increasing distance to the colony ($F_{2,91} = 3.55$, $P = 0.033$; Fig. 3). However, net feeding rate and pecking success did not change significantly with distance to the colony (ANOVA with the residuals of regression models
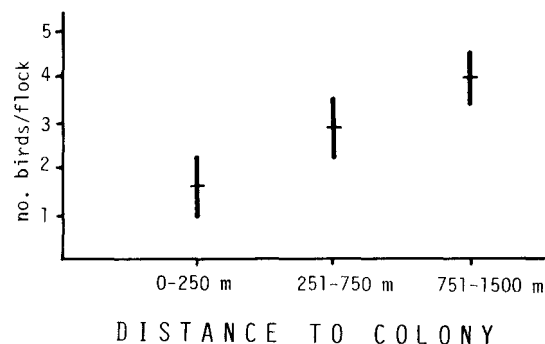

Fig. 3. Variation of aggregation size with distance to the colony. Vertical bars represent standard errors.

of both variables on aggregation size; net feeding rate: $F_{2,64} = 1.40, P = 0.26$; pecking success: $F_{2,64} = 0.57, P = 0.57$).

DISCUSSION

Our results show that aggregation enables foraging Storks to maximize food intake through a minimization of the time spent vigilant. This is surely of considerable adaptive value, given the low energetic content of earthworms (Cummins & Wuycheck 1971), their main prey in our study area. Moreover, minimization of the time necessary to obtain the daily food ration is surely advantageous for Storks since they need to devote a long time (approximately 50% of daytime) to breeding duties. Higher food intake rates in larger flocks have also been demonstrated in other bird species (e.g. Abramson 1979, Barnard 1980, Barnard & Stephens 1981, 1983, Lendrem 1984, Sullivan 1984, Glück 1986, 1987a, Popp 1986). The only cost of aggregation while foraging is a very small loss in feeding time (0.2%) due to a very low hostile interaction rate, only in aggregations of more than 7 birds (7 times in a sample of 51 birds and 233 minutes). However this cost is negligible compared to the time gained through reduction in vigilance (12.7%).

From the two possible tactics to reduce vigilance time when in larger aggregations, (a) reduce scan frequency and (b) reduce scan duration (see McVean & Haddlesley 1980, Lendrem 1984), Storks reduce scan duration but do not change scan frequency. Storks in large aggregations probably need only to scan for a few seconds just to assess that other flock members are still there, and devote proportionately less time to true predator detection, while the importance of these functions of vigilance could be inverted in birds foraging alone or in small or loose flocks (see e.g. Studd et al. 1983). We suggest that scanning rate might have been evolutionarily more fixed around certain critical levels necessary to warrant survival, mainly depending on predator approach time (cf. Pulliam 1973, Lendrem 1983, 1984, Hart & Lendrem 1984), or on the behaviour of other flock members (e.g. Studd et

al. 1983). By lengthening the scan duration Storks achieve a higher level of vigilance with lower frequency of changes between vigilant and non-vigilant states, thus saving the time and energy necessary to rise and lower their heads (see Studd et al. 1983) and not interrupting the search for hidden prey difficult to capture. Identical relationships between total vigilance time, mean scan duration and frequency of scans were found in House Sparrows Passer domesticus foraging in flocks (McVean & Haddlesley 1980, Studd et al. 1983). These results are also in accordance with the increased duration of scans observed in captive Goldfinches Carduelis carduelis just after appearance of a predator model, i.e. in situations of high predation risk (Glück 1987b).

Storks perform walking activity very differently when they are in small or large aggregations. In the former, birds walk more head-up due to their higher need to scan, loosing feeding time and spending extra energy on walking, whereas members of the later can concentrate their attention in looking for prey while walking head-down. The locomotion patterns of feeding birds are an interesting aspect of foraging behaviour which should receive more attention in the future.

As net intake rate does not change with distance travelled to the feeding site, we also interpret larger Stork aggregations at longer distances from the colony as a mechanism to compensate for the longer time needed to reach distant feeding areas. Joining a larger aggregation enables the individual to minimize vigilance time, with a consequent maximization of the absolute intake rate. This agrees with the idea of a higher foraging activity at longer distances from the central place (Orians & Pearson 1979, Lessels & Stephens 1983, see reviews in Barnard 1983, Stephens & Krebs 1986).

Resting and preening provide birds additional advantage for flocking since vigilance is shared among more individuals (see also Redpath 1988). However, the relative importance of this advantage is probably lower, since Storks devote most of their time outside the colony to foraging.

The results obtained demonstrate that Storks foraging in larger aggregations benefit from higher

absolute food intake rate due to decreased vigilance time. The alternative hypothesis of local enhancement in patches of higher food availability is also supported, given the correlation between the net intake rate and aggregation size. This has also been shown for many other bird species (e.g. Barnard 1980, Waite 1981, Goss-Custard 1984, Draulans 1987). We argue that the two hypotheses are non-exclusive, since partial correlations of net intake rate and total time head-up with aggregation size are both significant (respectively $r = 0.292$, $P = 0.014$, and $r = -0.394$, $P = 0.001$; $n = 67$).

We conclude that aggregation of foraging Storks is explained both as a response to predation pressure and as an adaptation to improving foraging efficiency through local enhancement.

ACKNOWLEDGEMENTS

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SAMENVATTING

Dit artikel gaat over het voordeel van foerageren in groepen. In dit geval zijn Ooievaars bestudeerd uit een broedkolonie in Midden Spanje, in de buurt van El Escorial. Er bestaan twee relevante hypothesen: (1) het foerageren in groepen geeft een betere bescherming tegen predatie, en (2) het foerageren in groepen leidt tot een toeneming in de foerageerefficiëntie. Hoewel deze vooronderstellingen elkaar niet uitsluiten, kunnen ze wel afzonderlijk onderzocht worden. De voorspellingen die uit beide hypothesen volgen, zullen elkaar slechts ten dele overlappen. Beide bleken geldig te zijn.

Bij de eerste hypothese passen de volgend resultaten: De tijd besteed aan waakzaam zijn was negatief gecorreleerd (vooral een effect op de duur van vlagen van waakzaamheid) aan de groepsgrootte. De tijd besteed aan rusten en poetsen bleek positief gecorreleerd (Fig.1). Er was geen duidelijk verband tussen groepsgrootte en de frequentie waarmee het foerageren werd onderbroken door waakzaamheid.

De volgende resultaten passen bij de tweede hypothese: waakzaamheid wordt ondermeer weerspiegeld door de locomotiehouding. Ooievaars die alleen foerageren lopen meer met de kop hoog, dan ooievaars die in groepen foerageren. De absolute, maar ook de netto voedselopname van solitair foeragerende ooievaars blijkt inderdaad kleiner te zijn dan die van individuen in groepen, vooral wanneer dat grote groepen zijn (Tabel 1). Interessant is dat de groepsgrootte toeneemt naarmate er verder van de kolonie gefoerageerd wordt (Fig. 3). Dit kan worden geïnterpreteerd als en afweging van de kosten van een grote reis tegen de baten van foerageren in een grote groep. - J.v.R.