

## **FLOCK SIZE AND FORAGING DECISIONS IN CENTRAL PLACE FORAGING WHITE STORKS, *CICONIA CICONIA***

by

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(With 1 Figure)  
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### **Summary**

We studied the foraging decisions of six individually marked white storks at a breeding colony in central Spain. Storks behaved as central place foragers, gathering in flocks to feed. Travel distance and patch residence time were positively correlated with the size of the foraging flock, but not with patch quality as estimated by the instantaneous food intake rate at the patch. Patch residence time was also positively correlated with travel distance to the patch, flock size being constant. In larger flocks individuals benefitted from a decrease in vigilance time and thus an increase in time spent actively feeding, which enabled birds to bring back to the nest a higher load size. These results suggest that storks followed simple rules of thumb based on flock size, rather than on the more complicated food availability estimations required by central place foraging models. We suggest that flock size could be the main cue used in foraging decisions by white storks and could be a simple rule for many other flock foraging species.

### **Introduction**

The main prediction derived from central place foraging (CPF) theory, that patch quality being equal patch residence time should increase as travel time between the central place and the patch increases (ORIAN & PEARSON, 1979), has been widely verified (see reviews in STEPHENS & KREBS, 1986; KREBS & KACELNIK, 1991). Most CPF studies, however, have been carried out with solitary foraging species. Few theoretical studies have directly addressed the question of social influences on forag-

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ing decisions in patches (CARACO, 1981; CLARK & MANGEL, 1986; VALONE, 1989). Empirical studies on such questions are also extremely scarce, and none of them has been carried out under completely natural conditions (PITCHER & MAGURRAN, 1983; MILINSKI, 1984; VALONE & GIRALDEAU, 1993).

A large number of studies have shown that foraging in flocks provides several benefits to flock members, mainly through enhanced predator avoidance and increased foraging efficiency (see reviews in MORSE, 1980; BARNARD, 1983; CLARK & MANGEL, 1984; PULLIAM & CARACO, 1984; KREBS & DAVIES, 1992). In a recent study on foraging behaviour of colonially breeding white storks, *Ciconia ciconia* (CARRASCAL *et al.*, 1990) we concluded that the main benefit obtained by individuals foraging in larger groups was an increase in food intake rate due to a decreased individual vigilance time. We interpreted larger feeding flocks at longer distances from the breeding colony as a mechanism to compensate, through flock feeding benefits, for the longer time needed to reach distant feeding patches. This suggested that white storks behaved as central place foragers which used flocking as a means to improve their feeding rate during foraging trips.

In the present study we hypothesize that storks departing from the colony to feed use foraging individuals as indicators of profitable patches and base their own foraging rules on the size of the flock which they join to feed. If flocks improve foraging efficiency through local enhancement (THORPE, 1963; see CARRASCAL *et al.*, 1990 for the white stork), and foraging in groups allows more time to feed, the size of a flock feeding in a patch might enhance the quality of that patch to the members of the flock or to a passing individual. Therefore, flock size could affect foraging decisions of gregarious foragers, independently of the food availability *per se* in the patch. We hypothesize that numbers of conspecifics already in patches would influence how far a bird should travel to feed and how long it should remain at a feeding patch. According to this hypothesis, we adapt the main predictions of CPF theory to a gregarious context by using flock size as an analogue of patch quality, and contrast the results with those obtained using the instantaneous food intake rate as an indicator of patch quality (the predictor variable in classical CPF models). The predictions tested were, first, that patch residence time should increase with increasing flock size. Second, that patch residence time and load size

should increase with distance travelled to the patch, flock size being constant (see Fig. 1). Third, that storks should therefore fly to increasingly distant patches only if large numbers of conspecifics are already feeding at these distant patches, because this enables individuals to increase load size through reduced vigilance time. Alternatively, if storks guide their foraging decisions on either their previous knowledge or their continuous assessment of intrinsic patch quality, they should fly longer distances and stay longer in patches where their instantaneous intake rate is higher.

### Study area and methods

The study area was located between El Escorial and Villalba (central Spain, 30°45'N, 04°05'W). It mainly consists of a large flat valley with wet pastures covered with dispersed Ash (*Fraxinus angustifolia*) and Elm (*Ulmus campestris*) trees, and open woods of Holm and Pyrenean oak (*Quercus rotundifolia* and *Q. pyrenaica*). The pasture land is used for extensive cattle grazing. The study area is crossed by two motor roads and several tracks, which are frequently used by farmers with dogs to visit the area. A large colony of ca. 60 white stork breeding pairs is located approximately in the middle of the study area. Storks feed in this area almost exclusively on earthworms (CARRASCAL *et al.*, 1990), which they capture in wet open pastures with streams and small ponds, their main foraging grounds. Birds avoid dense woodland areas, which offer a much lower food availability (ALONSO *et al.*, 1991).

In late March 1989 and 1990 we captured and radio-tagged nine birds (four males and

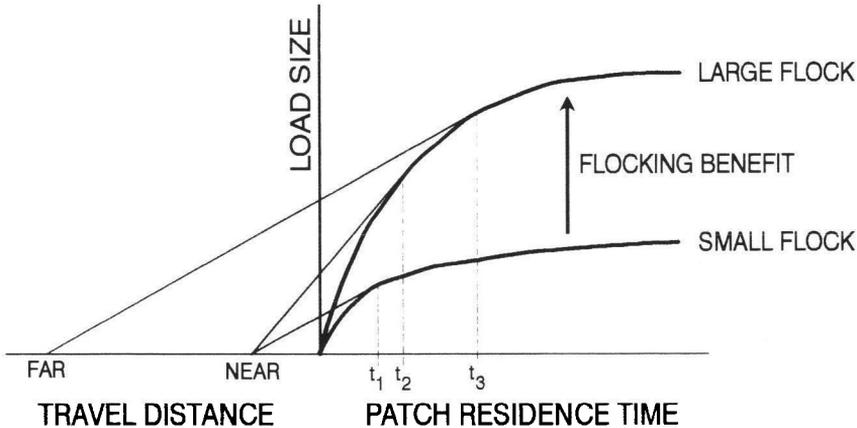


Fig. 1. Central place foraging model for multiple prey loaders when patch quality is dependent on flock size, rather than on food availability. For a given patch, quality as perceived by the individual increases in proportion to the decrease in the time each bird in a flock must devote to vigilance. The conversion of the vigilance time saved into feeding time allows flock members to increase intake rate, and thus load size. From this model the following predictions can be derived: a) patch residence time should increase in patches with large vs patches with small flocks ( $t_3$  vs  $t_1$ ); b) for a given patch (*i.e.* flock size), residence time should increase ( $t_2$  to  $t_3$ ) with increasing travel distance (near to far).

five females). Two of the males and one female did not breed successfully, and were not included in the analyses (in two cases they were immature birds, and the nest of the third bird was destroyed by a wind storm). We followed the six breeding birds (two in 1989 and four in 1990) during their foraging trips from the nest throughout the brooding period (from late April to mid June). Tracking was done by car or on foot, depending on the distance flown by the birds and the accessibility of each particular site. Storks spent most foraging bouts in flooded pastures or open ash groves where food availability reached the highest values in the study area (see ALONSO *et al.*, 1991). During each foraging bout we measured: (1) dispersal distance from the nest (to the nearest 10 m); (2) patch residence time (minutes); (3) initial size of the flock when the focal individual arrived at the patch, and mean flock size (averaging all changes in flock size at the patch); (4) time spent vigilant (seconds with head raised above the back level), vigilance rate (bouts per minute), and time (seconds) spent actively feeding (these activities were measured during one to several continuous observation periods of 3-12 minutes each per foraging trip); (5) number of prey captured and eaten (easily recognized by the characteristic swallowing movement of head and neck); (6) time (seconds) storks were engaged in non-foraging activities (short preening periods, hostile interactions). We used the instantaneous food intake rate, *i.e.* number of prey captured while head down actively feeding, without considering the time spent vigilant, as an estimate of food availability in the patch. Other authors have also suggested that what is relevant to energy maximization is not the standing density of food but rather the acquisition rate (*e.g.* SIH, 1980, p. 281; PYKE, 1984, p. 554; ARDITI & DACOROGNA, 1988, p. 843). Therefore, intake rate has frequently been used as an estimate of site quality in field studies (CARRASCAL *et al.*, 1990; EVANS, 1982a; GOSS-CUSTARD, 1984; MUNGER, 1984; VALONE, 1989, 1992).

Each foraging bout, which was limited by two brooding periods at the nest, was considered as an independent data point, since for each individual there was no autocorrelation in travel distance, patch residence time, and food intake and vigilance rates in the sample of foraging bouts. Foraging bouts were neither correlated with the previous time spent at the nest (correlations were not significant for any individual; chi-squared test for combined probabilities  $\chi^2_{1,12} = 10.102$ ,  $p > 0.1$ ). Bouts during which storks did not forage (*e.g.* looking for branches or straw for nest building or maintenance) were not considered. Samples were obtained throughout the whole day.

The CPF model, as an extension of the marginal value theorem, requires that intake rate is a decreasing function of time in the patch. We tested this assumption by comparing the gross intake rate during the first and last thirds of each patch residence time. We excluded those cases where any changes in flock size occurred.

Statistical analyses were conducted separately for each of the six individuals in order to avoid pseudoreplication, as well as to analyse interindividual differences in foraging strategies. We used simple correlations to test predictions about flock size, percentage of time spent vigilant, patch residence time, and travel distance. Data series were analyzed after logarithmic or arc-sin transformation. For testing predictions derived from the currently accepted CPF model, or benefits of flocking (see references above), we used one-tailed tests. The correlation between flock size and instantaneous intake rate was tested with two-tailed test because no clear directional relationship between both variables has been universally accepted (see discussions on local enhancement in EVANS, 1982b; MOCK *et al.*, 1988). The series of individual significance tests were used in a single test of combined probabilities from independent tests of significance (SOKAL & ROHLF, 1981, p. 779-782).

## Results

White storks left the nest to forage 8.6 times per day (range 3-22, SD = 3.8, N = 39 complete days). Mean values of foraging trip variables were

49 minutes for patch residence time (range 2-488, SD = 44.6), 1324 m for mean travel distance (range 40-12500, SD = 2734), 5.3 birds for initial flock size when the focal individual arrived at the patch (range 1-26, SD = 5.5), 10.5 s/min for vigilance time (range 0-60, SD = 10.4), and 3.8 prey items/min for instantaneous food intake rate (range 0-23.5, SD = 3.0) (see sample sizes in Tables 2-5).

Prey capture rate decreased significantly between the first and last thirds of patch residence time in three of six individuals, but the mean decrease for the sample of six birds was significant ( $t = 4.51$ ,  $p = 0.006$ , Table 1). We conclude that food intake rate by white storks in patches can be regarded as a decelerating process with increasing patch residence time.

The percentage time spent vigilant per bout decreased with increasing flock size in all individuals studied (Table 2). Although statistical significance was reached only in three of the six birds, all correlations were negative. This, and the high significance of the chi-squared test for combined probabilities ( $\chi^2_{1,12} = 53.44$ ,  $p < 0.001$ ) indicated that the pattern was consistent. Therefore, by converting vigilance time into foraging time, storks benefitted from a longer feeding time in large flocks.

Flock size was significantly correlated with instantaneous food intake rate only in one bird. The remaining five birds showed either positive (three birds) or negative (two birds), but nonsignificant correlations. Thus, there was no consistent relation between flock size and instan-

TABLE 1. Mean change (in percentage) in prey capture rate between the first and last thirds of each patch residence time for the six individuals

Bird	$\bar{x}$	SD	N	$p^1$
1	-41.7	30.0	7	0.01
2	-32.5	14.9	5	0.008
3	-29.0	59.2	12	0.118
4	-38.7	32.2	11	0.003
5	-32.2	54.2	3	0.411
6	1.7	39.0	9	0.901

Test with combined probabilities:  $\chi^2_{1,12} = 36.75$ ;  $p < 0.001$

One sample t-test <sup>2</sup>):  $t_5 = 4.51$ ;  $p = 0.006$

N = number of patches.

<sup>1</sup>) One-sample t-tests against the null hypothesis of no change.

<sup>2</sup>) One-sample t-test comparing the mean change for the six birds with the null hypothesis of no change.



**TABLE 3.** Correlations for travel distance to the patch with initial flock size when arriving and instantaneous food intake rate at the patch

Travel distance with:								
Bird	Initial flock size				Instantaneous food intake rate			
	b	r	p*	N	b	r	p*	N
1	1.114	0.529	0.0004	37	0.013	0.703	0.0001	23
2	0.919	0.560	0.000005	54	0.002	0.038	0.424	28
3	0.829	0.682	0.000001	51	0.000	0.000	0.500	25
4	0.344	0.341	0.005	55	-0.008	-0.214	0.768	33
5	0.607	0.401	0.007	37	-0.145	-0.690	0.999	19
6	0.442	0.366	0.005	49	-0.003	-0.080	0.358	36

Test with combined probabilities:  
 $\chi^2_{1,12} = 108.73; p < 0.001$                        $\chi^2_{1,12} = 12.05; p > 0.25$

One-sample t-test:  
 $t_5 = 5.87; p = 0.002$                                        $t_5 = 0.96; p = 0.381$

The one-sample t-test compares the mean slope for the six birds with the null hypothesis of no slope.

\* = one-tailed test.

**TABLE 4.** Correlations for patch residence time with flock size and instantaneous food intake rate at the patch

Patch residence time with:								
Bird	Flock size				Instantaneous food intake rate			
	b	r	p**	N	b	r	p**	N
1	0.369	0.321	0.026	37	7.852	0.232	0.144	23
2	0.428	0.412	0.0016	49	2.062	0.156	0.218	27
3	0.235	0.307	0.013	53	-1.793	-0.362	0.925	25
4	0.511	0.406	0.001	56	-2.815	-0.098	0.418	34
5	0.211	0.295	0.054	31	-1.608	-0.517	0.972	18
6	0.578	0.452	0.0007	47	0.273	0.011	0.475	35

Test with combined probabilities:  
 $\chi^2_{1,12} = 63.04; p < 0.001$                        $\chi^2_{1,12} = 10.37; p > 0.5$

One-sample t-test:  
 $t_5 = 6.84; p = 0.001$                                        $t_5 = 0.41; p = 0.697$

The one-sample t-test compares the mean slope for the six birds with the null hypothesis of no slope.

\*\* = two-tailed test.



supported by the combination of the results for the six individuals (all correlations were positive;  $\chi^2_{1,12} = 34.27$ ,  $p < 0.001$  for patch residence time,  $\chi^2_{1,12} = 32.56$ ,  $p < 0.001$  for load size, Table 5).

## Discussion

White storks leaving their nests must decide where to go to forage. This decision can be split up into two components: how far to fly and how long to stay. Our results show that both decision variables, distance travelled and patch residence time were highly and positively correlated with the size of the flock selected by the stork to forage, while they were independent of the instantaneous food intake rate, and thus, probably of the food availability at the patch. This did not necessarily mean that storks contradicted one of the main predictions of classical CPF models, namely that patch residence time and load size are positively correlated with patch quality (ORIAN & PEARSON, 1979). It simply suggests that for storks foraging gregariously, a higher flock size is frequently more important than small increases in food availability. Flock size could thus be the best cue to estimate patch quality.

In patch and CPF models the currency is assumed to be the maximization of the long-term average rate of energy intake. Animals are thought to be rate-maximizing foragers that have complete information about model's parameters, and recognize the quality of different patch types in the environment (STEPHENS & KREBS, 1986). Nevertheless, under natural conditions in an unpredictable environment it may be unrealistic to assume that foragers have accurate information about patch quality and that they can easily track fluctuations in resource levels, due to depletion by competitive exploitation, or temporal and spatial changes in food dispersion. If acquiring accurate information about the model's parameters is not possible or difficult, animals could base their foraging decisions on more simple "rules of thumb" which, although less efficient than currencies of classic models, enable them to choose the "best" decision among those available considering their behavioural or environmental constraints (see *e.g.* JANETOS & COLE, 1981). KREBS *et al.*, (1983) and CHEVERTON *et al.* (1985) interpreted these rules of thumb as refinements of the classical foraging models into which more realistic constraint assumptions are included (see STEPHENS & KREBS, 1986).

For several reasons one could expect correlations between foraging decisions and flock size. First, while in solitary foraging species an individual has to make its own foraging decisions, in gregarious species flocking and patch selection decisions must be taken simultaneously (*cf.* PULLIAM & CARACO, 1984; VALONE, 1989). Moreover, measuring patch quality is a costly, time and energy consuming process, since individuals have to land on a patch and spend some time foraging before they can assess local food availability. It is thus surely easier, while still approximately optimal, to join other birds found already foraging and make the pertinent decisions according to the size of the flock.

Second, flocking offers antipredator benefits in addition to the enhanced feeding time benefits. Since aggression rate does not increase with increasing flock size in storks (CARRASCAL *et al.*, 1990), selection for large flocks should be the optimal solution for a foraging stork.

Finally, even considering the feeding time benefits alone, we simply suggest that in our study storks perceived patch 'quality' as dependent on the number of birds foraging in the patch, rather than as the mere food abundance on it. This was so because the magnitude of the decrease in vigilance could be of much higher value for an individual than the comparatively smaller differences in food availability among selected food patches in our study area (see ALONSO *et al.*, 1991).

Our results show marked individual deviations from predictions of the CPF model, either considering intake rate maximization, or flock size selection, or both, as foraging currencies. The absence of a significant correlation in some of the individuals studied does not invalidate the proposed model, although it suggests that additional factors, not directly related to foraging decisions, might be responsible for the observed variability. Significant interindividual variation in foraging patterns has been shown for several species (*e.g.* SULLIVAN, 1988; EDWARDS, 1989; VAN BUSKIRK & SMITH, 1989; JANSEN, 1990; reviewed by LOTT, 1991). Due to these individual differences, data sometimes do not fit predictions from foraging models (foraging patterns of the 'average' individual).

#### A. The decision how far to fly.

Storks leave the nest when the mate returns from a foraging trip, and usually fly individually to look for food. Sometimes they fly repeatedly to

the same area, but many times they go to new sites (pers. obs.). On several occasions we have observed that storks gain height circling over the colony before deciding where to go. Due to their conspicuous black and white plumage pattern, flying storks leaving the colony can easily see the birds foraging in open ash groves, the preferred feeding habitat in our study area (ALONSO *et al.*, 1991). Thus, it must be relatively easy for birds leaving the nest in search for food to assess the size of the different foraging flocks in the surroundings. If an individual does not know about the relative qualities of the different foraging patches, flock size would probably be the best cue to make a rapid, simple and rather good decision. Our results clearly indicate that there was no relationship between the food availability at the patch, and the distance travelled to it. Therefore, storks did not seem to have precise information about patch quality when deciding where to fly. They rather seemed to follow a simple but good rule: fly far only if there is a large flock size to join.

#### B. The decision how long to stay.

Similarly, storks decided their patch residence times simply as a function of flock size. The larger the flock size in which the stork was foraging, the longer they remained in that patch, regardless of the local instantaneous food intake rate. Storks behaved as if the patch was profitable as long as several conspecifics were foraging in it, rather than from the food availability *per se* (VALONE, 1989). This foraging rule could probably be a rather general one among flock foraging species (see also ERWIN, 1985; the same result was also obtained for flock foraging common cranes, *Grus grus*, ALONSO *et al.*, in press).

Patch residence time also increased with increasing distance travelled from the colony to the patch. This relationship held even once the effect of flock size was removed. This result supports our version of the main prediction from multiple-prey CPF models (ORIAN & PEARSON, 1979). Storks compensate the higher cost of flying farther to feed with a longer patch residence time and, thus, a higher load size.

#### C. The benefit of larger flocks.

Our data show a clear positive relationship between flock size and the percent time an individual in a flock can devote to feeding. This increase

in feeding time was possible because individual vigilance time was reduced in larger flocks. This result had also been obtained in a previous study with unmarked storks at the same area (CARRASCAL *et al.*, 1990), and has been observed in many other gregarious species (reviewed in PULLIAM & CARACO, 1984). The increased feeding time enabled the individual to increase its load size when foraging in larger flocks. This last relationship between flock size and load size was significant ( $p < 0.05$ , one-tailed test) in four of six individuals, and the high significance of the combined probability test ( $\chi^2_{1,12} = 40.38$ ,  $p < 0.001$ ) suggests that this trend is probably true for most individuals. But even if an increase in intake rate or load size would not occur in all situations, only an increased time available for feeding would surely be of adaptive value, and could have been enough for the evolution of flock foraging in white storks, as well as in other species.

The absence of a relationship between flock size and the instantaneous food intake rate indicates that larger flocks did not necessarily forage at the best patches during the present study. This was probably so because all patches visited by the storks were of good enough quality (see ALONSO *et al.*, 1991). In such circumstances, the best choice was to select the largest flock to reduce vigilance time as much as possible, this allowing to increase load size.

With respect to the distance travelled, as the instantaneous food intake rate did not change with it, we also interpret larger flocks at longer distances from the colony as a mechanism to compensate for the longer time needed to reach distant feeding areas. Joining a larger flock enables the individual to minimize vigilance time, with a consequent maximization of the gross intake rate. The relatively small differences in food availability among the different patches probably exert a lesser influence on patch selection.

#### D. Conclusion.

We conclude that the size of a foraging flock could be the main cue used by white storks departing from the breeding colony to make some of their most important foraging decisions: where to go and how long to stay there. We hypothesize that storks could follow the simple rules of thumb: 'select the largest possible flock among those found', and 'stay longer the

larger the flock size'. Such rules, in spite of their simplicity, help storks perform approximately optimally. An additional classical CPF rule would be 'stay longer the farther from the nest'. We suggest that, contrary to solitary foragers, the distance travelled and the patch residence time do not seem to depend only on food availability in flock foragers. Local enhancement probably evolved because individuals selected the best patches for feeding, and the benefits derived from flock foraging have probably favoured the evolution of flock size as an appropriate cue in gregarious species. Flock foraging benefits should thus be considered when modelling CPF in these species.

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