

Habitat selection by foraging White Storks, *Ciconia ciconia*, during the breeding season

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Foraging habitat selection by breeding White Storks (*Ciconia ciconia*) was studied at two contrasting areas in Spain, in relation to physical features of the terrain, food availability, and distance to the colony. In the first area, where storks captured mainly orthopterans, they selected tall-grass pastures and recently ploughed cereal fields, which were the habitats with highest densities and largest average sizes of prey. In the second area, where storks preyed almost exclusively on earthworms, flooded and open ash groves with short grass and high densities of earthworms were the preferred habitat. In this area, marked storks dispersing farther to feed in selected open ash groves more often than in dense ones. Foraging bouts, were longer, aggregations were larger, and food intake rates were greater, in open ash groves than in dense ones, owing to greater earthworm availability and accessibility. Depletion of earthworms led to an increased distance of dispersal to forage in the second area, but not in the first, where because of rapid reproduction of orthopterans, the birds were not forced to forage at greater distances later in the season.

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Le choix du site de quête de nourriture a été étudié chez des Cigognes blanches (*Ciconia ciconia*) en deux habitats très distincts d'Espagne, et certaines caractéristiques ont été observées plus particulièrement, notamment les caractéristiques physiques du terrain, la disponibilité de la nourriture et la distance de la colonie. Au premier site, où elles capturaient surtout des orthoptères, les cigognes choisissaient des champs de végétation herbeuse haute et des champs de céréales labourés depuis peu et c'est là que les proies avaient les plus fortes densités et les tailles moyennes les plus élevées. Au second site, où les cigognes capturaient surtout des vers de terre, les bosquets inondés et clairsemés de frêne à végétation herbeuse basse supportaient les plus grandes densités de vers de terre et étaient les habitats favoris des cigognes. A ce site, les cigognes marquées qui s'éloignaient le plus de la colonie choisissaient de préférence les bosquets clairsemés aux bosquets denses de frênes. Les cigognes passaient aussi plus de temps à se nourrir, se ressemblaient en groupes plus importants et avaient des taux de consommation de nourriture plus élevés dans les plantations clairsemées que dans les plantations denses, parce que la disponibilité des vers de terre y était plus grande et qu'ils étaient plus accessibles. La chute de densité des vers de terre entraînait une augmentation de la distance parcourue en quête de nourriture au second site alors qu'au premier site, le renouvellement rapide des orthoptères ne forçait pas les oiseaux à se déplacer davantage en fin de saison.

[Traduit par la rédaction]

Introduction

The habitat preferences of birds are determined by an individual's ability to obtain food and shelter against predators and weather, which are the main selective pressures related to fitness (see reviews in Hildén 1965; Cody 1985). Animals tend to feed in areas of high food availability (reviews in Nilsson 1972; Newton 1980; Herrera 1981; Goss-Custard 1983, 1984; Birkhead and Furnes 1985; Wiens 1989a) and low predation risk (e.g., Barnard 1980; Grubb and Greenwald 1982; Lima *et al.* 1987; Ekman 1987; Hogstad 1988).

Studies of habitat selection by birds have usually focused on defining the relationship between vegetation structure and bird density or presence. Nevertheless, the associations described in these correlation analyses do not show the causal mechanisms underlying habitat preferences in the ecological and evolutionary sense (Sherry and Homes 1985). A better way to define the functional importance of habitat features to birds is through the study of several aspects of behaviour (Morse 1980; Wiens 1973, 1985, 1989b). For example, if territories are used as feeding areas, study of food abundance and the birds' foraging behaviour should explain the birds' distribution and habitat use patterns.

This behavioural approach to habitat selection has shown that habitat use shows important interindividual, spatial, and temporal differences, in contrast to the previous idea of a species-specific fixed pattern (e.g., Noon *et al.* 1980). Also, consideration of recent foraging theory (Pyke 1984; Stephens and Krebs 1986) in the analysis of bird habitat selection allows testable predictions to be defined. Through this behavioural perspective, habitat preferences can be understood as a complex phenomenon resulting from the interaction between the costs and benefits derived from habitat use (foraging time available, travel distance, food intake rate, etc.).

In this paper we study habitat selection by White Storks (*Ciconia ciconia*) in Spain. Although some studies have dealt with habitat selection by this species in Central Europe, under relatively homogeneous environmental conditions (e.g., Pinowska and Pinowski 1989), little is known about storks' habitat preferences in the Iberian Peninsula, where the species reaches its highest population densities in Europe (Lázaro *et al.* 1986). In many areas of central Spain several habitat types can be distinguished near stork colonies, and birds have to decide which habitats to use, how long to stay in them, and how far to fly to

reach feeding areas. Our purpose was to describe habitat selection patterns in two contrasting areas in relation to prey abundance. The following specific questions were addressed: (i) do dispersal and habitat use patterns of White Storks relate to food availability? (ii) do storks deplete their food resources? and (iii) is habitat use dependent on distance from the colony through a trade-off between travel costs and foraging benefits?

Study area

We selected two different areas, each containing a White Stork colony, to represent the two main biotopes utilized by this species in Iberia during the breeding season (Lázaro *et al.* 1986). The first area lies in western Spain, close to El Gordo (39°52'N, 5°18'W, 300 m asl), and consists of 2000 ha of cereal fields (wheat, rye, and oats) and dry pasture land partly used for sheep grazing, around a large reservoir, with some woodlots containing holm oak (*Quercus rotundifolia*), pine (*Pinus* spp.), and eucalyptus trees (*Eucalyptus* spp.; see Fig. 1). The climate is Mediterranean, with an average yearly temperature of 15–16°C, warm dry summers, and low precipitation (400–500 mm annually). All 16 stork pairs of this colony nest on roofs of buildings in the village (10 birds on a single roof) and feed almost exclusively on arthropods (mainly orthopterans; of the identified prey ingested by 21 focal birds surveyed for at least 5 min, more than 95% were arthropods (personal observation)). The second area, near El Escorial (40°35'N, 4°05'W, 900 m asl), contains the largest White Stork colony in central Spain. It 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 oak and Pyrenean oak (*Q. pyrenaica*). This area has a colder and more humid climate than the first, with a yearly mean temperature of 9–10°C, cool springs with freezing night temperatures, sometimes even during May, and annual precipitation of 700 mm (Elías and Ruiz 1977). The food of adult storks consists of almost exclusively of earthworms (Carrascal *et al.* 1990).

Methods

Habitat selection

Both areas were surveyed between early April and late June 1988, using previously (late March) established itineraries which were fixed according to the dispersal of storks from the colonies. The total length of these survey routes was 29 km in El Gordo and 12 km in El Escorial. Transects driven along them by car in both areas lasted 1.5–2 h and were carried out 3 times per field day: early morning (06:00–08:00), midday (11:00–13:00), and late afternoon (16:00–19:00). The locations of all sighted storks were plotted on maps (1 : 25 000) of the study areas, and the type of habitat was recorded. Storks spent almost all their time outside the nest foraging (Carrascal *et al.* 1990). We considered observations made during each of the three daily transects to be independent, since the time elapsed between them was always longer than 3 h, though foraging bouts last 15 min – 2 h (unpublished data from radio-tagged birds). Availability of the different habitat types was estimated using the same transects, recording the habitat type at each side of the transect every 200 m. In El Gordo we considered the following habitats: (i) woods (*Pinus* spp., *Eucalyptus* spp., and holm oak); (ii) pasture land, which we divided into three categories according to the height of the grass: <10, 10–30, and >30 cm; (iii) fields being tilled that day; (iv) fields tilled at least 1 day prior to observation; (v) cultivated cereal fields; and (vi) the shores of the reservoir. In El Escorial the following habitats were considered: (i) streams and ponds, (ii) oak woods, and (iii) ash groves. The transect was repeated 13 times in El Escorial and 12 times in El Gordo. As the main foraging habitat in El Escorial, ash groves (see below), was homogeneous, we studied it in more detail. At intervals of 50 footsteps we recorded the degree to which ash groves were swamped, measuring the water level (cm) where water was present, and the height of the grass (cm). We also counted the number of trees >2.5 m tall within a radius of 25 m at 100-footstep intervals along random transects established in pastures both visited and not visited by foraging storks.

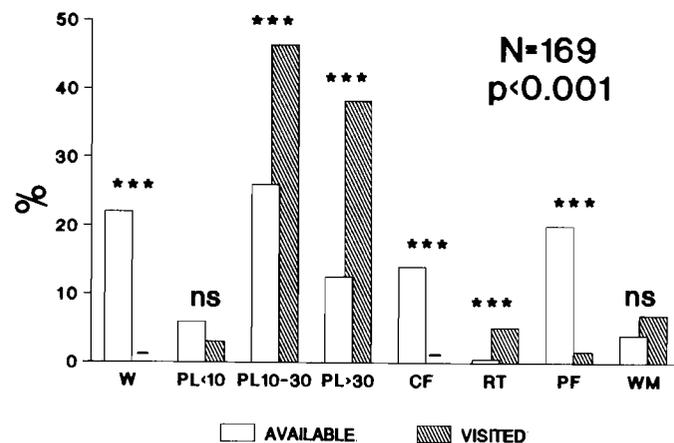


FIG. 1. Habitat availability and use by White Storks in El Gordo, Spain. W woods; PL, pastureland (grass <10, 10–30, or >30 cm high). CF, cultivated fields; RT, recently tilled fields; PF, ploughed fields; WM, water reservoir margins. The results of *t*-tests for proportions comparing paired percentages are indicated above the bars as follows: ns, not significant; ***, $p < 0.001$. The p value shows the significance of χ^2 test comparing availability and use distributions. N is the number of birds.

Individual foraging behaviour

In 1989 we captured and radio-tagged five birds in El Escorial. Three were females (two of these bred successfully, the third was an immature bird) and two were males (a breeding one and an immature). We followed the three breeding storks by car or on foot, depending on the distance flown by the bird and the accessibility of the foraging site, and studied their foraging behaviour during the incubation period (20 field days), i.e., dispersal from the nest, patch residence time, habitat selection, food intake, and vigilance time. Each foraging bout was considered to be an independent observation, since for each individual there was no autocorrelation in travel distance, patch residence time, and food intake and scanning rates in the sample of foraging bouts. Consecutive foraging bouts were separated by an incubating bout or defined by a change in foraging site by a distance of >500 m covered by flight. Periods during which the storks did not forage were not considered. For analysis we combined the data from the three individuals, since there were no significant differences in their foraging behaviour (feeding rate, vigilance time, habitat use, length of foraging bouts, and distance between foraging site and nest).

Food availability and depletion of food resources

We counted arthropods >1 cm in length (mainly orthopterans and beetles) seen while walking slowly along transects 25 m long \times 2 m wide in both areas (see Folse 1982 and Blancher and Robertson 1987 for a similar approach). Earthworms and hypogeal insect larvae were counted in earth samples of 20 \times 20 \times 5 cm taken with a shovel and crumbled by hand. The length and width of each earthworm and larva, and the approximate length of arthropods, were estimated to obtain an approximation of its biomass, assuming a cylindrical form for earthworms and larvae and a ellipsoidal or a hemiellipsoidal form for arthropods. To estimate the availability of prey near the shores of the reservoir in El Gordo, we sampled 24 transects 50 m long \times 2 m wide along the shores most frequently visited by the storks, counting aquatic prey (fishes, newts, frogs, and macroinvertebrates). Although this method did not allow precise measurement of the real availability of prey to the storks, it provided a reliable index of prey abundance for comparison among the habitats.

Depletion of food resources by the storks was estimated by measuring prey abundance at selected foraging sites before and 15 (El Gordo) or 10 (El Escorial) days after storks had been foraging on them.

Statistical procedures

We used Student's *t*-test to compare means and proportions in independent series, χ^2 tests to compare series of proportions, and simple

TABLE 1. Food availability in the two study areas

	Number/sample		g/sample	
	\bar{x}	SD	\bar{x}	SD
El Gordo (arthropods)				
Woods—shrublands (22)	4.0	3.7	1.0	1.8
Pasture land				
Grass <10 cm (10)	17.0	16.5	2.9	2.8
Grass 10–30 cm (32)	115.6	93.6	15.3	12.2
Grass >30 cm (8)	173.9	179.6	27.1	31.6
Cultivated fields (25)	9.7	14.9	2.0	3.8
Recently tilled fields (9)	6.3	4.6	3.5	3.7
Ploughed fields (14)	2.6	2.6	0.9	1.4
El Escorial (hypogean invertebrates)				
Woods (50)	0.1	0.3	0.1	0.3
Nonvisited ash groves (50)	1.8	2.9	0.6	1.2
Visited ash groves (43)	3.1	2.9	2.1	2.7

NOTE: As storks did not feed on hypogean invertebrates in El Gordo or on arthropods in El Escorial, these data are not given (see Results for data). Numbers in parentheses show sample size.

and partial regression analyses. Data series were analyzed after logarithmic transformation. Habitat selection was estimated through Ivlev's (1961) eligibility index ($U_i - A_i/U_i + A_i$), where U_i and A_i are the proportions of use and availability, respectively, of the different habitats. This index varies between -1 (complete avoidance) and $+1$ (complete preference).

Results

Food availability

Earthworms were more abundant in El Escorial ($\bar{x} = 2.11$, $SD = 2.74$, $n = 43$) than in El Gordo ($\bar{x} = 0.11$, $SD = 0.31$, $n = 50$) (t -test, $p < 0.001$). Arthropods, however, were much less abundant in the first area ($\bar{x} = 0.2$, $SD = 0.2$, $n = 26$) than in the second ($\bar{x} = 17.7$, $SD = 17.9$, $n = 40$) (t -test, $p < 0.001$). In El Escorial the density and biomass of earthworms and other hypogean invertebrates were significantly higher in ash groves than in oak woods (t -test, $p < 0.001$; see Table 1). In El Gordo there were more arthropods in tall-grass pastures than in other pastures, cultivated land, or woods (t -tests, $p < 0.05$; see Table 1). However, in fields being ploughed, arthropods were much larger (mean 0.6 g) than in other habitats (0.15–0.3 g), although their density was as low as in cultivated land and short-grass pastures.

Habitat selection

Frequency distributions of habitats available to and visited by the storks differed significantly, in both El Gordo (χ^2 test, $p < 0.001$; Fig 1) and El Escorial (χ^2 test, $p < 0.001$; Fig. 2). Storks clearly selected some types among all available habitats in the two study areas. In El Gordo they avoided cereal-sown ground and wooded areas and visited ploughed fields only sporadically, except for those being ploughed on the same day, which were positively selected. They also selected tall-grass pastures, but were indifferent to short-grass pastures and the shores of the reservoir (Fig. 1).

The eligibility index for the seven terrestrial habitats in El Gordo was significantly correlated with the average density and mean weight of prey on each (partial correlation coefficients; $r = 0.96$, $p < 0.01$ for density and $r = 0.94$, $p < 0.01$ for weight). These two variables explained 93% of the variance in eligibility for any of the seven habitats ($p < 0.01$ in the multiple regression analysis).

TABLE 2. Characteristics of the ash groves used and not used by white storks in El Escorial

	Ash groves not visited	Ash groves visited
Degree of flooding		
% sites with water	14	71
n	251	216
Height of grass (cm)		
Mean	32.1	13.5
SD	12.6	9.9
n	36	30
No. of trees/0.2 ha		
Mean	12	6
SD	10.0	5.8
n	36	30

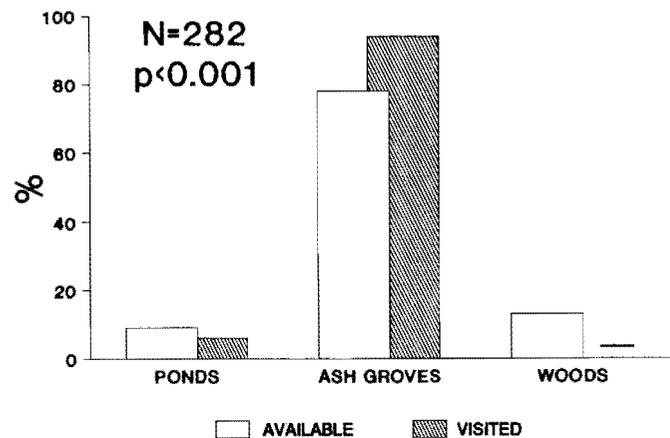


FIG. 2. Habitat availability and use by White Storks in El Escorial. See Fig. 1 for details.

In El Escorial, storks selected ash groves but avoided wooded areas and did not use ponds and streams in proportion to their availability (Fig. 2). Ash groves selected by the storks had fewer trees ($p < 0.01$) and shorter and grass ($p < 0.001$) and were more flooded ($p < 0.001$, t -tests) than those not used (Table 2). Also, the density and biomass of earthworms and other hypogean invertebrates were significantly greater in ash groves used by the storks ($p < 0.001$, t -tests).

Foraging behaviour

Individually marked storks dispersed farther and their foraging bouts were longer in open than in dense ash groves (Table 3). The absolute food intake rate and mean aggregation size were also greater in open ash groves. To exclude the influence of the larger aggregations, which are associated with a shorter vigilance time (Table 3), we calculated the net food intake rate (only with head down), which better reflects the quality of the foraging site (see Carrascal *et al.* 1990). The net food intake rate was also significantly higher in open ash groves.

Food depletion and dispersal from the colony

The abundance of arthropods in pastures increased in El Gordo at a site regularly visited by storks during 15 days in May, as a consequence of the high reproductive and growth rates of arthropods (mainly orthopterans) during spring (Fig. 3). In contrast, in El Escorial the density of earthworms decreased in May after 10 days of regular use by storks (Fig. 3). Since there

TABLE 3. Foraging parameters of White Storks feeding in El Escorial

	Open ash groves			Dense ash groves			
	\bar{x}	SE	<i>n</i>	\bar{x}	SE	<i>n</i>	
Patch residence time (min)	69.3	11.8	45	31.2	7.9	21	***
Dispersal distance (m)	457.2	84.0	47	206.5	38.6	21	**
Flock size	6.2	0.8	46	1.9	0.37	19	***
Vigilance time (s/min)	19.8	2.6	29	34.3	11.5	9	*
Absolute intake rate (no./min)	3.2	0.4	27	1.3	0.4	9	**
Net intake rate (no./min)	4.0	0.4	27	1.6	0.5	9	**

NOTE: ANOVA between open and dense ash groves: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

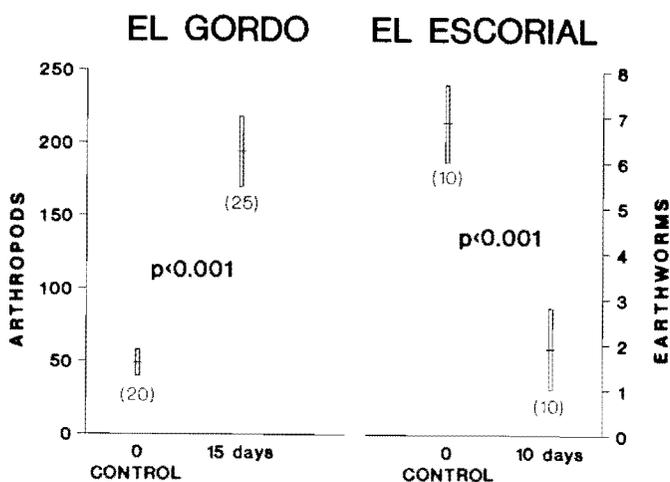


FIG. 3. Changes in prey availability (mean \pm 95% confidence interval) at a site regularly visited by White Storks during 15 days in El Gordo and 10 days in El Escorial. Numbers in parentheses show sample size. The significance of *t*-tests is indicated.

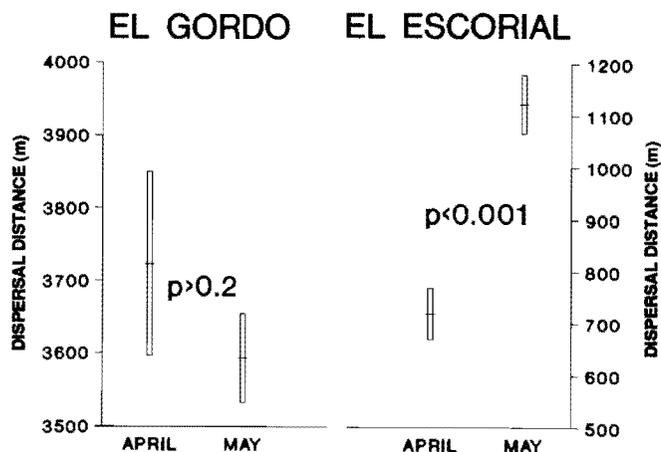


FIG. 4. Monthly changes in dispersal distance from the colony to foraging areas (mean \pm 95% confidence interval). The significance of *t*-tests is indicated.

were no significant numbers of other predator species feeding on the same prey, we conclude that in El Gordo, storks did not deplete food resources (mainly grasshoppers), whereas in El Escorial they did significantly deplete their main prey (earthworms).

The mean distance that storks dispersed to feed increased

significantly between April and May in El Escorial, whereas it did not change significantly, and even showed a slight decreasing trend, in El Gordo (Fig. 4).

Discussion

The results of this study show that food availability is an important causal factor in habitat selection and foraging dispersal of White Storks from the breeding colony. Similar results have been obtained by researchers working with other bird species (e.g., Newton (1979, 1986) with raptors, Grzybowski (1982), Boag and Grant (1984), and Grant and Grant (1987) with granivorous birds, Goss-Custard (1983, 1985) with waders, Bailey and Titman (1984) with ducks, Ford and Paton (1985) with nectarivorous birds, and Terril and Ohmart (1984), and Brush and Stiles (1986) with insectivorous birds). These results agree with the prediction from foraging theory of a higher use of patches with greater food availability owing to the higher benefit obtained by individuals foraging in them (Schoener 1971; Krebs *et al.* 1983; Pyke 1984; Stephens and Krebs 1986). The absolute food intake rate of marked individuals in El Escorial was indeed higher in open ash groves, which were selected by foraging storks over any other habitat. This high absolute intake rate in open ash groves could be a consequence of (i) decreased vigilance time and (or) (ii) greater food availability. An increase in vigilance time with decreasing visibility in the habitat has been recorded in shorebirds (Metcalf 1984), and tits (Hogstad 1988), and attributed to the greater vulnerability of a foraging individual surrounded by objects such as trees, foliage, rocks, or banks. However, though foraging storks spent more time vigilant in dense ash groves, this was mainly a result of the smaller flocks in these areas, because of inverse relationship between feeding and vigilance. Dense ash groves in El Escorial are probably not so dense as to cause a significant increase in vigilance. Thus, the main cause of the higher food intake rate in open ash groves was probably the greater food availability, since the net food intake rate, which excludes the effect of vigilance, was higher in open ash groves (see also Carrascal *et al.* 1990). Higher food intake rates in patches with greater food availability have also been recorded for other bird species (e.g., Krebs *et al.* 1972; Barnard 1980; Goss-Custard 1984; Blancher and Robertson 1987; Draulans 1987).

Not only were open ash groves visited more frequently by storks, but the foraging bouts in them, and the distance covered by the birds to reach them, were longer than for dense ash groves. These results agree with two predictions of the patch model for central place foragers: that patch residence time should be longer in better patches, and in more distant patches (see

Stephens and Krebs 1986). When storks flew longer distances to feed, they not only prolonged their foraging bouts, but also selected open ash groves more frequently. The percentage of open ash groves visited at distances greater than 250 m from the colony was 81% ($n = 26$) compared with 62% ($n = 42$) for closer sites. Dispersal distance to foraging sites and duration of foraging bouts were positively correlated, as predicted by central place models ($r = 0.30$, $n = 66$, $p = 0.016$).

Three facts suggest that in addition to food abundance, other factors influenced habitat selection by White Storks. First, the eligibility of ash groves with shorter grass suggests that prey accessibility or detectability was probably also important in determining storks' preference for a patch (e.g. small earth piles left on the surface by earthworms is one of the clues to their presence). Similar conclusions were drawn by Pinowska and Pinowski (1989) from the study of another White Stork population, and by Brownsmith (1977) for starlings (*Sturnus vulgaris*) feeding on pasture land.

Second, habitat eligibility in El Gordo was independently correlated with abundance and size of the prey. Indeed, the highest eligibility index values were for recently ploughed fields, which offered the largest prey (large hypogeal invertebrates and small vertebrates turned up by the plough). This result is not surprising, given the higher energy intake rate per prey unit provided by larger prey, which allows search time to be reduced (see Pyke 1984; Stephens and Krebs 1986). The low selection for the shores of the reservoir, which offered even larger prey, ca. 200 carp 20–50 cm/100 m² of water surface, is explained by the long handling time required to capture and swallow these fishes (personal observations).

Third, the presence of storks already feeding at a site is probably one of the main causes of passing individuals being induced to land, which enhances the use of profitable patches. By joining other foraging individuals, storks thus obtain both feeding and antipredator advantages (Carrascal *et al.* 1990). Therefore, such enhancement is surely decisive in feeding site selection by foraging storks, as has also been shown for other species (Krebs *et al.* 1972; Baker *et al.* 1981; Andersson *et al.* 1981; Clark and Mengel 1984; Ekman and Hake 1988).

White Storks monitored food availability throughout the breeding season, measuring the degree of resource depletion and modifying the dispersal distance between colony and foraging site accordingly. This conclusion is supported by the clear differences found in the patterns of prey availability and dispersal of foraging storks from the colony between the two study areas. In El Gordo, where the availability of grasshoppers and other arthropods increased notably throughout the spring, we did not record a seasonal increase in the distance travelled by the storks to feed. In contrast, in El Escorial, where earthworms were depleted because of their lower reproductive rate, storks did increase their foraging trip distance throughout the season. These results show the importance of a knowledge of food depletion in understanding the distribution patterns of feeding animals in relation to food availability (for studies of the different relationships among bird density, food abundance and depletion rates see Goss-Custard (1983), Folse (1982), Jordano (1987), and Pulliam and Dunning (1987)).

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- ANDERSSON, M., GÖTMARK, F., and WIKUND, C. 1981. Food information in the black-headed gull, *Larus ridibundus*. *Behav. Ecol. Sociobiol.* **9**: 199–202.
- BAILEY, R. O., and TITMAN, R. D. 1984. Habitat use and feeding ecology of postbreeding redheads. *J. Wildl. Manage.* **48**: 1144–1155.
- BAKER, M. C., BELCHER, C. S., DEUTSCH, L. C., SHERMAN, G. Y., and THOMPSON, D. B. 1981. Foraging success in junco flocks and the effect of social hierarchy. *Anim. Behav.* **29**: 137–142.
- BARNARD, C. J. 1980. Flock feeding and time budgets in the House Sparrow (*Passer domesticus*). *Anim. Behav.* **28**: 295–309.
- BIRKHEAD, T. R., and FURNESS, R. W. 1985. Regulation of seabird populations. *In Behavioural ecology: ecological consequences of adaptive behaviour.* Edited by R. M. Sibly and R. H. Smith. Blackwell Scientific Publications, Oxford. pp. 145–167.
- BLANCHER, P. J., and ROBERTSON, R. J. 1987. Effects of food supply on the breeding biology of western kingbirds. *Ecology*, **68**: 723–732.
- BOAG, P. T., and GRANT, P. R. 1984. Darwin's Finches (*Geospiza*) on Isla Daphne Major, Galápagos: breeding and feeding ecology in a climatically variable environment. *Ecol. Monogr.* **55**: 463–489.
- BROWNSMITH, C. B. 1977. Foraging rates of starlings in two habitats. *Condor*, **79**: 386–387.
- BRUSH, T., and STILES, E. W. 1986. Using food abundance to predict habitat use by birds. *In WILDLIFE 2000: modeling habitat relationships of terrestrial vertebrates.* Edited by J. Verner, M. L. Morrison, and C. J. Ralph. The University of Wisconsin Press, Madison. pp. 57–63.
- CARRASCAL, L. M., ALONSO, J. C., and ALONSO, J. A. 1990. Aggregation size and foraging behaviour of White Storks *Ciconia ciconia* during the breeding season. *Ardea*, **78**: 399–404.
- CLARK, C., and MENGEL, M. 1984. Foraging and flocking strategies: information in an uncertain environment. *Am. Nat.* **123**: 626–641.
- CODY, M. L. 1985. Habitat selection in birds. Academic Press, Orlando.
- 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**: 479–493.
- EKMAN, J. 1987. Exposure and time use in willow tit flocks: the cost of subordination. *Anim. Behav.* **35**: 445–452.
- EKMAN J., and HAKE M. 1988. Avian flocking reduces starvation risk: an experimental demonstration. *Behav. Ecol. Sociobiol.* **22**: 91–94.
- ELÍAS, F., and RUIZ, L. 1977. Agroclimatología de España. I.N.I.A., Cuaderno, No. 7. Madrid.
- FOLSE, L. J. 1982. An analysis of avifauna–resource relationships on the Seregeti plains. *Ecol. Monogr.* **52**: 111–127.
- FORD, H. A., and PATON, D. C. 1985. Habitat selection in Australian Honeyeaters, with special reference to nectar productivity. *In Habitat selection in birds.* Edited by M. L. Cody. Academic Press, Orlando. pp. 367–388.
- GOSS-CUSTARD, J. D. 1983. Spatial and seasonal variations in the food supply of waders (Charadrii) wintering in the British Isles. *In Proceedings of the Third Nordic Congress on Ornithology.* 1981. pp. 85–96.
- 1984. Intake rates and food supply in migrating and wintering shorebirds. *In Shorebirds: migration and foraging behavior.* Edited by J. Burger and B. L. Olla. Plenum Publishing Corp. New York. pp. 233–270.
- 1985. Foraging behaviour of wading birds and the carrying capacity of estuaries. *In Behavioural ecology: ecological consequences of adaptive behaviour.* Edited by R. M. Sibly and R. H. Smith. Blackwell, Scientific Publications, Oxford. pp. 169–188.

- GRANT, P. R., and GRANT, B. R. 1987. The extraordinary El Niño event of 1982–1983: effects on Darwin's Finches on Island Genovesa, Galápagos. *Oikos*, **49**: 55–66.
- GRUBB, T. C., and GREENWALD, L. 1982. Sparrows and a brushpile: foraging response to different combinations of predation risk and energy cost. *Anim. Behav.* **30**: 637–640.
- GRZYBOWSKI, J. A. 1982. Population structure in grassland bird communities during winter. *Condor*, **52**: 137–152.
- HERRERA, C. M. 1981. Organización temporal de las comunidades de aves. *Doñana Acta Vertebr.* **8**: 79–101.
- HILDÉN, O. 1965. Habitat selection in birds. *Ann. Zool. Fenn.* **2**: 53–75.
- HOGSTAD, O. 1988. Rank-related resource access in winter flocks of willow tit *Parus montanus*. *Ornis Scand.* **19**: 169–174.
- IVLEV, V. S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven.
- JORDANO, P. 1987. Avian fruit removal: effects of fruit variation, crop size, and insect damage. *Ecology*, **68**: 1711–1723.
- KREBS, J. R., MACROBERTS, M. H., and CULLEN, J. M. 1972. Flocking and feeding in the Great Tit *Parus major*—an experimental study. *Ibis*, **114**: 507–530.
- KREBS, J. R., STEPHENS, D. W., and SUTHERLAND, W. J. 1983. Perspectives in optimal foraging. *In Perspectives in ornithology. Edited by A. H. Brush and G. A. Clark.* Cambridge University Press, New York. pp. 165–216.
- LÁZARO, E., CHOZAS, E., and FERNÁNDEZ-CRUZ, M. 1986. Demografía de la Cigüeña Blanca (*Ciconia ciconia*) en España. Censo Nacional de 1984. *Ardeola*, **33**: 131–169.
- LIMA, S. L., WEIBE, K. L., and DILL, L. M. 1987. Protective cover and the use of space by finches: is closer better? *Oikos*, **50**: 225–230.
- METCALFE, N. B. 1984. The effects of mixed-species flocking on the vigilance of shore birds: who do they trust? *Anim. Behav.* **32**: 986–993.
- MORSE, D. H. 1980. Behavioral mechanisms in ecology. Harvard University Press, Cambridge, MA.
- NEWTON, I. 1979. Population ecology of raptors. T. & A. D. Poyser, Ltd., Stoke and Trent, U.K.
- . 1980. The role of food in limiting bird numbers. *Ardea*, **68**: 11–30.
- . 1986. The Sparrowhawk. T. & A. D. Poyser, Ltd., Stoke on Trent, U.K.
- NILSSON, L. 1972. Habitat selection, food choice, and feeding habits of diving ducks in coastal waters of south Sweden during the non-breeding season. *Ornis Scand.* **3**: 55–78.
- NOON, B. R., DAWSON, D. K., INKLEY, D. B., ROBBINS, C., and ANDERSON, S. H. 1980. Consistency in habitat preference of forest bird species. *Trans. North Am. Wildl. Nat. Resour. Conf.* **45**: 226–244.
- PINOWSKA, B., and PINOWSKI, J. 1989. Feeding ecology and diet of the White Stork *Ciconia ciconia* in Poland. *In Weißstorch—White Stork. Edited by G. Rheinwald, J. Ogden, and H. Schulz.* International Council for Bird Preservation, Walsrode, Germany. pp. 381–396.
- PULLIAM, H. R., and DUNNING, J. B. 1987. The influence of food supply on local density of sparrows. *Ecology*, **68**: 1009–1014.
- PYKE, G. H. 1984. Optimal foraging theory: a critical review. *Annu. Rev. Ecol. Syst.* **15**: 523–575.
- SCHOENER, T. W. 1971. The theory of foraging strategies. *Annu. Rev. Ecol. Syst.* **2**: 369–404.
- SHERRY, T. W., and HOLMES, R. T. 1985. Dispersion patterns and habitat responses of birds in northern hardwood forests. *In Habitat selection in birds. Edited by M. L. Cody.* Academic Press, Orlando. pp. 283–309.
- STEPHENS, D. W., and KREBS, J. R. 1986. Foraging theory. Princeton University Press, Princeton.
- TERRILL, S. B., and OHMART, R. D. 1984. Facultative extension of fall migration by Yellow-rumped Warblers (*Dendroica coronata*). *Auk*, **101**: 427–438.
- WIENS, J. A. 1973. Interterritorial habitat variation in grasshopper and savannah sparrows. *Ecology*, **54**: 877–884.
- . 1985. Habitat selection in variable environments: shrub-steppe birds. *In Habitat selection in birds. Edited by M. L. Cody.* Academic Press, Orlando. pp. 227–251.
- . 1989a. The ecology of bird communities: processes and patterns. Vol. 2. Cambridge University Press, New York.
- . 1989b. The ecology of bird communities: foundations and patterns. Vol. 1. Cambridge University Press, New York.