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Effect of food abundance on laying date and clutch size in the White Stork *Ciconia ciconia*

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Capsule Food independently affects both laying date and clutch size, suggesting that seasonal decline in clutch size is related to a decrease in food availability.

Aim To test the effect of food abundance on laying date and clutch size of the White Stork and identify the cause of seasonal decline in the number of eggs laid.

Methods During 1991 and 1996 we recorded clutch size and laying date of pairs breeding next to rubbish dumps (food abundant and constant throughout the breeding season) and birds breeding far from rubbish dumps (using natural food sources).

Results In 1991 there was no difference in mean laying date between pairs nesting at rubbish dumps and control pairs. Clutch size was significantly larger at rubbish dump nests. In contrast, mean laying date was earlier in control pairs in 1996 and there was no significant differences in clutch sizes, even when controlling for laying date effect.

Conclusion The results support the hypothesis that food availability independently affects both laying date and clutch size. The seasonal decline in clutch size close to rubbish dumps was negligible (1991) or much smaller than in the control zone (1996) suggesting that a progressive deterioration of natural food sources is the most probable reason for a decline in clutch size as the season advances.

Many studies suggest that there are two main factors affecting intraspecific clutch size variation: food availability (Newton & Marquiss 1981, Korpimäki & Wiehn 1998) and laying date (Meijer *et al.* 1988, Korpimäki & Wiehn 1998). Of these two factors, date seems to affect single-brooded and multiple-brooded species differently. Laying pattern in single-brooded species usually show a seasonal decline (Murphy 1986, Stutchbury & Robertson 1988), while multiple-brooded species lay their largest clutch in the middle of the breeding season (Seel 1968, Davies & Lundberg 1985). Moreover, laying date may be modified by food availability (Nager *et al.* 1997, Ramsay & Houston 1997).

Field studies where supplementary food has been added to breeding territories have shown contradictory results (reviews in Martin 1987, Gehlbach & Roberts 1997). An advance in laying date has been commonly observed; less frequently clutch size or egg size increased when extra food is provided. The threshold hypothesis (Martin 1987, Boutin 1990) suggests that supplementary food will only affect populations when food availability is below a threshold value. If this is so, then little or no response of individuals to supplementary food would be expected when natural conditions are favourable. Accordingly, experimental birds would only lay larger clutches than controls when conditions during the experiment are poor or relatively unfavourable.

Two major hypotheses are commonly suggested to explain seasonal declines in clutch size. First, there may be a condition threshold decreasing with time, which is governed either via an internal annual programme or via some external variable independent of food (e.g. day length). Crossing the threshold would induce laying, which in turn determines clutch size (Reynolds 1972, Daan *et al.* 1988) probably through the effect of prolactin levels (Meijer *et al.* 1990). Second, differences in quality between individuals and/or territories could mean that pairs in better condition breed earlier and lay more eggs than those in worse condition or in bad territories; the progressive deterioration of food sources may lead to the seasonal decline (Askenmo 1982, Newton & Marquiss 1984, Winkler & Allen 1996). In this case, food availability would indepen-

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dently affect both laying date and clutch size and changes in these two breeding traits would be expected from changes in food availability (Aparicio 1994). Although studies with different species give mixed results, many recent experiments have documented that supplementary feeding before and during egg-laying increases clutch size independent of laying date (review in Korpimäki & Wiehn 1998).

The White Stork *Ciconia ciconia* is a long-lived single-brooded species, whose clutch size fluctuates between one to six eggs and declines as the breeding season advances (Tortosa 1992). At present, many White Storks in southern Spain breed close to rubbish dumps as domestic garbage provides an abundant and constant food source for them and many other bird species (Donázar 1992, Gómez-Tejedor & de Lope 1993). The food provided by garbage seems to affect migrating habits of White Storks (Tortosa *et al.* 1995). Breeding performance is also known to be affected by food availability at dumps as reported in the White Stork (Tortosa *et al.* 2002) and Herring Gulls *Larus argentatus* (Pons & Migot 1995).

We analyse the effect of food availability and date on clutch size in the White Stork. According to the hypothesis that food availability affects clutch size independently of laying date, we would predict that (a) clutch size of pairs breeding close to an artificial food source will be larger than in control pairs breeding at the same dates, and (2) seasonal decline in clutch size will be negligible or, at most, weak in storks with extra food compared with control pairs.

METHODS

The study was conducted during 1991 and 1996 in Andalusia, southern Spain. Data collection in 1991 was carried out in three breeding colonies. We recorded clutch size and laying date of 29 pairs in a control zone (i.e. nests situated far from any rubbish dump) and 23 pairs distributed among two colonies adjacent to a rubbish dump. There were also two nests in a control zone and six near a rubbish dump for which the laying date remained unknown. In 1996 we recorded data from 28 pairs breeding close to a rubbish dump, with nine nests used as controls.

We considered a breeding pair to be under the influence of a rubbish dump when the nest was located less than 1 km away. Control nests were greater than 25 km from a rubbish dump. The habitat around control and rubbish dump populations was similar, comprised mainly *dehesa* (mediterranean oak savanna).

Analysis

Laying date was defined as when the first egg of the clutch was laid. In 1991 we did not find differences in mean laying date between the two colonies adjacent to a dump (t-test: $t = 1.03$, df = 21, $P = 0.31$) or in mean clutch size (t-test: $t = 1.73$, df = 26, $P = 0.09$). In both colonies, clutch size was unaffected by laying date ($r_S = -0.21$, $n = 8$, $P = 0.60$ and $r_S = -0.01$, $n = 15$, $P > 0.05$, respectively). Therefore, all data from White Stork nests breeding close to rubbish dumps were pooled for analysis.

All data had a normal distribution so we used parametric tests (t-tests) except when variances where not homogeneous.

RESULTS

No significant differences were found when we compared mean laying dates between control birds and those breeding near rubbish dumps in 1991 ($t = 1.4$, df = 48, $P = 0.16$), whereas in 1996 birds breeding close to rubbish dumps laid on average 16.6 days earlier than controls (Mann–Whitney U-test, $P < 0.005$) (Table 1).

In 1991 clutch size was significantly larger in nests near rubbish dumps than in controls ($t = 4.26$, df = 55, $P < 0.05$) (Table 1). These differences were not attributable to earlier nesting as there was no significant difference in mean laying date. An ANCOVA using the zone (control or rubbish dump) as factor variable and age as covariate confirmed the lack of a date effect ($F_{1,47} = 18.4$, $P < 0.005$). In contrast, in 1996 no effect of food abundance on clutch size was detected since there were no differences in the mean number of eggs per clutch at nests in rubbish dump (3.7 ± 0.9, $n = 28$) and control zones (3.5 ± 1.3, $n = 9$) (t-test: $t = 0.38$, df = 35, $P = 0.70$) (Table 1), even when controlling for laying date effect (ANCOVA: $F_{1,34} = 2.31$, $P = 0.13$).

Table 1. Laying date and clutch size of White Storks nesting near rubbish dumps and at control sites. Results are mean ± sd with *n* in parentheses. For laying date, day 1 = 1 January.

	Rubbish dumps	Control
Laying date		
1991	82.3 ± 14 (23)	88.0 ± 14.0 (23)
1996	68.6 ± 9.3 (28)	85.2 ± 18.0 (9)
Clutch size		
1991	4.1 ± 0.8 (28)	3.0 ± 1.1 (29)
1996	3.7 ± 0.9 (28)	3.5 ± 1.3 (9)

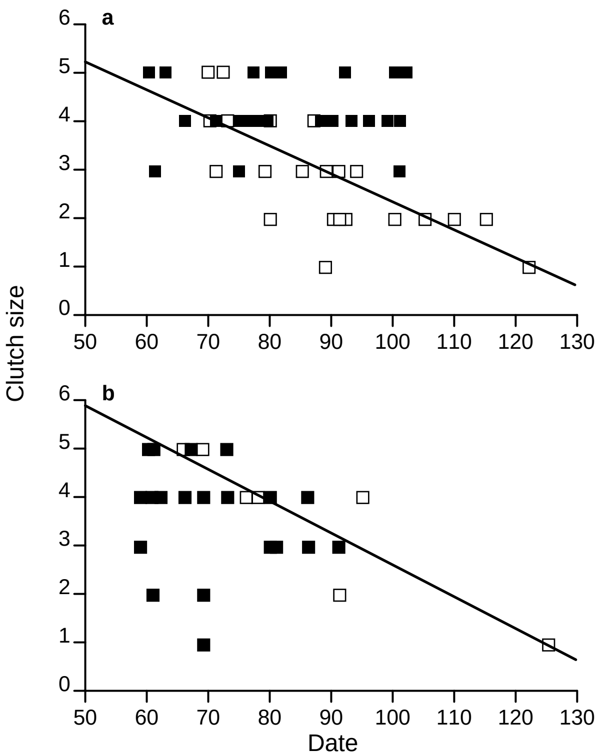

Figure 1. Clutch size in relation to laying date in (a) 1991 and (b) 1996 (day 1 = 1 January) in rubbish dumps (■) and control sites (□). Regression lines are only added for control sites, where they are of statistical significance.

There was no effect of laying date on clutch size in White Stork populations breeding close to the rubbish dumps ($r = 0.035$, $n = 23$, $P = 0.87$), clutch size being almost constant during the 1991 breeding season. In contrast, clutch size in control birds strongly decreased as the season advanced ($r = -0.72$, $n = 27$, $P < 0.001$) (Fig. 1), the slopes being significantly different (ANCOVA, $F_{1,46} = 14.9$, $P < 0.001$). Likewise, in 1996 the decline in clutch size was not significant in nests near rubbish dumps ($r = -0.25$, $n = 28$, $P = 0.19$), but there was a strong decline in clutch size in the control pairs ($r = -0.90$, $n = 9$, $P < 0.001$) (Fig. 1), although slopes did not differ significantly between these two populations (ANCOVA, $F_{1,33} = 2.38$, $P = 0.13$).

DISCUSSION

The seasonal decline in clutch size near rubbish dumps was negligible (1991) or much smaller than in the control zone (1996), suggesting that the progressive deterioration of natural food sources as the season advances may be the cause (at least in part) of the seasonal decline in clutch size, as also found by Siikamäki (1998) and Korpimäki & Wiehn (1998).

In 1991, the clutch size was larger in those pairs that bred close to rubbish dumps, where food was more abundant, compared with control pairs. This difference in mean clutch size is not attributable to differences in laying date, which was not different between these two sites. In 1996 the effect of food availability differed from the results in 1991, since clutch size was similar in control nests and those near rubbish dumps, although mean laying date was earlier near the latter. These results support the hypothesis that food availability independently affects both laying date and clutch size as proposed by Newton & Marquiss (1981), Askenmo (1982) and Aparicio (1994).

An additional explanation for the differences found between control pairs and those near rubbish dumps could be a bias in bird quality; birds that breed nearer to rubbish dumps could be more competitive and therefore able to defend the best territories or nest sites. However, nest sites on evergreen oaks around rubbish dumps are not limited and food in the rubbish is abundant and spread through a relatively large area, suggesting that it is not nest-sites or food that constrain the number of breeding pairs near the rubbish dumps.

A similar positive relationship between food abundance in rubbish dumps and clutch size was found by Pons & Migot (1995) in Herring Gulls. Reduction in food supply, resulting from the closure of a rubbish dump, was followed by a decrease of 6.7% in mean clutch sizes and a 50% reduction in production of young.

The threshold hypothesis (Martin 1987, Boutin 1990) suggests that clutch size might only increase with food addition when natural food supplies are low. This hypothesis has found empirical support in several studies such as those of Hiom *et al.* (1991), Svensson & Nilsson (1995) and Nager *et al.* (1997). Accordingly, we should expect greater differences in clutch size between nests near rubbish dump and those in control areas under poor natural conditions. The 1991 season was the first of several dry years in Spain (INM 1991), so food for control pairs was scarce and decreased, while those pairs breeding close to the rubbish dumps had a constant, abundant and predictable food source. In contrast, 1996 was a good year with abundant rainfall (INM 1996). In accordance with the threshold hypothesis, in 1991 we detected food-dependent differences in clutch size between nests near rubbish dumps and those in control areas – that is, during a year with low food availability.

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