Food supply and seasonal variation in breeding success: an experiment in the European coot

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SUMMARY

We investigated experimentally the seasonal role of food supply in brood survival of the European coot *Fulica atra*. For two breeding seasons, individual pairs were offered supplemental food the first ten days after their young hatched. Under natural conditions this period was largely responsible for the seasonal variation in brood survival. Our experiment tested three hypotheses: (1) food supply is not involved in breeding success at any date (*other factors hypothesis*), (2) food supply limits success independently of date (*elevation hypothesis*), and (3) food supply affects success seasonally and is responsible for the natural seasonal trend in success (*date hypothesis*). Experimental pairs with supplemental food raised heavier, larger and more chicks than control pairs. Consistent with the *date hypothesis*, food supplementation abolished seasonal variation in chick survival. Chick growth under supplemental food was in agreement with the *elevation-hypothesis*. This discrepancy was probably due to the limited supply of additional food. We conclude that seasonal variation in offspring production was in essence the result of seasonal variation in food availability.

1. INTRODUCTION

Most birds show a marked pattern of reproductive output with nesting date. Offspring survival often declines as the season progresses, as do other measures of reproductive output, such as clutch size, fledging success, and offspring survival to breeding age (Klomp 1970; Perrins 1970; Daan *et al.* 1989; Rohwer 1992). Seasonal variation in food supply during the brood care period is one important explanation for variation in fledging success with hatching date (Lack 1968; Perrins 1970; Martin 1987; Daan *et al.* 1989). Studies of species with precocial young have suggested alternative hypotheses, such as marked seasonal trends in weather conditions (Bengtson 1972; Erikstad & Anderson 1983), predation rate (Cooke & Findlay 1982; Elridge & Krapu 1988), or parasite loads as the cause of the seasonal pattern in offspring survival (Møller 1994). Examination of natural variation in predation or harsh weather might, however, be deceptive. For instance, predation risk might be directly related to starvation, as revealed in experiments with eider ducklings (*Somateria mollissima*, Swennen 1989). Similar interactions may exist between the condition of young and their susceptibility to parasites (Møller 1994). Therefore, experimental manipulations of suggested factors are needed to unravel the mechanism behind seasonal variation in breeding success.

Experimental studies have confirmed that food supply during the brood care period may restrict offspring survival, as success increased following food supplementation during that period alone (Harris

1978; Simons & Martin 1990; Ens *et al.* 1992; Richner 1992; but see Verhulst 1994). The same applies to predation, as predator reduction experiments in several grouse showed that reproductive success may increase following reduced predation on young (Marcström *et al.* 1988). Experimentally increased parasite levels have reduced growth rates in nestlings (Møller 1994). To our knowledge, however, no empirical study has addressed the question of whether food supply, predation, parasitism or any other factor causes the seasonal trends in fledging success.

Whereas in most bird species there is a decline in fledgling production with advancing breeding date (Daan *et al.* 1989; Rohwer 1992), in the European coot, *Fulica atra*, the number of young raised to independence typically shows a convex seasonal pattern. There is a slight increase in numbers of young fledged early in the season, followed by a protracted decline in fledging after a peak early in the season (Brinkhof *et al.* 1993). We have previously shown that this pattern is caused by seasonal variation in the environment, rather than by systematic variation in quality between pairs breeding at different dates (Brinkhof *et al.* 1993). Thus, late pairs (presumably of low quality) enjoyed enhanced reproductive success when their breeding time was experimentally advanced. This result indicated that date itself, rather than quality differences between early and late breeders, was responsible for the seasonal variation in chick survival. Which aspects of the environment were responsible for the seasonal pattern was unclear, but we suggested that seasonal variation in food supply could have played a role. Here we report the results of

Figure 1. Expected results under different hypotheses for the role of food supply on the seasonal variation in chick survival. The natural seasonal trend in survival of young is given by the control pairs (open circles, broken line). The arrows give the expected effect of food supplementation. If food supply is not limiting success (*other factors hypothesis*), the survival rate of young for experimental pairs (closed circles, solid line) will not be affected by the supplementation of food at any date (a). If food supply limits success independent of date (*elevation hypothesis*), food supplementation should lead to an increase in the level of survival of young throughout the season (b). If food supply limits success seasonally (*date hypothesis*), food supplementation should not only raise the level, but also result in the disappearance of the seasonal trend in survival (c). Remark: the visual difference in slopes between the curves in (b) is due to the assumption of a logistic response in modelling survival rates (see data analysis).

a food supplementation experiment, carried out to investigate this possibility.

The seasonal pattern in fledgling production is largely the result of a convex seasonal pattern in chick survival during the first two weeks after hatching (Brinkhof *et al.* 1993), and therefore food supplementation was carried out during this period. We consider three hypotheses for the role of food supply during this critical period. These hypotheses are not mutually exclusive, but they lead to different predictions for the outcome of experimental manipulations of food supply. First, the seasonal variation in hatchling survival may be due to factors other than the food supply (*other-factors hypothesis*). Under this hypothesis we expect no effect of food supplementation on hatchling survival at any date (figure 1a). Second, food supply may limit hatchling survival independent of season. In this case food supplements should equally enhance chick survival throughout the season, so the normal seasonal variation is unchanged (*elevation hypothesis*; figure 1b). Third, seasonal trends in the food supply may create seasonal trends in survival (*date hypothesis*). This hypothesis predicts that food supplementation would enhance the survival of early and late young more than of young hatched at the time when survival is normally highest, and thereby lead to a disappearance of the seasonal trend in success (figure 1c). The aim of this study was to distinguish experimentally between these three hypotheses by supplementary feeding of coot families during the first ten days after hatching.

2. MATERIALS AND METHODS

(a) Study area and study species

The experiments were done in 1990 and 1991 at Lake Westeinderplassen (52° 18' N, 4° 42' E), 17 km south-west of Amsterdam, The Netherlands (see also, Cavé & Visser 1985). The majority of breeding pairs of the European coot in the

study area (147 and 148 pairs in 1990 and 1991, respectively) were marked with steel bands and numbered plastic neck collars.

Coots are highly territorial during the breeding season, with both male and female defence (Kornowski 1957). The coot is a facultative double-brooded species, in which only the earliest breeding pairs produce a second brood. The young are semi-precocial. For two weeks after hatch, chicks are dependent on feeding and brooding provided by both parents (Horsfall 1984). Thereafter, young gradually become self-supporting by 7–9 weeks of age (Kornowski 1957; Horsfall 1984).

(b) Determination of breeding variables

From March to June we searched the area at least once per week to locate nest sites, mark eggs with permanent ink, determine clutch size, and identify marked parents. Laying date of the first egg was determined by backdating, assuming a laying frequency of one egg per day. The clutch was considered complete when no egg was laid on three consecutive days. Incubation starts before the clutch is completed, and eggs hatch asynchronously. The mean hatching date of the clutch (50% hatched) was used in analyses (see Brinkhof *et al.* 1993).

(c) Experimental procedure and determination of breeding success

Throughout the breeding season, 80 control (1990, $n = 52$; 1991, $n = 28$) and 42 experimental pairs (1990, $n = 25$; 1991, $n = 17$) were randomly chosen. For the latter pairs, the experimental procedure started approximately five days before hatching with a habituation period when a plastic feeding tray was placed 2–4 m from the nest. These trays were initially baited with bread to get birds to use the trays. From hatch to day 10 after hatching, experimental pairs were supplemented twice a day (10:00 and 15:00 hrs) with small mealworms (*Alphitobius diaperinus*) and some pelleted poultry starter (Kenner™, main components as indicated by the supplier: 16% crude protein, 4% fat, 4.5% fibre, with

supplements of vitamin A, D3 and E). The supply of live mealworms was restricted to about 15 g per young per day, while the pellet food was provided *ad libitum*. On day 11 food supplementation was stopped and the tray removed.

Five experimental pairs abandoned their clutch before hatch, possibly because the food tray was placed too near (< 2 m) to their nest. These pairs and two pairs whose trays were monopolized by mallards (*Anas platyrhynchos*) were excluded from the analyses. Chicks of food-supplemented pairs were fed with supplemental food in all cases. In 25 cases the coot parents made exclusive use of the tray, but in ten cases other species of birds, mainly mallard and moorhen (*Gallinula chloropus*), also used the food. These 35 experimental pairs were compared with the 80 control pairs. Control (CO) and food-supplemented (FS) pairs showed a similar variation in laying date (mean $\pm$ s.e.; for CO: 103.06 ± 1.29 ; for FS: 104.97 ± 2.52), clutch size (for CO: 7.22 ± 0.14 ; for FS: 7.17 ± 0.21) and hatching success (for CO: 0.94 ± 0.02 , for FS: 0.91 ± 0.03). Clutch size ($n = 115$) declined with date, but the level and slope of the decline did not vary between years or between control and experimental pairs (ANCOVA with treatment (control, experimental) as the class variable; for level, $F_{1,112} < 0.01$, $p = 0.96$; for slope, $F_{1,111} = 0.65$, $p = 0.42$).

The number of surviving young in each brood was determined on day 10 after hatching (i.e. the end of the feeding period). In addition, young were caught where possible to measure body mass and tarsus length as parameters for growth.

(d) Data analysis

Analyses were carried out using GLIM (Francis *et al.* 1993). Logistic regression was used for the analysis of survival rates; multiple regression for the analysis of body mass and tarsus length. In logistic regression analyses, the residual scaled deviance of the final model was considerably larger than the residual degrees of freedom, so William's adjustment for overdispersion in data with binomial errors was used (see Crawley 1993). Dates are presented as day of the year (i.e. May 1 = day 121).

The three hypotheses considered for the role of food supply (figure 1) give explicit predictions for the effect of food supplementation on the seasonal trend in breeding success. The normal convex seasonal pattern of the response variable (R) representing survival (Brinkhof *et al.* 1993) or growth (unpublished results) of chicks can be expressed as a quadratic function of hatching date (HD):

$$R = a + bHD - cHD^2. \quad (1)$$

We assume a logistic response in survival rate and a linear response in growth, which implies an additive effect of the covariates on either the log-odds of survival (i.e. $\ln(s/(1-s))$) or growth rate. The effects of food supplementation (FS; controls: FS = 0, food supplemented broods: FS = 1) can then be expressed as:

$$R = a + bHD - cHD^2 + (a'FS + b'HDFS + c'HD^2FS). \quad (2)$$

The term in the right-hand parentheses gives the potential effects of additional food, and allows us to distinguish between the three hypotheses for the role of food supply. Under the *other factors hypothesis* (figure 1a) none of the terms involving FS (a' , b' , c') will be significantly different from 0, reducing equation (2) to equation (1). Under the *elevation hypothesis* (figure 1b), additional food raises the level of success only; thus $a' > 0$, $b' = 0$ and $c' = 0$. Under the *date hypothesis* (figure 1c) food supplementation affects not only the level of

R , but also counteracts the natural seasonal trend. Thus $a' > 0$, $b' = -b$ and $c' = -c$, and equation (2) can be rewritten as:

$$R = a + a'FS + bHD(1 - FS) - cHD^2(1 - FS). \quad (3)$$

3. RESULTS

(a) Survival over the feeding period

Logistic regression was used to analyse the variation in survival rates for the first ten days following hatching. In the control pairs, *YEAR* (as factor), HD and HD^2 contributed significantly to the explained variation (table 1a). The significance of the variable *YEAR* means that the survival of chicks differed between years, the rates in 1990 being higher than in 1991 (figure 2). However, the seasonal trend in survival was not noticeably different between years for control birds, as the interactions of year with HD ($F_{1,75} = 2.09$, $p = 0.15$) and of year with HD^2 ($F_{1,74} = 1.33$, $p = 0.25$) were not significant. Survival of chicks over the first ten days after hatching for both years followed a convex seasonal pattern, with maximum values around day 125 (May 5) (figure 2).

For the food-supplemented broods, *YEAR*, HD , HD^2 and their interactions did not significantly contribute to the explained variance in survival (table 1b). Survival rate for the ten food-supplemented broods where we observed other species of birds taking food from the tray was not significantly different from broods with exclusive use of the supplemental food ($F_{1,33} = 1.42$, $p = 0.24$). For broods receiving additional food, survival rates were independent of year and season (figure 2).

The finding that there was no seasonal variation in survival in food-supplemented broods (table 1b), while seasonal variation was present among control pairs (table 1a), suggests the *date hypothesis* (figure 1c). To test formally if food supplementation affected the seasonal trend in chick survival we intended to fit equation (2) to the data. However, since chick survival varied significantly between years in the control group (table 1a), we added *YEAR* as a factor to this model. In addition, the interaction between year and food supplementation (FS) was added, because chick survival varied between years in the control group, but not in the food-supplemented group.

The resulting model after fitting equation (2) including the terms *YEAR* and *YEAR*·FS is given in table 1c. All major terms, except the interaction between *YEAR* and food supplementation, were significant, and all underlying terms were retained in the model. As can be seen in table 1c, the coefficients $-b'$ and $-c'$ were close to the coefficients b and c respectively (see equation (2)). This implies that the food supplement counteracted the convex seasonal pattern in chick survival, as predicted by the *date hypothesis*. Further, the level of survival within food-supplemented broods was significantly higher than in control broods.

Finally, we tested whether the effect of the food supplement solely counteracted the convex seasonal trend in chick survival, without creating any further date-effect. We therefore compared the fit of the model

Table 1. *Effect of food supplementation on the seasonal variation in survival of young*

(Logistic regression analysis of the survival of young for the first ten days after hatching for control broods (*a*), food-supplemented broods (*b*) and control and food-supplemented broods combined (*c*). Supply of additional food was tested as group (food-supplemented broods $FS = 1$, controls $FS = 0$). For 'YEAR' the mean estimate of the constant over the two years is given. Williams's adjustment with *F*-tests was used in testing the significance of the variables retained in the final model since there was considerable overdispersion (ratio of scaled deviance to d.f. was 2.1, 1.6 and 2.0 for the models (*a*), (*b*) and (*c*) respectively). For further explanation see text.)

parameter	(increase in)		<i>p</i>	estimates of coefficients		
	deviance	d.f.		in model	s.e.	in eqn (2)
(<i>a</i>) null model	200.56	79				
final model	93.50	76				
constant		1				
YEAR	6.86	1	0.02	−34.6	17.0	
hatching date (<i>HD</i>)	4.90	1	0.05	0.553	0.260	
<i>HD</i> ²	5.52	1	0.04	−0.00221	0.000985	
(<i>b</i>) null model	53.27	34				
final model	38.98	34				
constant		1		0.857	0.162	
(<i>c</i>) null model	303.62	114				
final model	130.03	108				
constant		1				
YEAR	5.29	1	0.04	−35.3	16.5	a
food supplement (<i>FS</i>)		1		59.4	26.2	a'
hatching date (<i>HD</i>)		1		0.564	0.253	b
<i>HD</i> ²		1		−0.00226	0.000960	c
<i>HD</i> · <i>FS</i>	5.49	1	0.03	−0.910	0.397	b'
<i>HD</i> ² · <i>FS</i>	5.85	1	0.03	0.00352	0.00149	c'
<i>Rejected term</i>						
YEAR· <i>FS</i>	1.82	1	0.29

Figure 2. Seasonal variation in the survival rate of young over the first ten days after hatching for control (1990: open circles, broken line; 1991: open triangles, dotted line) and food-supplemented (1990: closed circles; 1991: closed triangles; solid line for years combined) broods. The mean values (± 1 s.e.) in the experimental group within years (1990, $n = 20$; 1991, $n = 15$) were calculated over five broods each, which were grouped according to hatching date. To allow a direct comparison of the mean values between control and experimental groups within years, the mean values for the control pairs were calculated over a range of hatching dates corresponding to each group of five experimental pairs. The analysis was of the ungrouped data and the logistic regression lines of the best (maximum likelihood) fit are given.

in table 1c with the fit to equation (3) (including the term YEAR), in which the coefficients b' and c' were forced to be exactly opposite to the coefficients b and c respectively. The difference between the two models was not significant (Δ deviance = 2.59, Δ d.f. = 2, $F_{2,108} = 2.15$, $p = 0.12$). This proves that the supply of extra food merely eliminated the seasonal variation in chick survival. It affirms that seasonal variation in chick survival is caused by food supply.

(b) Growth over the feeding period

Body mass and tarsus length of 115 young were determined at the end of the feeding period in 18 (1990, $n = 5$; 1991, $n = 13$) out of 80 control and 25 (1990, $n = 12$; 1991, $n = 13$) out of 35 food-supplemented broods. The average number of young caught was 2.5 (93% of those present) and 2.8 (54%) in the control and food-supplemented broods, respectively. It was assumed that these young were representative of the brood. The young were between 8 and 12 days old, and body mass and size change approximately linearly over this period (Visser 1974). Growth measures were averaged per brood and analysed using multiple regression.

Controlling for the age differences, YEAR, HD, *HD*², the interactions of year with HD and *HD*², and food-supplementation (*FS*) contributed significantly to the explained variance in mean body mass and mean tarsus length (table 2). This implies that the level and the seasonal variation in growth was significantly

Table 2. *Effect of food supplementation on the seasonal variation in growth of young*

(Multiple regression analyses of the variance in the growth measures body mass and tarsus length of young at the end of the feeding period averaged per brood. The data were weighed for the number of young assessed per nest. R^2 values were calculated hierarchically in the order as shown in the table.)

parameter	d.f.	body mass			tarsus length		
		R^2 (%)	F	p	R^2 (%)	F	p
AGE (days)	1	26	23.74	< 0.01	24	18.31	< 0.01
YEAR	1	30	5.28	0.03	29	5.05	0.03
hatching date (HD)	1	38	3.60	0.07	33	3.45	0.07
HD ²	1	38	3.73	0.06	33	3.44	0.07
YEAR·HD	1	43	4.83	0.03	40	4.57	0.04
YEAR·HD ²	1	50	4.40	0.04	46	4.12	0.05
food supplement	1	58	6.15	0.02	54	6.18	0.02
residual	35

Figure 3. Seasonal variation in residual mean body mass and mean tarsus length (both corrected for age) of chicks in control (open circles, broken lines) and food-supplemented (closed circles, solid lines) broods for 1990 and 1991. Symbols represent data from individual broods. The regression lines give the best (least squares) fit for the data combined.

different between years. In 1990, both body mass and tarsus length declined with date. In 1991, body mass and tarsus length showed a convex relationship with date (figure 3). Body mass and tarsus length of young of experimental broods were significantly higher than those of young of control broods. The seasonal variation in growth within the experimental group was, however, not significantly different from the natural seasonal variation (table 2; figure 3).

4. DISCUSSION

The results support the hypothesis that brood survival is limited by food supply during the early

brood care period. At the end of the ten-day feeding period, brood sizes and chick growth of food supplemented coot pairs were greater than those of the controls. More importantly, food supplementation counteracted the convex seasonal trend in survival. This was in accordance with the *date hypothesis* (figure 1c). However, seasonal variation in growth persisted, as predicted by the *elevation hypothesis* (figure 1b).

The discrepancy between results for survival and growth may have been due to the smaller data set available for the growth analysis, offering less potential to discriminate between the *level* and *date* hypotheses. Alternatively, the divergence could reflect our inability to supply mealworms *ad libitum*; on most visits none

remained in the feeding trays. Coot parents preferred to feed mealworms to their young rather than pellet food. Moreover, food-supplemented parents fed their young with natural foods (e.g. insects) as well. This may have been due to the limited quantity or quality of the mealworms supplied. In either case, food-supplemented broods were to some extent subject to natural seasonal variation in food supply, which may have manifested itself in the growth of chicks, but not in their survival. The number of mealworms delivered to the young was partially determined by the parents, who ate some of the mealworms, especially when the young showed signs of satiation.

We may conclude that seasonal variation in food supply gives rise to the seasonal pattern in chick survival, and our data also indicate the mechanism causing this pattern. The influence of food supply could have been mainly direct, through starvation, or indirect, through enhancing predation or parasitism (McNamara & Houston 1987; Swennen 1989). Indeed, the seasonal trend in survival could have been entirely due to seasonal variation in predation rate, with supplemental food reducing the exposure to predation. However, the seasonal trend in growth which, although more variable than survival, was always downwards towards the end of the season, gives strong support for a direct effect of food shortage. Moreover, measurements of natural food (i.e. insects on the water surface) revealed a convex seasonal pattern that closely matched the seasonal pattern in chick survival in the first ten days after hatching (Brinkhof 1995). The more marked effect of food supplementation on survival than on growth suggests that, although extra food was enough to take the young over a starvation threshold, it was inadequate to compensate fully for the effect of the natural seasonal trend in food supply.

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