Reduced parental effort in relation to laying date in house sparrows (*Passer domesticus*): a study under controlled conditions

Gregorio Moreno-Rueda*

Departamento de Biología Animal y Ecología, Facultad de Ciencias, Universidad de Granada, E-18071 Granada, Spain

Abstract

It is known that breeding success in birds declines with an advance in the laying date. In this paper, breeding success diminished with laying date in a house sparrow (*Passer domesticus*) population breeding in captivity. The principal cause of the cline in breeding success with date was a decrease in the female feeding rate. The parental effort in females decreased with the advance of the laying date, although food access was ad libitum throughout the breeding season. Consequently, this cline in breeding success may be due to a reduced parental investment with the advance of the laying date or to exhaustion due to previous reproductive events in the season. Hypotheses usually used to explain the cline in breeding success with date can not explain results in this study.
© 2004 Elsevier B.V. All rights reserved.

Keywords: Breeding success; Parental investment; House sparrow; *Passer domesticus*; Laying date

1. Introduction

Several studies have shown that, in birds, breeding success declines as the laying date advances (Klomp, 1970; Perrins and Birkhead, 1983; Moreno, 1998). Most hypotheses explaining this descent may be grouped in two blocks: the "timing" and the "quality" hypotheses. The "timing" hypotheses state that environmental conditions deteriorate as the laying date advances, reducing breeding success in later broods. Food reportedly diminishes at later dates (Lack, 1968; Martin, 1987). Ectoparasite loads appear to be heavier in second broods (Brown and Brown, 1999; Merino et al., 2000). Moreover, chicks fledging from later broods have a competitive disadvantage with respect to those from earlier broods, which have al-

ready achieved a stronger ability to compete, and this may diminish survival prospects for later fledglings (Nilsson and Smith, 1988; Sandell and Smith, 1991). Loss due to predation may also be heavier for later broods (Birkhead, 1977). A second group of hypotheses holds that parents breeding later are poor quality, either because they are in poor condition (Price et al., 1988), or because they are inexperienced parents (Forslund and Larsson, 1992; Perdeck and Cavé, 1992), or because they acquire territories of lower quality (Svensson and Nilsson, 1995).

The two groups of hypotheses are not mutually exclusive. In fact, some studies have found an effect of both parental quality and time of breeding on the relationship between breeding success and date (Verhulst et al., 1995; Nilsson, 2000). That environmental conditions deteriorate as the date advances seems clear, and when such environmental deterioration is controlled for breeding success is higher (De Lope and

* Tel.: +34 958243082; fax:+34 958243238.
  E-mail address: gmr@ugr.es (G. Moreno-Rueda).

Møller, 1993; Siikamäki, 1998; Brown and Brown, 1999). Nevertheless, the "quality" hypothesis would not explain differences in breeding success between first and later broods in multi-brooded species (e.g., great tit, *Parus major*; Sanz, 1998).

In short, because of a worsening in environmental conditions with date, later broods become infested with more ectoparasites, and thus have higher energetic requirements (Christe et al., 1996). Moreover, food availability in the environment for later broods is lower. Although parents successfully raise fledged chicks with the same quality as earlier broods, they would be in a competitive disadvantage with respect to earlier fledglings (above). This implies that later broods should have lower reproductive values than earlier ones. Indeed, the probability of recruitment for chicks declines with the fledging date (Svensson, 1997; Verboven and Visser, 1998). On this basis, because reproduction is expensive (Clutton-Brock, 1991; Stearns, 1992), lower parental investment (sensu Carranza, 2002) would be predicted in these later broods (Curio, 1983), allowing parent birds higher survival or future reproductive success (e.g., Gustaffson and Sutherland, 1988). This lower parental investment would not cause the decline in breeding success with later date, it would be a consequence (Moreno, 1998). There are few works in which this hypothesis has been tested, because most of studies seek to test the "timing" and "quality" hypotheses.

For the testing of this hypothesis a type of measurement of parental effort is required, for example, feeding rate, which is related to parental energy expenditure (Tinbergen and Verhulst, 2000). Nevertheless, the studies cited in this introduction have measured parameters of breeding success, but they have seldom measured any parameter of parental effort. Studies that have found a feeding rate or nest attendance decline with advanced laying date (Kelly and van Horne, 1997; Naef-Daenzer et al., 2000) did not determinate whether that lower feeding rate was due to environmental deterioration or a reduction in parental investment. Even in studies which controlled for environmental deterioration and eliminated the decline in breeding success (e.g., Siikamäki, 1998), we cannot rule out the possible existence of a cline in parental investment that would have been masked by the experimental treatment. For example, in the study of Siikamäki (1998), extra food was supplied to pairs

forced to lay a replacement brood. These pairs were more successful than other pairs that were forced to lay a replacement brood but without being given extra food. However, pairs with extra food initiated moult earlier, while they fed nestlings, suggesting that they had a great surplus of food. This surplus could enable a high breeding success with lower parental investment.

Nevertheless, some studies give some support to the hypothesis of lower parental investment with an advancing laying date. Brown and Brown (1999), studying the cliff swallow (*Petrochelidon pyrrhonota*), found that females laying later in the season had higher probabilities of winter survival, suggesting that those females invested less in reproduction.

In the present work, I studied whether parental effort declined with an advancing laying date in an aviary where house sparrows (*Passer domesticus*) have bred successfully since 1999. The food supply did not vary with date, being provided ad libitum. First, I examined whether breeding success declined with an advance in the laying date although individuals breeding in captivity were provided with food ad libitum. Because a cline in breeding success with an advancing laying date was detected (see Section 3), I also examined whether parental effort declined at a later date and whether it explained such cline in breeding success.

2. Material and methods

This study was conducted during the breeding season of the year 2001 in an indoor aviary sited in the Faculty of Sciences at the University of Granada (Granada City). The aviary, with a volume of 20.5 m^3, was visually isolated to avoid stress to birds. Ad libitum access to food and water, as well as to nest material and nest-boxes, were provided throughout the breeding season. Light in the aviary simulated the natural photoperiod. Temperature increased with time, but it was more constant than in the field. House sparrows had bred successfully since 1999. They were captured in December 1998 near the lagoon of Padul and in the city of Granada (both in the province of Granada, SE, Spain). In 2001, 22 pairs bred in the aviary and their reproductive parameters resembled those found in nature (Moreno-Rueda and Soler, 2002). For a more detailed description of captivity conditions, see Moreno-Rueda and Soler (2002).

All birds in the aviary had colour rings, and their histories were known. Periodic observations provided data concerning the pairs formed and nest-boxes used. Pairs formed remained stable during the study. At the same time each day nest-boxes were examined, and their content was recorded (number of eggs or nestlings). The record of the first egg found in the nest was considered the laying date. The number of fledglings per nest also was noted. In some broods randomly selected, feeding rates by male and female were recorded during one-hour observation periods. A total of 43 broods observed had small chicks (3–5 days old) while 24 broods had large chicks (10–12 days old).

A Kolmogorov–Smirnov test revealed that all variables were normally distributed, and thus, parametric statistics were used according to Sokal and Rohlf (1995), using the computer program Statistica (Statsoft, 2001). Analyses of reproductive parameters and feeding rates with date implied General Linear Models (GLM) that controlled by pair. The results are given as mean ± S.D. All statistical tests were two-tailed.

3. Results

Laying date had no significant effects on clutch size (date: $F_{1,34} < 0.01$, $P = 0.98$; pair: $F_{21,34} = 1.07$, $P = 0.42$; Fig. 1A) or number of hatchlings (date: $F_{1,34} = 1.05$, $P = 0.31$; pair: $F_{21,34} = 1.12$, $P = 0.37$; Fig. 1B). Nevertheless, the number of fledglings per nest did decline significantly with the advance of the laying date (date: $F_{1,34} = 16.15$, $P < 0.001$; pair: $F_{21,34} = 1.05$, $P = 0.44$; Fig. 1C). Yearling females laid their first clutch later than did experienced females (yearling females, $n = 7$, median: 05/06/01, experienced females, $n = 15$, median: 04/14/01, median test, $\chi^2_1 = 5.25$, $P = 0.02$; see Fig. 1). Yearling females showed no decline in number of fledglings with an advance in the laying date (date: $F_{1,9} = 0.16$, $P = 0.70$; pair: $F_{6,9} = 0.53$, $P = 0.77$), while experienced females did (date: $F_{1,24} = 21.98$, $P < 0.001$; pair: $F_{14,24} = 1.32$; $P = 0.26$; Fig. 1C). Using a GLM to control for a possible effect of hatchling number, I found that the number of fledglings continued to decline with laying date ($F_{1,33} = 15.33$, $P < 0.001$; laying date and hatchlings as continuous predictors,

pair as categorical predictor). Therefore, a decline in breeding success existed in the aviary.

The feeding rate of females was significantly higher than for males when the nests contained large chicks (Fig. 2). Females increased their feeding rate significantly when chicks were larger, while males did not (Fig. 2). When there were small chicks in nests (3–5 days old, $n = 43$), the feeding rate of females declined with the advance of laying date (date: $F_{1,21} = 12.36$, $P = 0.002$; pair: $F_{20,21} = 1.29$, $P = 0.28$; Fig. 3), while males showed no significant trend (date: $F_{1,21} = 1.98$, $P = 0.18$; pair: $F_{20,21} = 0.08$, $P = 0.81$). The feeding rate of yearling females did not decline with the advance of the date (date: $F_{1,6} = 0.29$, $P = 0.61$; pair: $F_{6,6} = 0.42$, $P = 0.84$), but the feeding rate of experienced females did (date: $F_{1,15} = 12.17$, $P < 0.01$; pair: $F_{12,15} = 0.54$, $P = 0.84$; Fig. 3). When nestlings were 10–12 days old ($n = 24$), the feeding rate of females decreased with the advance of the laying date (date: $F_{1,5} = 9.98$, $P < 0.05$; pair: $F_{16,5} = 1.87$, $P = 0.25$). Males showed no significant trend (date: $F_{1,5} = 2.27$, $P = 0.19$; pair: $F_{16,5} = 2.23$, $P = 0.19$).

The number of nestlings (small and large) in the nest when observations were performed registered a significant decline with the advance of laying date ($r = -0.27$, $P < 0.05$, $n = 67$). When nestlings were small, the male feeding rate increased with brood size ($r = 0.50$, $P = 0.001$), whereas the female feeding rate showed a non significant trend ($r = 0.24$, $P > 0.1$). When nestlings were bigger, the feeding rates of males as well as females increased with brood size (for both sexes: $r > 0.40$, $P < 0.01$). To control for a possible effect by brood size on the relationship between feeding rates and date, I performed four General Linear Models with the feeding rate of each sex as dependent variables and with date, pair and brood size as independent variables, distinguishing small and large nestlings. When the nestlings were small ($n = 43$) brood size, but not date, almost significantly affected the male feeding rate (brood size: $F_{1,20} = 3.60$, $P = 0.07$; date: $F_{1,20} = 0.81$, $P = 0.38$; pair: $F_{20,20} = 0.52$, $P = 0.92$). Nevertheless, the female feeding rate was affected negatively by date, but not by number of chicks in the nest (date: $F_{1,20} = 10.20$, $P < 0.01$; brood size: $F_{1,20} = 0.18$, $P = 0.68$; pair: $F_{20,20} = 1.22$, $P = 0.33$). When nestlings were larger ($n = 24$) models were not significant ($P > 0.05$).

Lastly, I performed a GLM with number of fledglings per nest as dependent variable and laying date, pair and feeding rate to small nestlings (of females and males pooled) as independent variables. Only feeding rate, but not laying date, significantly explained variance in the productivity of fledglings (feeding rate: $F_{1,11} = 11.35$, $P < 0.001$; date: $F_{1,11} = 0.15$, $P = 0.71$; pair: $F_{16,11} = 0.87$, $P = 0.62$). This implies that feeding rate, but not laying date, affected fledgling productivity.
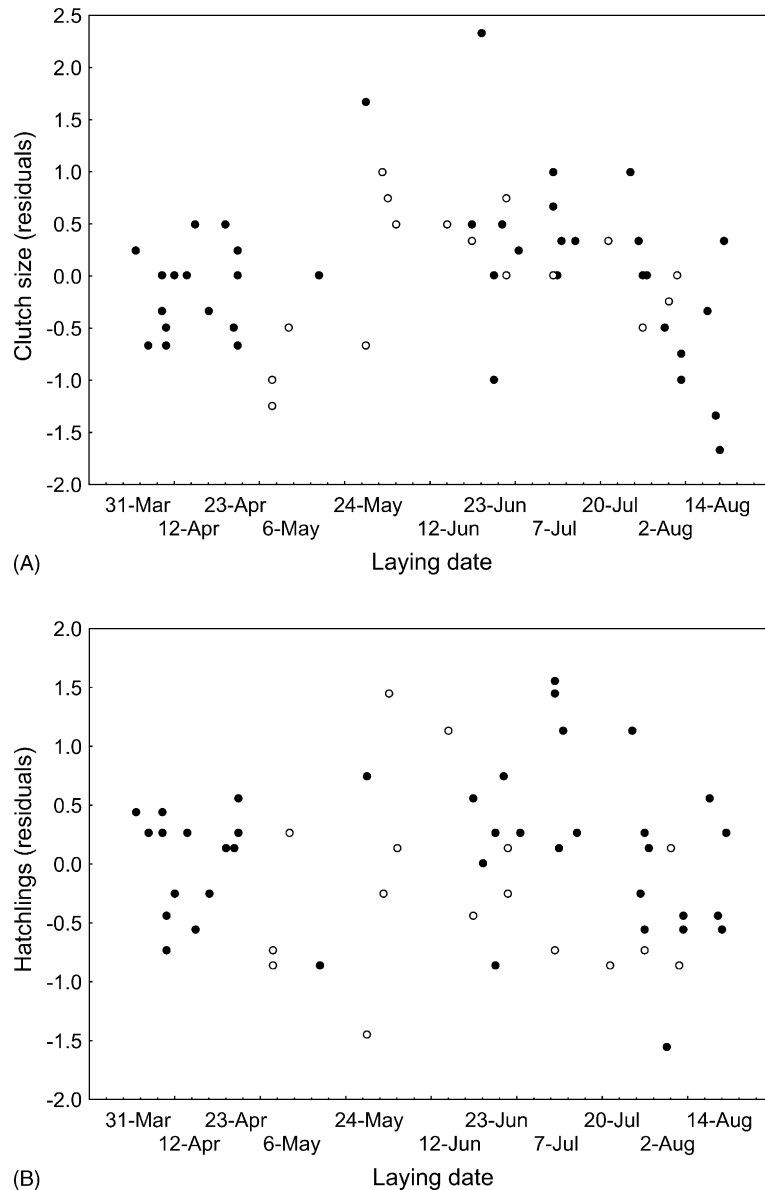
Fig. 1. Relationship between date and residuals of reproductive variables controlled for pair. $N = 57$ broods. Experienced females ($n = 40$): solid circles, yearling females ($n = 17$): empty circles. (A) Residuals of clutch size plotted against laying date. (B) Number of hatchlings per nest (residuals) plotted against laying date. (C) Number of fledglings per nest (residuals) plotted against laying date.
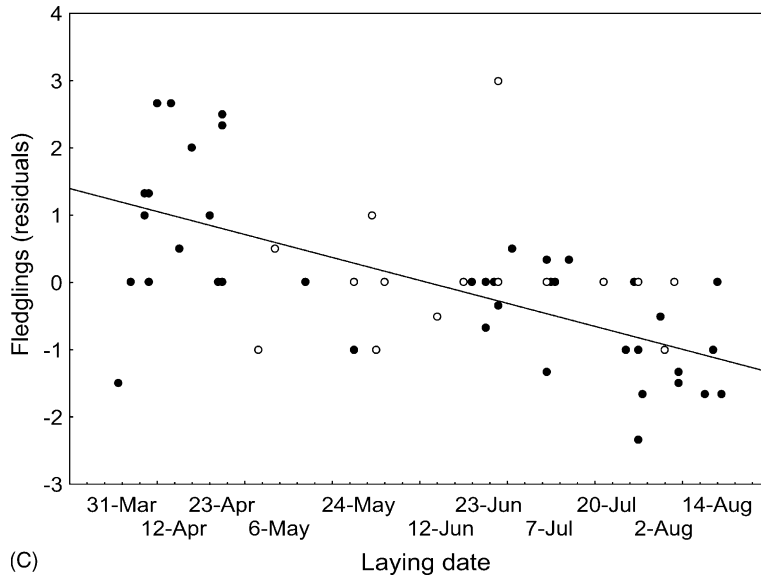
(C)

Fig. 1. (*Continued*)

4. Discussion

This work analyses the variation in breeding success with laying date in a captive population of house sparrows, showing that fledgling success declines as laying date advances, although clutch size and hatching success were not affected. These results are consistent with others reported in the wild (Lack, 1968; Klomp, 1970; Perrins and Birkhead, 1983; Martin, 1987; Moreno, 1998; Verboven and Visser, 1998; Brown and Brown, 1999; and others, including studies with taxa other than birds: Landa, 1992; Schultz,
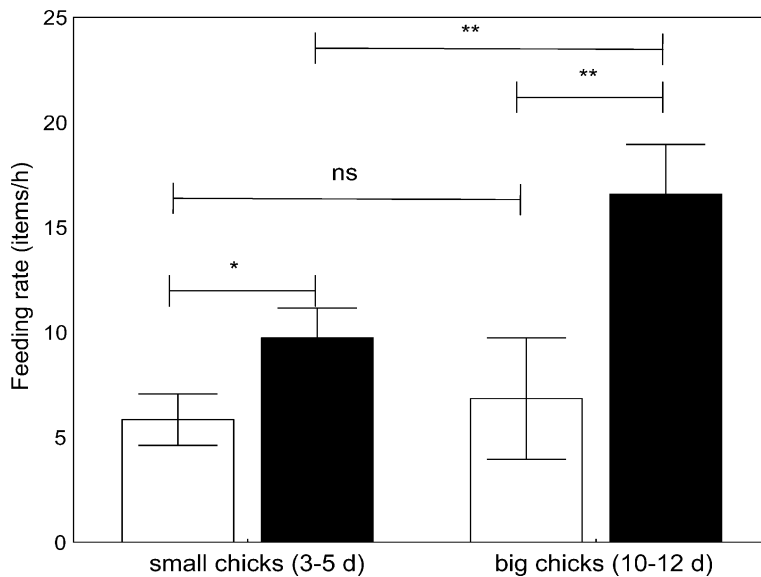

Fig. 2. Feeding rates of males (white) and females (black) according to nestling age. Lines are standard error. Paired *t*-test, $n = 19$; [**]$P < 0.01$, [*]$P < 0.10$, [ns]$P > 0.10$.
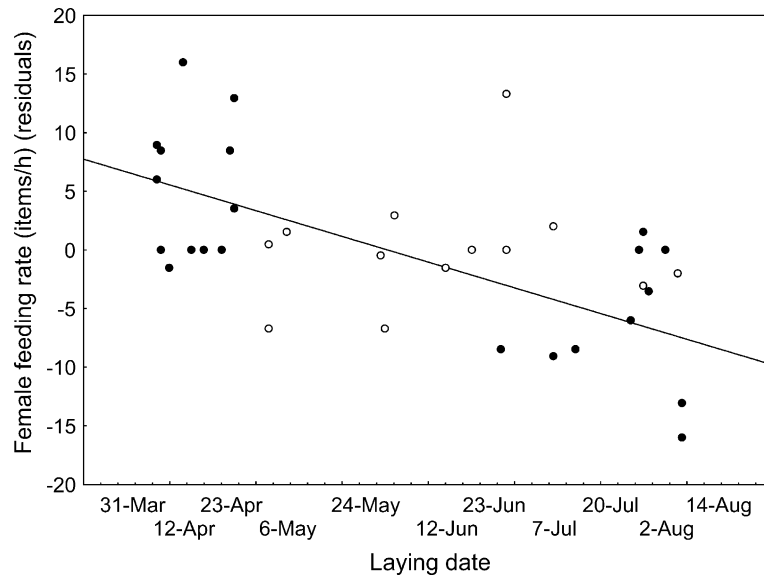
Fig. 3. Relationship between female feeding rate (residuals after controlling for pair) to small nestlings (3–5 days old) and date. Solid circles are experienced females ($n = 29$). Empty circles are yearling females ($n = 14$).

1993; Sinervo and Doughty, 1996). This study, to my knowledge, is the first to report these results for a population breeding in captivity. Below, I discuss hypotheses that could explain these results.

4.1. Quality hypotheses

These hypotheses hold that breeding success declines with an advance laying date due to differences in the quality of reproductive pairs (Price et al., 1988). Indeed, in the present study, experienced females laid earlier than did yearling ones, but laying date had a negative effect on breeding success in successive broods, although individual differences were statistically controlled. This implies that factors other than variation in quality affected breeding success. Variation in territory quality, of course, could not affect the results in this study.

4.2. Timing hypotheses

These hypotheses say that breeding success declines with an advancing laying date because environmental conditions become less favourable as the season progresses (see Section 1). For example, the food supply may decline over a year (Martin, 1987), but this was not the case in the present study. The density of birds in the aviary increased as fledglings left their nests, and such factor could affect breeding success by reducing food access due to increased competition. Nevertheless, this possibility is improbable for three reasons: (1) Adults are dominant over the young (Senar, 1999), and thus, it is improbable that the fledglings would have appreciably affected the access of adults to food. (2) Feeders remained unused for many hours (personal observations), showing that there was no apparent limit on the ad libitum access to food. (3) A stronger effect would be predicted of density on competition among fledglings (Nilsson and Smith, 1988; Sandell and Smith, 1991), predicting reduced fledgling survival at later laying dates, but this did not occur, because fledging date was not different between fledglings that survived and fledglings that died before October first when statistically controlled by fledgling mass (ANCOVA, $F_{1,42}$ $= 1.0$, $P = 0.41$; survival or non-survival as categorical predictor, fledgling mass as covariate). Increase in depredation with an advancing date (Birkhead, 1977), logically, was not a factor in the aviary. Temperature increased positively with the advance of the laying date in the aviary ($r = 0.96$, $P \ll 0.01$, $n = 110$ registers), but temperature would be expected to alter breeding success and feeding rates in a way contrary to that found, that is, as temperature increases

the nutritional needs of the chicks and parents diminish, lengthening the time available for foraging and feeding (e.g., Caraco and Bayham, 1982). Parasite density in the nest is known to increase over the season, and this could affect breeding success (many studies show a negative effect of parasites on breeding success, Moss and Camin, 1970; Møller, 1990). I did not control for ectoparasites, but their quantity in the aviary were very low in comparison with natural nests (personal observations), thus, probably their effect, if any, would be low. Another possibility is that nestlings received lower quantities of food over the day as a whole because daylight hours (i.e., photoperiod) shortened over the year. Nevertheless, as the photoperiod initially increases to the summer solstice and then decreases, a concave up relationship would be predicted, but this was not found.

Most of the variance in breeding success was explained by a cline in feeding rate with an advance in the laying date. This decline in female feeding rate can not been satisfactorily explained by either of the foregoing hypotheses. A possible explanation is that, because the reproductive value of chicks declines with the advancing laying date, it would be expected that parental investment (reflected by feeding rate) declines at later dates (Curio, 1983; Fig. 1 in Moreno, 1998). Females but not males would reduce their parental investment at later laying dates because their investment is higher than that of males (Fig. 2). The house sparrow's breeding success in the wild, as in other multi-brooded birds, shows a peak in the middle of the breeding season, with lows at the beginning and end (Summers-Smith, 1988). This may be due to a peak of food availability in the middle of the breeding season (Lack, 1968). However, fledglings in the first broods may have higher quality because, as stated above, later fledglings would be at a competitive disadvantage (Nilsson and Smith, 1988; Sandell and Smith, 1991). Indeed, house sparrow chicks from later broods often do not breed the next year (Summers-Smith, 1988). Nevertheless, Ringsby et al. (1998) found that later house sparrow chicks had higher probabilities of survival than earlier chicks, and similar results were reported by Murhpy (1978). On the other hand, these results may not be conclusive. For example, Brown and Brown (1999), in a 11-year study on cliff swallows, found that the direction of the relationship between date and fledgling survival was highly variable among years.

Alternatively, female feeding rates could decline with an advancing laying date because of physical exhaustion (Gebhardt-Henrich et al., 1998). This hypothesis would explain why males did not reduce their feeding rate over the season, because their feeding rates were very low. Moreover, yearling females did not reduce their feeding rates over the season, either, maybe because, like the males, they invested less in reproduction (McNamara and Houston, 1996; see Figs. 1 and 3, empty circles), and were less exhausted late in the season.

In short, this study shows that breeding success declines with advancing laying dates in a population of house sparrows breeding in captivity. Such decline in breeding success was primarily due to a decline in female feeding rate over the season. The results do not exclude the importance of the "timing" and "quality" hypotheses, and, indeed, some results support these hypotheses. Nevertheless, the present results clearly show that an additional factor, maternal effort (measured as the feeding rate) affected breeding success. This descent in feeding rates can be explained by two no mutually exclusive hypotheses: (1) Because reproductive value of nestlings decreases with the advance in the laying date, females could diminish their investment over time; however, more data in the wild are necessary to demonstrate that the reproductive value of nestlings declines with an advancing laying date. (2) The female feeding rate could also decline over time due to exhaustion, then, because birds had ad libitum access to food, this effect should be more notable in the wild.

Acknowledgements

References

Birkhead, T.R., 1977. The effect of habitat and density on breeding success in the Common Guillemont (*Uria aalge*). J. Anim. Ecol. 46, 751–764.

Brown, C.R., Brown, M.B., 1999. Fitness components associated with laying date in the cliff swallow. Condor 101, 230–245.

Caraco, T., Bayham, M.C., 1982. Some geometric aspects of house sparrow flocks. Anim. Behav. 30, 990–996.

Carranza, J., 2002. La evolución del cuidado parental. In: Soler, M. (Ed.), Evolución. La base de la Biología. Proyecto Sur de Ediciones, Granada, pp. 193–212.

Christe, P., Richner, H., Oppliger, A., 1996. Begging, food provisioning, and nestling competition in great tit broods infested with ectoparasites. Behav. Ecol. 7, 127–131.

Clutton-Brock, T.H., 1991. The Evolution of Parental Care. Princeton University Press, Princeton.

Curio, E., 1983. Why do young birds reproduce less well? Ibis 125, 400–404.

De Lope, F., Møller, A.P., 1993. Effects of ectoparasites on reproduction of their swallow hosts: a cost of being multi-brooded. Oikos 67, 557–562.

Forslund, P., Larsson, K., 1992. Age-related reproductive success in the barnacle goose. J. Anim. Ecol. 61, 195–204.

Gebhardt-Henrich, S.G., Heeb, P., Richner, H., Tripet, F., 1998. Does loss of mass during breeding correlate with reproductive success? A study on Blue Tits *Parus caeruleus*. Ibis 140, 210–213.

Gustaffson, L., Sutherland, W.J., 1988. The costs of reproduction in the collared flycatcher *Ficedula albicollis*. Nature 335, 813–815.

Kelly, J.F., Horne, B.V., 1997. Effects of food supplementation on the timing of nest initiation in belted kingfishers. Ecology 78, 2504–2511.

Klomp, H., 1970. The determination of clutch-size in birds: a review. Ardea 58, 1–124.

Lack, D., 1968. Ecological Adaptations for Breeding in Birds. Methuen, London.

Landa, K., 1992. Seasonal declines in offspring fitness and selection for early reproduction in nymph-overwintering grasshoppers. Evolution 46, 121–135.

Martin, T.E., 1987. Food as a limit on breeding birds: a life-history perspective. Annu. Rev. Ecol. Syst. 18, 453–487.

McNamara, J.M., Houston, A.I., 1996. State-dependent life histories. Nature 380, 215–221.

Merino, S., Møller, A.P., de Lope, F., 2000. Seasonal changes in cell mediated immunocompetence and mass gain in nestling barn swallows: a parasite-mediated effect? Oikos 90, 327–332.

Moreno, J., 1998. The determination of seasonal declines in breeding success in seabirds. Etología 6, 17–31.

Moreno-Rueda, G., Soler, M., 2002. Cría en cautividad del Gorrión Común *Passer domesticus*. Ardeola 49, 11–17.

Moss, W.W., Camin, J.H., 1970. Nest parasitism, productivity, and clutch size in purple martins. Science 168, 1000–1003.

Møller, A.P., 1990. Effects of parasitism by a haematophagous mite on reproduction in the barn swallow. Ecology 71, 2345–2357.

Murhpy, E.C., 1978. Seasonal variation in reproductive output of house sparrows: the determination of clutch size. Ecology 59, 1189–1199.

Naef-Daenzer, L., Naef-Daenzer, B., Nager, R.G., 2000. Prey selection and foraging performance of breeding great tits *Parus major* in relation to food availability. J. Avian Biol. 31, 206–214.

Nilsson, J.-Å., 2000. Time-dependent reproductive decisions in the blue tit. Oikos 88, 351–361.

Nilsson, J.-Å., Smith, H.G., 1988. Effects of dispersal date on winter flock establishment and social dominance in mars tits *Parus palustris*. J. Anim. Ecol. 57, 917–928.

Perdeck, A.C., Cavé, A.J., 1992. Laying date in the coot: effects of age and mate choice. J. Anim. Ecol. 61, 13–19.

Perrins, C.M., Birkhead, T.R., 1983. Avian Ecology. Blackie, Glasgow.

Price, T.D., Kirkpatrick, S., Arnold, S.J., 1988. Directional selection and the evolution of breeding date in birds. Science 240, 798–799.

Ringsby, T.H., Sæther, B.-E., Solberg, E.J., 1998. Factors affecting juvenile survival in house sparrow *Passer domesticus*. J. Avian Biol. 29, 241–247.

Sandell, M.I., Smith, H.G., 1991. Dominance, prior occupancy and winter residency in the great tit (*Parus major*). Behav. Ecol. Sociobiol. 29, 147–152.

Sanz, J.J., 1998. Effects of geographic location and habitat on breeding parameters of great tits. Auk 115, 1034–1051.

Schultz, E.T., 1993. The effect of birth date on fitness of female dwarf perch, *Micrometrus minimus* (Perciformes: Embioticidae). Evolution 47, 520–539.

Senar, J.C., 1999. Plumage coloration as a signal of social status. In: Adams, N.J., Slotow, R.H. (Eds.), Proceedings of the 22nd International Ornithology Congress. BirdLife South Africa, Johannesburg, pp. 1669–1686.

Siikamäki, P., 1998. Limitation of reproductive success by food availability and breeding time in pied flycatchers. Ecology 79, 1789–1796.

Sinervo, B., Doughty, P., 1996. Interactive effects of offspring size and timing of reproduction on offspring reproduction: experimental, maternal, and quantitative genetic aspects. Evolution 50, 1314–1327.

Sokal, R.R., Rohlf, F.J., 1995. Biometry, 3rd ed. Freeman, New York.

Statsoft, I., 2001. STATISTICA for Windows [Computer program]. Statsoft, Inc., Tulsa.

Stearns, S.C., 1992. The Evolution of Life-Histories. Oxford University Press, Oxford.

Summers-Smith, J.D., 1988. The Sparrows, A Study of the Genus *Passer*. T & AD Poyser, Calton.

Svensson, E., 1997. Natural selection on avian breeding time: causality, fecundity-dependent, and fecundity-independent selection. Evolution 51, 1276–1283.

Svensson, E., Nilsson, J.-Å., 1995. Food supply, territory quality, and reproductive timing in the blue tit (*Parus caeruleus*). Ecology 76, 1804–1812.

Tinbergen, J.M., Verhulst, S., 2000. A fixed energetic ceiling to parental effort in the great tit? J. Anim. Ecol. 69, 323–334.

Verboven, N., Visser, M.E., 1998. Seasonal variation in local recruitment of great tits: the importance of being early. Oikos 81, 511–524.

Verhulst, S., van Balen, J.H., Tinbergen, J.M., 1995. Seasonal decline in reproductive success of the great tit: variation in time or quality? Ecology 76, 2392–2403.