

SEASONAL DECLINE IN CLUTCH SIZE OF THE MARSH TIT (*PARUS PALUSTRIS*) IN RELATION TO DATE-SPECIFIC SURVIVAL OF OFFSPRING

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ABSTRACT.—This paper documents and evaluates seasonal trends in reproductive performance in the Marsh Tit (*Parus palustris*) in southern Sweden. Clutch size decreased for nests started later in the season. This pattern held true both for second-year and older females when analyzed separately. Individual females adjusted clutch size in relation to the relative time of season they produced a clutch a particular year. The seasonal decline in clutch size was also evident for clutches produced in the same territory at different parts of the season in different years. Females breeding for several years demonstrated a high consistency in relative laying date and clutch size. The same was not true for males or for territories. The length of the incubation period normally decreased with season. Nestling mass and survival did not show any systematic seasonal trend. Nest predation was probably more prevalent late in the season. Fledglings that hatched later had poorer survival until autumn. This effect was evident for males, but not for females. Hatching date did not influence fledglings' survival to the next breeding season, but sample sizes were small. I suggest that the Marsh Tit adjusts clutch size to the survival probability of nestlings, this being affected by the probability of nest predation and by fledgling survival. Hence, late-laying females are not prepared to accept as large reproductive costs as early laying females. Received 5 November 1992, accepted 17 November 1993.

A COMMON PATTERN among altricial birds living in seasonal environments is for clutch size to decline with the progress of season (e.g. Klomp 1970, Murphy 1986, Stutchbury and Robertson 1988, Crick et al. 1993). Most hypotheses explaining this seasonal trend rely on assumptions about constraints on either laying date or clutch size (Daan et al. 1990).

The seasonal decline in clutch size might be due to quality differences between females or territories. For example, young females may lay later and produce smaller clutches (e.g. Klomp 1970). Females of poor quality or on poor territories might not be able to mobilize resources necessary for egg laying until later in the season and, at the same time, the poor quality of the bird/territory will make the optimal clutch size small (e.g. Daan et al. 1988).

Another kind of explanation suggests that the seasonal decline in clutch size is related to general seasonal trends in reproductive success. For example, food availability might decline with season, reducing the optimal clutch size (e.g. Perrins 1965). Alternatively, the survival probabilities of young might be lower later in the season which, if parents pay a reproductive cost related to brood size, will select for smaller clutch sizes (Hussell 1972). Hence, if birds are

constrained in when they can lay, a seasonal decline in clutch size will result.

Daan et al. (1990) elegantly combined these two approaches and removed the need for constraints on laying date or clutch size. They suggested that the seasonal decline in clutch size was the result of a simultaneous optimization of laying date and clutch size when territory (or individual) quality differed. The model relies on a number of assumptions: (1) there should be a general increase in the availability of food over the season; (2) there should be a reproductive cost dependent on clutch size; (3) there should be decline in the reproductive value of eggs caused by the progress of season; and (4) individuals or territories should differ in quality.

To evaluate the models, data on seasonal trends in fitness components for different species should be collected. In this paper I document and evaluate the seasonal trends in reproduction in the Marsh Tit (*Parus palustris*). It is a suitable species for this since much is known about its social organization and mating system (e.g. Nilsson and Smith 1985, 1988, Nilsson 1989). The Marsh Tit is nearly exclusively monogamous (unpubl. data) and rears only one clutch per season (repeat clutches might follow

breeding failure). Furthermore, it is year-round resident (Southern and Morley 1950, Nilsson and Smith 1988), making it possible to document survival of both adults and juveniles.

MATERIALS AND METHODS

The study was performed in the Revinge area 20 km east of Lund, southern Sweden. The study area consists of woods varying in size from small groves to larger forests. The majority of the woods are deciduous, although some areas contain planted pine forest. Nest boxes were first established in 1982. The study area was enlarged to 64 km² in 1983 and then remained constant throughout the breeding season of 1987. The number of nest boxes was approximately 355, but varied somewhat among years. All of the nest boxes were of similar size. To attract Marsh Tits, the boxes were made with a small entrance hole (26 mm diameter). To avoid having Blue Tits (*Parus caeruleus*) exclude Marsh Tits from breeding in the boxes, they were put up in pairs or trios with a distance of about 10 m between boxes in the same pair/trio. Each year considerable effort was also spent locating natural nest holes and nest boxes in private gardens. Except for analyses of fledgling survival, only Marsh Tits breeding in the nest boxes above were included.

Nest boxes were visited at least once every week during the egg-laying period, and the date of laying of the first egg was established assuming that Marsh Tits lay one egg per day. Laying interruptions are rare in Marsh Tits (unpubl. data). After having established clutch size, the nest box was again visited daily around hatching to establish the day the clutch started to hatch.

Nestlings were banded when 13 days old with an individual combination of color bands and weighed to the nearest 0.1 g using a Pesola balance. Parents were captured, banded and weighed on the same day or sometimes the day before or day after. Sex was determined by inspecting for a brood patch, and age was determined based on the form and color of wing coverts and tail feathers (see Svensson 1984). Aging was not done systematically until the breeding season of 1984. After offspring left the nest, the nest boxes were cleaned and searched for any remaining nestlings to determine fledgling success. Only first clutches (i.e. no repeat clutches) were used in the analyses.

Survival of fledglings was determined during regular surveys of the study area (for details, see Nilsson and Smith 1988). A central part of the study area (5 km²) was surveyed two to six times each winter 1983–1984 until 1986–1987. An extensive study area (25 km²) was surveyed during the winters of 1983–1984 and 1984–1985. Since Marsh Tit juveniles establish themselves permanently soon after independence (Nilsson and Smith 1988), I used all observations after 1 September.

During each autumn and winter, Marsh Tits were captured in mist nets using temporary feeders or playback. In the central study area, a large fraction of the Marsh Tits were caught from 1983–1984 and the majority from 1984–1985 (see Nilsson and Smith 1988, Nilsson 1989). In the remainder of the study area, Marsh Tits were mainly caught in conjunction with studies of Great Tits (*Parus major*; see Smith et al. 1989). Captured Marsh Tits were measured, weighed, aged and sexed (see Nilsson 1992).

Since nest-box groups were situated far apart, I could use nest-box group as an indicator of territory identity. Hence, I assumed that birds breeding in different years in the same nest-box group had the same territory. In most cases this was true, although territories may vary in size (unpubl. data). Clearly, Marsh Tits sometimes bred in different nest-box groups different years while actually occupying the same territory.

All parametric analyses are performed using the least-squares methods of MGLH in SYSTAT (Wilkinson 1990). Since the variance of laying date for true first clutches differed between years (11.8–50.1; Bartlett test, $X^2_4 = 27.39$, $P < 0.001$), I standardized laying date of first clutches each year to a mean of 0 and a variance of 1. Partial correlations, when controlling for a categorical variable, were performed by creating dummy variables.

Survival was analyzed using logistic regression with SYSTAT (Steinberg and Colla 1991). To do this, I had to assume that the survival of one fledgling was independent of that of other fledglings from the same brood after taking into account hatching date and nestling mass. This has been found to be a reasonable assumption in other studies (Hochachka and Smith 1991), and the logistic regression approach is superior to other approaches since it is less restrictive in its assumption that parametric methods (Hosmer and Lemeshow 1989). I used backward stepwise elimination with the limitation that main effects were not allowed to leave the model before interactions and quadratic effects. To control the robustness of models, analyses were repeated using forward inclusion.

Sample sizes differ slightly between different analyses. This is mainly due to the fact that nests abandoned due to human disturbance or included in experiments were excluded from the point of disturbance/experimentation. Four fledglings that were removed from the study area in autumn were not included in the analyses of survival until the next breeding season.

RESULTS

Seasonal decline in clutch size.—First clutches varied in size between 5 and 12 eggs, and were initiated over a period of approximately three weeks each year. For all years, there was a significant decline in clutch size with season (Ta-

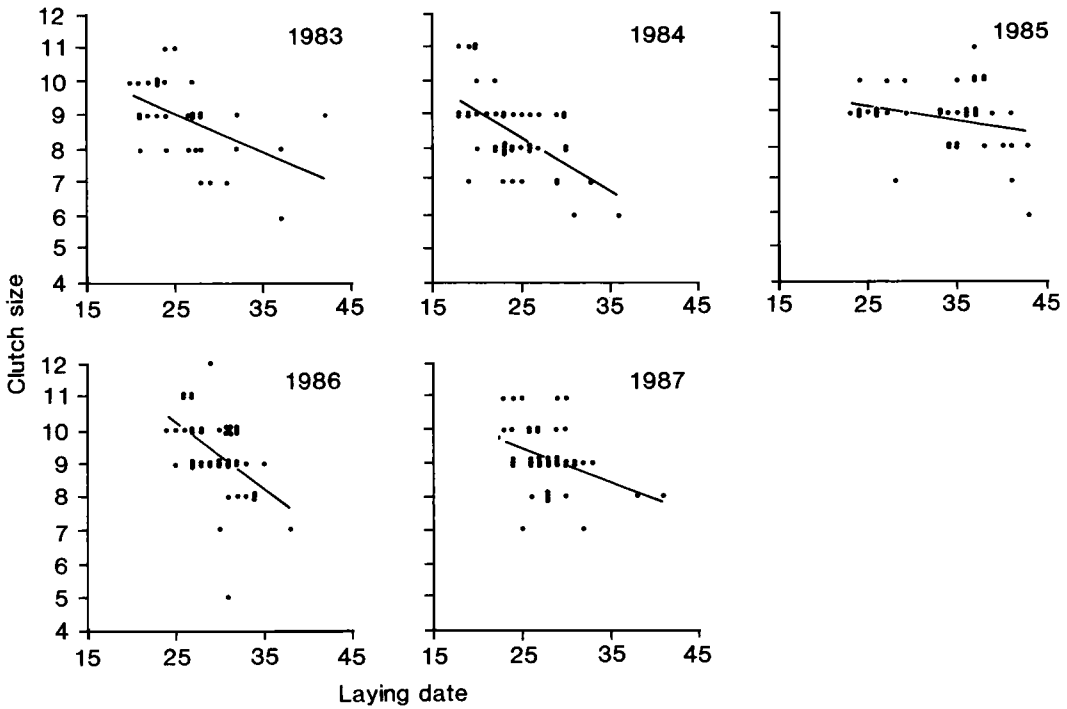


Fig. 1. Relationship between clutch size and laying date (1 = 1 April). Linear regression: 1983, $b = -0.11$, $n = 33$, $t = 3.24$, $P = 0.003$; 1984, $b = -0.16$, $n = 47$, $t = 4.66$, $P < 0.001$; 1985, $b = -0.04$, $n = 42$, $t = 1.74$, $P = 0.089$; 1986, $b = -0.20$, $n = 48$, $t = 3.83$, $P < 0.001$; 1987, $b = -0.10$, $n = 44$, $t = 2.52$, $P = 0.016$.

ble 1, Fig. 1). The slope of this relationship did not differ between years (interaction in an ANCOVA, $F_{4,204} = 1.47$, $P = 0.21$). However, if the analysis was repeated using data that were not standardized, there was a significant interaction since clutch size tended to decrease faster with season when laying-date variation was small (interaction in ANCOVA, $F_{4,204} = 3.06$, $P = 0.018$). The negative relationship between clutch size and laying date was significant, or nearly so, for each year separately (Fig. 1). The relationship was linear, since a higher-order term did not improve fit ($P > 0.1$).

Since young females lay their first egg later in the season than older ones (Smith 1993), the decline in clutch size with season potentially could be explained by age differences between birds. To analyze this, I looked at the relationship between clutch size and laying date separately for second-year (SY) and older (after-second-year; ASY) females. For both categories, clutch size declined with season (Table 2, Fig. 2). Also, when female age and year were held constant, the relationship between clutch size and laying date still was significant (ANCOVA

with year and female age as factors; the effect of laying date, $F_{1,167} = 39.20$, $P < 0.001$). Male age did not affect laying date (Smith 1993) and, thus, did not contribute to the relationship between clutch size and laying date.

To investigate if seasonal trends in clutch size were only due to lower-quality females or females in poor territories laying later and, therefore, a smaller clutch, I analyzed how clutch size for individual females and individual territories changed when laying date differed among years. For these analyses, when effects across years were examined, clutch size for each year was standardized to a mean of 0 and a

TABLE 1. Analysis of covariance of effect of date of laying of first egg on clutch size. Laying date standardized to mean of 0 and variance of 1 each year.

Variable	Slope	Sum-of-squares	df	F-ratio
Year		18.93	4	4.80***
First egg date	-0.491	51.11	1	51.83***
Error		205.09	208	

***, $P < 0.001$.

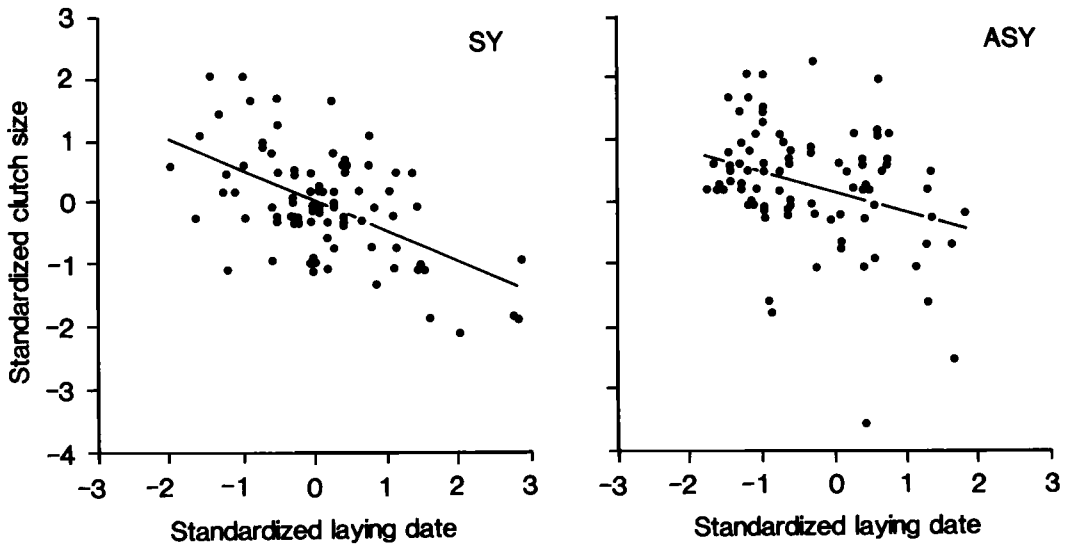


Fig. 2. Relationship between clutch size and laying date for second-year females (SY) and after-second-year (ASY) females. Clutch size and laying date standardized each year to mean of 0 and a variance of 1.

variance of 1. When the same female laid clutches on different dates in different years, clutch size varied in relation to the time of season she laid (ANCOVA with female identity as factor; the effect of relative laying date, $b = -0.39$, $F_{1,52} = 9.53$, $P = 0.003$, based on 38 females breeding more than one year). This was not simply an age effect, since the effect held true when female age was also introduced as a covariate ($F_{1,47} = 4.64$, $P = 0.036$). The same was true when females laid eggs at different dates within the same territory in different years (ANCOVA with territory identity as factor; the effect of relative laying date, $b = -0.47$, $F_{1,92} = 28.60$, $P < 0.001$,

based on 57 territories with more than one breeding).

Seasonal trends in incubation, growth and survival.—The length of the incubation period decreased with season most years, but the slope of the relationship differed among years (Table 3, Fig. 3). This relationship was not due to smaller clutches late in the season being incubated more efficiently, since the effect was significant when clutch size (and year) was partialled out ($r_{199} = -0.36$, $P < 0.01$).

Nestling mean mass did not show any systematic seasonal trend (ANCOVA with year as a factor; the effect of hatching date, $F_{1,167} = 0.067$, $P = 0.80$; Fig. 4). Inclusion of brood size as a covariate did not affect the result $F_{1,166} = 0.011$, $P = 0.92$). Moreover, the proportion of nestlings fledgling from nests where at least one nestling fledged did not depend on season (ANCOVA on square-root arcsine-transformed proportions with year as a factor; the effect of hatching date, $F_{1,164} = 0.001$, $P = 0.97$). However, the probability of total nest failure increased for later nests. To demonstrate this I performed a logistic regression with nest failure as the dependent variable and year, hatching date and the interaction as independent variables. Backward stepwise elimination showed that year ($-2 \text{ Log LR} = 15.22$, $df = 4$, $P = 0.004$) and hatching date ($-2 \text{ Log LR} = 9.07$, $df = 1$, $P = 0.003$) affected the probability of total failure. Total nest fail-

TABLE 2. Analysis of covariance of effect of date of laying of first egg on clutch size for SY females and ASY females separately. Laying date standardized to mean of 0 and variance of 1 each year.

Variable	Slope	Sum-of-squares	df	F-ratio
Second-year females				
Year		12.23	4	3.71**
First egg date	-0.618	29.25	1	35.47***
Error		65.97	80	
Older females				
Year		7.35	4	1.56 ^{ns}
First egg date	-0.396	11.08	1	9.44**
Error		96.30	82	

** $P < 0.01$; *** $P < 0.001$; ^{ns} $P > 0.05$.

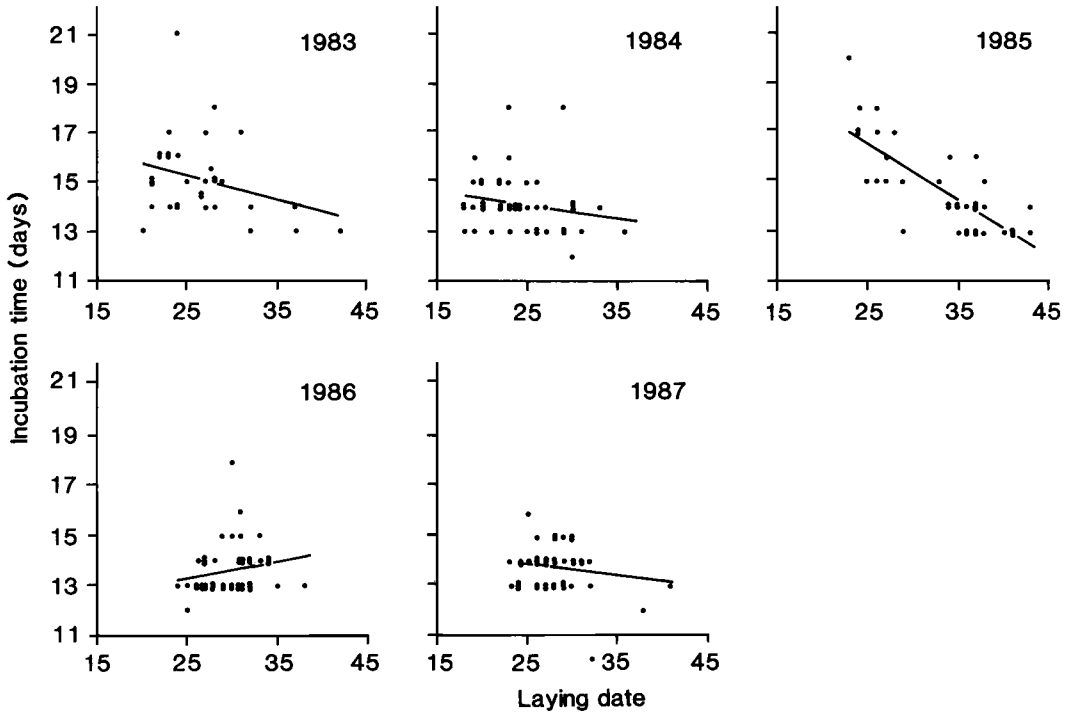


Fig. 3. Relationship between length of incubation time and date of laying of first egg (symbols as in Fig. 1).

ures were due to predation (91%) and nests being abandoned for unknown reasons (9%). However, these figures should be interpreted with caution, since nests were sometimes protected from predation.

Quality differences between birds and territories.—To investigate whether there were consistent differences in quality between birds or territories, I calculated repeatabilities (Lessells and Boag 1987) for laying date, clutch size and nestling mass. Since I was interested in the relative quality of birds, I used measures standardized within years as above. However, since repeatabilities calculated this way do not compare to conventionally calculated repeatabilities, the latter are also given (Table 4). Female Marsh Tits showed a high repeatability for laying date, whereas males did not and the repeatability for territories was low (Table 4). For clutch size, repeatability was again high for females, but low for males and territories (Table 4). Finally, for nestling mass repeatability was high for females and low for males (Table 4). It was moderately high for territories, but not if only occasions when different females occupied it were considered (using standardized data,

12.3%, 29 territories with 65 successful nests). Hence, it seems that differences between females had a large impact on reproductive success.

Seasonal decline in fledgling survival.—A methodological problem in all analyses of survival of fledglings is that the probability that an individual will be recaptured depends on where it was born—birds born at the border of the study area will have a lower probability of being recaptured. This problem existed also in this study. Furthermore, the central parts of the study area were searched more intensively during

TABLE 3. Analysis of covariance of effect of date of laying of first egg on length of incubation time. Laying date standardized to mean of 0 and variance of 1 each year.

Variable	Sum-of-squares	df	F-ratio
Year	57.88	4	11.00***
First egg date	32.89	1	24.99***
Interaction	55.93	4	10.62***
Error	256.65	195	

***, $P < 0.001$.

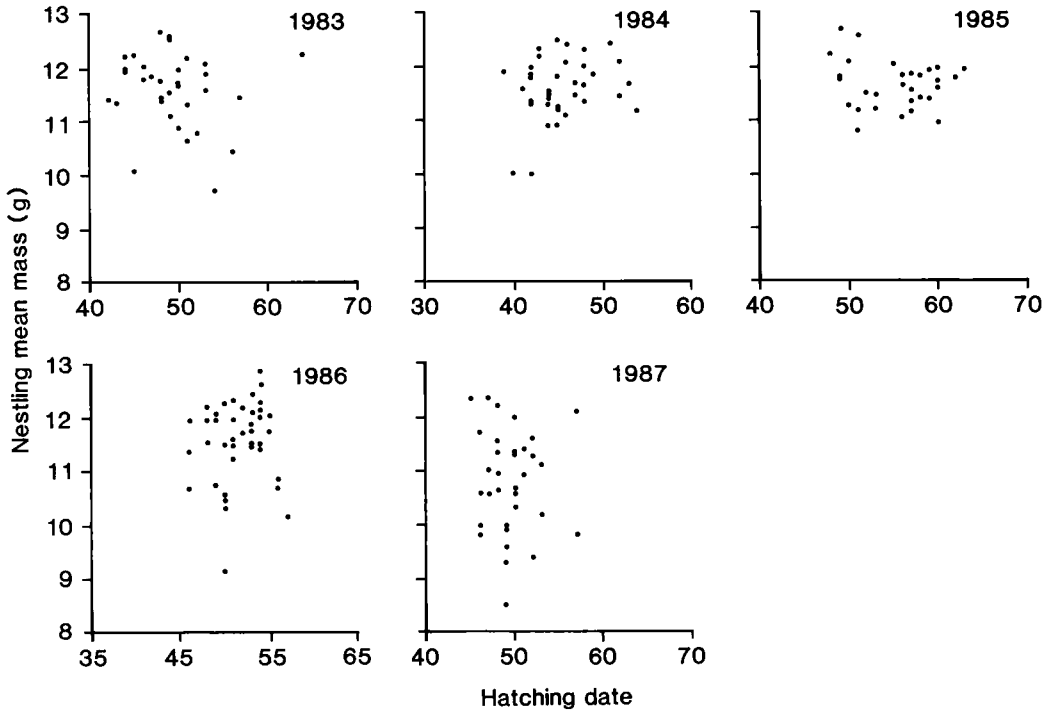


Fig. 4. Relationship between nestling mass and hatching date.

winter. Hence, when analyzing survival until autumn it is important to consider where a bird was born. This was done by introducing the distance and the squared distance from the central point of the study area in which the bird was born in the logistic regressions below. I allowed for eight additional factors in the regression model: year, interaction between year and distance to central point, mass of bird as nestling, square of this mass, interaction be-

tween year and mass, hatching date (standardized within years), square of hatching date, and interaction between year and hatching date. Intercorrelation between independent factors was low (spearman rank correlation coefficient varied between -0.02 and 0.11).

When analyzing survival until autumn, both backward elimination and forward inclusion produced identical results. Of interest in the final model was that survival seemed to depend

TABLE 4. Repeatability for laying date of the first egg, clutch size and nestling mass for Marsh Tit females, males and territories. Repeatabilities are given both for untransformed data and for data standardized to a mean of zero and a variance of 1 within years.

Trait	Category	Individuals	Observations	Repeatability	Repeatability of standardized data
Laying date	Female	38	91	0.273	0.495
	Male	35	86	0.068	0.214
	Territory	59	156	0.043	0.141
Clutch size	Female	41	98	0.332	0.394
	Male	38	92	0.026	0.084
	Territory	59	158	-0.066	-0.001
Nestling mass	Female	34	77	0.363	0.424
	Male	30	69	-0.088	0.102
	Territory	45	114	0.130	0.265

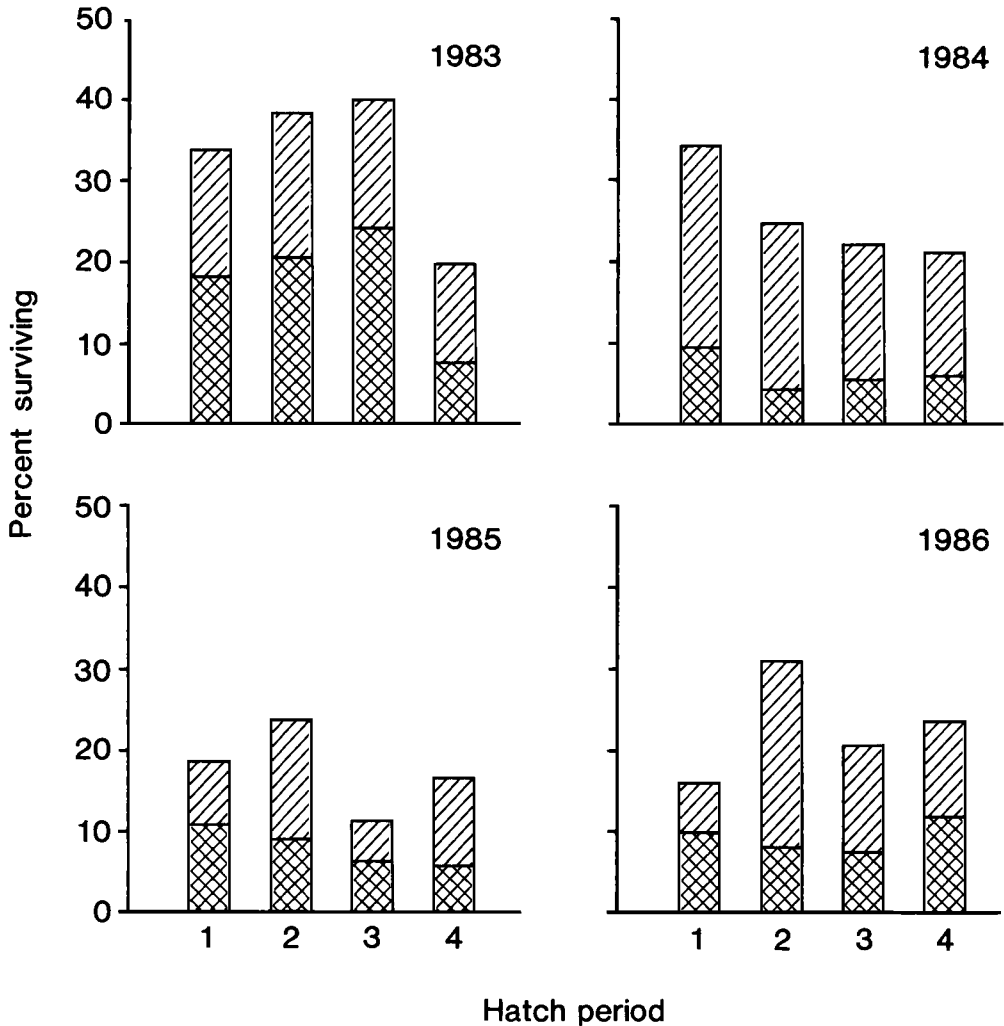


Fig. 5. Survival until after 1 September and until next breeding season (cross-hatched part of bars) of Marsh Tit fledglings in relation to hatching date. Hatching date divided into four periods each year with approximately equal numbers of fledglings.

positively on the bird's mass as a nestling and negatively, although not significantly so, on its hatching date (Table 5, Fig. 5). The effect of mass as nestling is difficult to interpret, since I recovered a higher number of males than females, and males have a higher mass in the nest (pairwise comparison of males and females using means within nests for nests where individuals of both sexes were recaptured, $\delta = 0.51$, $\text{prdt}_{48} = 5.07$, $P < 0.001$).

To look for effects on males and females separately, the same analyses as above were performed separately on males and females. Since the sexes could not be distinguished in the nest,

I instead treated only the recovered birds of the sex in question as recovered, all other birds as not recovered. For males, backward elimination and forward inclusion produced identical results. For females, backward elimination resulted in a model that, in addition to the factors included by the forward inclusion, also had hatching date and squared hatching date as factors. However, since both these factors could be excluded without a significant loss of explanatory power ($-2 \text{ Log LR} = 5.15$, $P = 0.08$) the simpler model was chosen (Table 5). Interestingly, the results seemed to differ for males and females (Table 5; Fig. 6). For males, survival

TABLE 5. Survival of fledgling Marsh Tits from fledging until after 1 September analyzed with logistic regression. Analyses based on 1,277 fledged young producing 324 recoveries of which 116 were sexed as males and 91 as females.

Variable	-2Log LR	df	P	Coefficient
Both sexes				
Constant				-1.454
Year	24.18	3	0.0001	
Distance	81.26	1	0.0001	-0.005
Mass	5.25	1	0.022	0.182
Hatch date	2.64	1	0.104	-0.112
Males				
Constant				-9.601
Distance	51.88	1	0.0001	-0.006
Mass	31.42	1	0.0001	0.734
Hatch date	11.13	1	0.0009	-0.369
Females				
Constant				-40.316
Distance	18.78	1	0.0001	-0.004
Mass	12.49	1	0.0004	7.491
Mass × mass	14.24	1	0.0002	-0.358

depended positively on mass and negatively on hatching date. For females, however, mass and mass squared related to recapture probability. Again, the effect of nestling mass is difficult to interpret due to the difference in nestling mass between the sexes. Inclusion of hatching date for females did not improve fit ($-2 \text{ Log LR} =$

TABLE 6. Survival of fledgling Marsh Tits from fledging until after 1 April in year after they were hatched analyzed with logistic regression. Analyses based on 1,273 fledged young producing 130 recoveries.

Variable	-2 Log LR	df	P	Coefficient
Constant				-4.617
Year	24.76	3	0.0001	
Mass	5.35	1	0.021	0.266

0.23, $P = 0.63$), whereas it seemed to influence males (Table 5). When looking at the survival until breeding, only mass affected this survival (Table 6). Addition of hatching date to the model in Table 6 did not improve fit ($-2 \text{ Log LR} = 1.24$, $P = 0.26$). Too few birds were recruited for males and females to be analyzed separately.

DISCUSSION

SEASONAL DECLINE IN CLUTCH SIZE

As in many other single-brooded passerines inhabiting seasonal environments, the clutch size of the Marsh Tit showed a marked seasonal decline (Klomp 1970, Murphy 1986, Daan et al. 1988). Laying date explained about 27% of the within-year variation in clutch size, a figure that was somewhat higher for young (31%), than for old females (12%).

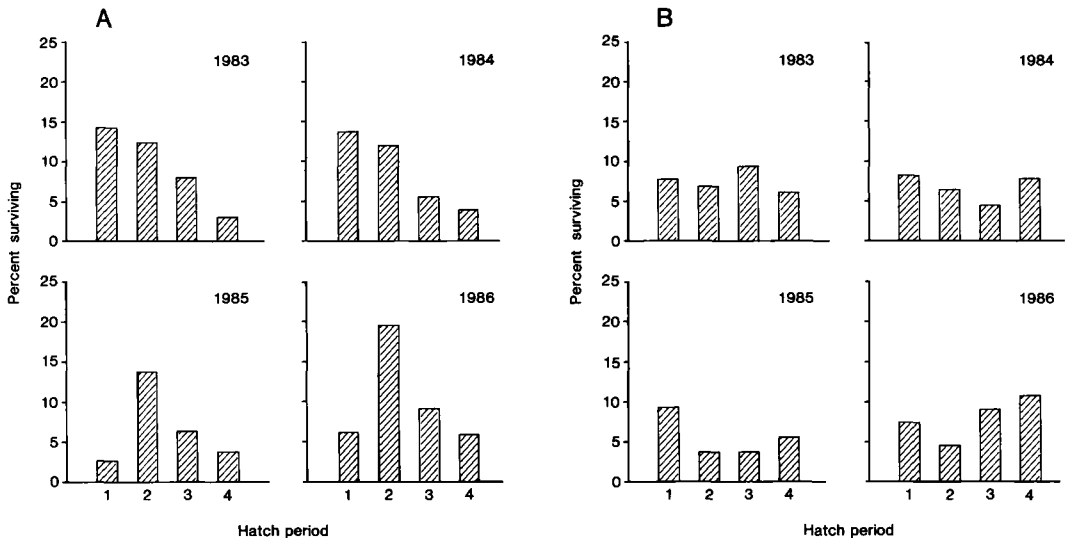


Fig. 6. Survival until after 1 September of (A) male and (B) female Marsh Tit fledglings in relation to hatching date. Hatching date divided into four periods each year with approximately equal numbers of fledglings.

Effect of quality differences between birds and territories.—The seasonal decline in clutch size could be due to quality differences between birds or territories, with birds of lower quality, or on territories of lower quality, laying both later and producing smaller clutches. The most obvious difference between birds is age, and young females also produced clutches that were both later and smaller. However, clutch size declined with the progress of season for both SY and ASY females when analyzed separately. Hence, even if age differences between birds could contribute to the seasonal decline, it is not the sole explanation for the phenomenon. Also, clutch size of other passerine birds has been found to decline with season for homogeneous age groups (see Stutchbury and Robertson 1988).

The calculation of repeatabilities for laying date, clutch size, and nestling mass suggested that some females were consistently better than other females. For males and territories, the repeatabilities were considerably lower. Such quality differences between females could explain the seasonal trend. However, the seasonal trend also held true for the same female (and for the same territory) when laying date differed among seasons. This suggests that the pattern observed is due to birds adjusting clutch size to time of season per se. This is consistent with the findings of Verhulst and Tinbergen (1991), who experimentally showed that females forced to lay repeat clutches followed the seasonal trend. In my study, the few repeat clutches also followed the general seasonal trend (unpubl. data).

Seasonal decline in food availability.—A seasonally declining clutch size could be a response to a declining food availability with the progress of season (Perrins 1965). For tits this is probably due to declining availability of caterpillars with season (van Balen 1973). In my study there was no general trend in nestling mass or breeding success to suggest a general decline in food availability with season. However, the lack of a seasonal trend in reproductive success could be due to the adjustment of clutch size to food availability. Nur (1987) demonstrated, by holding clutch size constant, that the reproductive success of Blue Tits decreased with season.

Adjustment to reproductive value of young.—Females could adjust their effort to declining survival prospects of late-born young. The survival probabilities of young declined with season, both due to higher nest predation and to re-

duced survival probabilities of fledged young. The effect of hatching date on fledgling survival was rather weak and could only be detected when analyzing male survival separately and not when analyzing survival until the next breeding season. However, the effect of nest predation was probably underestimated since nest boxes tend to protect birds from nest predation (e.g. Nilsson 1984).

If the date of laying of the first egg is fixed, a bird could, by laying fewer eggs, terminate laying earlier and obtain a higher fledgling survival. However, for this effect to cause a bird not to lay an extra egg, the decline in offspring survival per day must be much more severe than has been documented here (cf. Perrins and McCleery 1989). Also, for this to cause a seasonal decline in clutch size, the penalty in terms of reduced offspring survival of laying an extra egg has to be more severe late in the season. Instead, for a difference in offspring survival to make birds adjust clutch size, reproductive costs must increase with clutch size.

Synthesis.—Several of the results of this study are consistent with the model of Daan et al. (1990). The reproductive value of offspring declined with season and females seemed to differ in quality. However, there are reasons to believe that food availability does not increase with season, since tits predominantly feed on caterpillars, a resource which often declines sharply with season (van Balen 1973). If food availability does not increase with season, we would expect all birds to lay as early as possible rather than to optimize laying time as Daan et al. (1990) suggested.

A number of supplemental feeding experiments on tits have produced an advancement of laying, but the effect has sometimes been small (Daan et al. 1988). However, rather than the start of egg laying being the energetic bottleneck, it could be the incubation period (e.g. Mertens 1987). In this study, early-laying females sometimes seemed to delay the onset of incubation since their incubation periods were far above what is normal for tits (Fig. 3; see also Nilsson 1993). Hence, it is likely that Marsh Tits are energetically constrained in when they can start breeding. If laying time is constrained, then the seasonal trend in reproductive effort could be due to adjustment to female quality (poor quality females laying late), and/or to seasonal declines in food availability and survival probabilities of young. Since individual females fol-

lowed the same seasonal trend as all females, the latter alternative seems most likely.

It is difficult to distinguish between the effect of declining food availability and declining reproductive value of young, and they might both contribute to the seasonal trend in clutch size. However, for clutch size to be adjusted to the reproductive value of the offspring, there must be a clutch-size-dependent reproductive cost. A number of brood-size-manipulation studies on tits have produced conflicting results (e.g. Boyce and Perrins 1987, Nur 1988, Tinbergen and Daan 1990, Pettifor 1993). A problem with some of these studies is that they have been performed on double-brooded species, where production of second clutches might confound results on survival. Another problem is that investigators have not always established that parents actually respond to an increase in clutch size by increasing their effort; such a response should not always be expected (see Winkler and Wallin 1987). Finally, most previous studies have not evaluated the risk of predation to parents feeding chicks (Magnhagen 1991). There is clearly a need for more detailed studies on the occurrence of reproductive costs.

FLEDGLING SURVIVAL

There are some problems with evaluating fledgling survival in the Marsh Tit, the most important being that I could not sex the nestlings. Thus, if the recovery rate differs between the sexes, any sex difference in the nestling characters analyzed will enter the analysis. Therefore, it was not surprising that mass explained fledgling survival for the sexes combined. The only way I could analyze the sexes separately was to use recoveries from only one sex, which does not solve this problem. Since the primary sex ratio seems to be 1:1 in birds (Clutton-Brock 1986, but see Dijkstra et al. 1990), and most hatchlings fledged (90%), there was probably no sex difference in hatching date, making conclusions about its effect more robust. However, late-born young may exhibit longer dispersal distances and, thus, have a lower probability of being recaptured (Nilsson 1989; e.g. Dhondt and Hublé 1968, Kluyver 1971).

A seasonal decline in the reproductive value of offspring seems to be a relatively common pattern among birds (e.g. Daan et al. 1988, Hochachka 1991). In Great Tits, survival of fledglings has been found to decrease with later

hatching (Kluyver 1951, Perrins 1965, Perrins and McCleery 1989, Smith et al. 1989, but see Tinbergen and Boerlijst 1990). Verhulst and Tinbergen (1991), by forcing Great Tits to lay later, demonstrated the causal connection to laying date. The lower survival of late-born young is probably due to an effect of timing of dispersal on establishment success and subsequent dominance (Nilsson and Smith 1988). That competition with earlier-born fledglings hampered survival was shown experimentally for Great Tits (Kluyver 1971), and Nilsson (1990) demonstrated experimentally that establishment success in Marsh Tits depended on dispersal date.

An interesting effect was that hatching date seemed to affect male survival, but not that of females. Since a major reason to expect an effect of hatching date on survival is that prior residency affects dominance (Nilsson and Smith 1988, Sandell and Smith 1991), this could mean either that dominance is more important in males, or that other factors are more important in explaining dominance in females.

ACKNOWLEDGMENTS

The study was supported by grants from the Swedish Natural Sciences Research Council to S. Erlinge and H. Smith.

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