Is there a cost of reproduction for Marsh Tits *Parus palustris* in a primeval forest?

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We looked for evidence of a cost of reproduction in the Marsh Tit *Parus palustris* living in the last fragments of primeval temperate forest (Białowieża National Park, eastern Poland). Potential nest-holes were superabundant but the birds had to cope with a diverse set of predators, dangerous both to broods and to parents. Taking advantage of the natural variation in realized reproductive investment that this caused in terms of the loss of nests or mates, we expected to find differences in survival and future fecundity between birds which had lost broods (reduced effort), had reared young (controls) or were either provisioning young single-handed or had laid replacement clutches (increased effort). Despite 13 years of observation, even during seasons with very strenuous conditions, we have failed to demonstrate that the observed range of variation in parental investment caused any demographic cost of reproduction. Incubating females were regularly killed on the nest, which could indicate the existence of a cost operating in the earlier stages of the breeding cycle. Overall, these results suggest that the reproductive rate in Marsh Tits is not controlled proximately by reproductive cost.

Ever since Williams (1966a, 1966b) introduced the term 'residual reproductive value', the idea of a cost of reproduction, i.e. a demographic trade-off between investment in current and future reproduction, has remained central both to life-history theory and empirical studies of demographic trade-offs (reviews in Lindén & Møller 1989, Lessells 1991, Stearns 1992, Dhondt 2001). The cost of reproduction can take two main forms (Bell 1980): an increase in present reproduction can have a negative influence either on the probability of surviving until the next season (survival cost), on the reproductive value of the next age class (fecundity cost), or on both.

Despite a large body of observational and experimental work, the evidence for trade-offs at the phenotypic level is mixed; the expected relationships have often been found, yet in many cases the postulated effects have not been detected. Replicated studies on the same species have sometimes produced conflicting outcomes (see reviews above; Sinervo & Svensson 1998). To some extent, these contradictory results could be artefacts of study design. The majority of investigators carried out observations only for one or two seasons, and Sinervo and Svensson (1998) clearly demonstrated that the direction of relationships could vary considerably across years. Lindén and Møller (1989) list other possible sources of bias in avian studies. Many of these studies were made on increasing or unusually dense populations of birds breeding in nestboxes. In addition, nestboxes were frequently designed to reduce or eliminate predation, whereas predation is an important cause of death of adults and offspring in natural conditions.

These equivocal results have led some authors to question the existence of the demographic cost of reproduction. Alerstam and Högstedt (1984) and Stearns (1992) investigated whether interseasonal reproductive costs existed in small passerines, income breeders with high nutrient turnover rates, which would quickly obliterate any negative effects of current reproductive effort. For Stearns (1992) it was, thus, not surprising that Pettifor *et al.* (1988) found no evidence for a trade-off between clutch size and the cost of reproduction in Great Tits *Parus major* and more surprising that Nur (1984) did find such evidence.
in Blue Tits Parus caeruleus. However, two possible mechanisms that could also produce trade-offs in such birds have been proposed since then. Gustafsson et al. (1994) suggested that the costs of reproduction arose because of suppression of the immune system following heavy investment in current reproduction. Svensson and Nilsson (1997), by contrast, proposed that prolongation of breeding resulted in time/energy constraints during moult, which in turn forced birds to produce feathers with low insulating capacity. The birds with poor-quality plumage would survive less well and would reproduce less successfully in the following season. Indeed, Blue Tits that reared experimentally delayed broods followed this scenario (Nilsson & Svensson 1996).

Here we look for signs of demographic costs of reproduction in the Marsh Tit Parus palustris, a small passerine (body mass of c. 10 g), living in the last fragments of the primeval temperate forest preserved in the Białowieża National Park (eastern Poland, hereafter BNP). This park offers a unique opportunity to study the adaptive value of behaviour, as here one can still observe organisms living under conditions that existed in European forests before their transformation by humans (Wesołowski 1983, Tomiałojć et al. 1984, Tomiałojć & Wesołowski 1990). Especially important for the current study is preservation in the BNP of an entire assemblage of nest predators that use diverse detection and attack techniques (Tomiałojć et al. 1984, Tomiałojć & Wesołowski 1990, Jędrejewska & Jędrejewski 1999), as well as the presence of a superabundant array of natural holes potentially suitable for nesting (Wesołowski 1989, 1996a, 2002). Living under such conditions, Marsh Tits have an opportunity to choose safe breeding holes (Wesołowski 2002). Nevertheless, broods are regularly depredated and the remains of killed parents are found, not infrequently, in the nests (Wesołowski 2002). The fitness consequences of nest failure are especially strong in this species, as Marsh Tits rear only one brood a year and, as a rule, do not lay replacement clutches (Wesołowski 1998, 2000, 2002). Widespread parasitism by blowfly Protocalliphora falcozi larvae puts an additional burden on the birds breeding there (Wesołowski 2001a).

In these exacting circumstances we expected to find clear signs of reproductive costs. We anticipated that parents investing heavily in reproduction in one season would survive less well and/or would lay smaller clutches and/or commence egg-laying later in the following season than birds which had not worked as hard in the previous year. Although laying date is not strictly a demographic variable, we include it here as it has a very strong effect on Marsh Tit clutch size (Nilsson 1991, Smith 1993, Wesołowski 1998, 2000). As direct phenotypic correlations cannot provide valid measures of trade-offs (Lessells 1991, Stearns 1992), we use here a quasi-experimental approach, taking advantage of the natural variation in the realized reproductive investment caused by the loss of a nest or mate. The birds that reared young served as ‘controls’. We assume that when deciding on when and how many eggs to lay, birds should assess their own condition and estimate the future share that their partner would contribute to parental care, i.e. they should optimize their workload. This workload should vary individually (Högstedt 1980, Pettifor et al. 1988, 2001) as each pair must set its own optimum. Thus, in an average season birds fledging young successfully should carry out an amount of work for which they had been prepared, although this might be increased by the cost associated with parasites in infested broods (Wesołowski 2001a).

If brood rearing incurs demographic costs, we should not find birds paying those costs to be better off. Nest loss could therefore be treated as the ultimate ‘brood-reduction’ experiment. Provided that the failed birds were not of lower quality, and that they did not have to replace the lost broods, they saved much of the effort necessary to rear a brood (along with parasites) to independence. Hence, they should survive better and/or lay larger clutches than the successful birds in future seasons.

Consequently, when these, usually, single-brooded birds attempt to replace a lost brood, or when one of a pair disappears and the remaining parent tries to rear the brood alone, the birds have to work much harder than would typically be the case, i.e. equivalent to a ‘brood-enlargement’ experiment. We expect such overworked birds to survive less well than the ‘controls’ and/or to be less fecund in the future.

In general, we expect to find a gradient of increasing reproduction costs from the ‘failed’ birds through the ‘successful’ to the ‘replacing/single’ birds. All these differences should be especially pronounced in the years following an extremely strenuous season (Lindén & Möller 1989). Therefore, the cold and rainy spring of 1999 with heavy nest loss, the most difficult season in the whole 13 years of study (Rowiński & Wesołowski 1999, our unpubl. data), should provide the most critical test of our expectations.
STUDY AREA AND METHODS

Study area
The Białowieża Forest complex is situated at the Polish–Belarussian border. Its western part (610 km², c. 41% of the area) belongs to Poland. The forest represents a remnant of the vast lowland forests that once covered large parts of temperate Europe. Its present unique features result from its considerable size and an exceptionally good state of preservation (Tomiałojć & Wesolowski 1990, Wesolowski & Tomiałojć 1995). The majority of tree stands in the Polish part are now under management, but a block of the best preserved primeval old-growth stands has been strictly protected within the BNP.

Data were gathered in the strictly protected part, in four large (33–50-ha) sample plots, 1–2 km apart. Three of these (plots C, M and W) were situated in upland Oak–Lime–Hornbeam stands composed mostly of Hornbeam Carpinus betulus, Lime Tilia cordata, Pedunculate Oak Quercus robur, Spruce Picea abies and Continental Maple Acer platanoides; the fourth (plot K) was located in a swampy riverine forest made up mainly by Alder Alnus glutinosa, Ash Fraxinus excelsior and Spruce (see Wesolowski 1996a, 1998 for detailed descriptions). Natural holes were in excess of that required by the birds in all the plots (Walankiewicz 1991, Wesolowski 1996a, 2001b).

Data collection
Intensive observations of Marsh Tit pairs, aimed at mapping the distribution of territories and finding the holes of all breeding pairs, were made in 1987–89 and 1993–2003. To gather data on the course of breeding, and fate of nests, the breeding holes were checked regularly following procedures described in detail in Wesolowski (2002). Almost all nests were found in most seasons, thus providing an unbiased sample of laying dates, clutch size and nest outcomes.

Adults carrying food for nestlings were caught in door-traps or mist-nets placed at the hole entrance, and colour-ringed. The majority of birds (up to 90% in some years) were ringed by the end of the season. In the following spring, we searched carefully for all the marked birds in the plots, and it was assumed that absent birds had died. This could be justified by the extremely sedentary habits of Marsh Tits: in 13 years of study, the birds stayed in their previous year’s territory or moved to one formerly occupied by a neighbour in all but just two cases (Wesolowski 2001a, our unpubl. data). Such extraordinary site fidelity has been described for the Marsh Tit in other areas (Glutz von Blotzheim 1964, Berndt & Winkel 1987, Rost 1988, Haftorn 1997, Markovec 2001, Amann 2003).

Analysis
We used all observations of colour-ringed birds which either fledged young or survived brood destruction. Birds known to have been killed on the nest by a predator were excluded as they could have no prospects for survival or future reproduction.

We allocated all observations to one of three groups, differing in the amount of effort spent on breeding activities. These were defined as follows:
- reduced effort – the brood was lost, the bird survived nest destruction but did not try to rear a replacement brood;
- standard effort (control) – the bird reared a brood successfully, with at least one young fledged;
- elevated effort – the brood was lost, and the bird tried to rear a replacement brood, or having lost the partner, the single bird strove to rear the brood alone.

Following Wesolowski (1998), we treated as replacements all late clutches, commenced 10 days or more after the median laying date of a season. All birds undertaking such broods, irrespective of their outcome, were included here, as by the very fact of producing two clutches in a season the birds had to invest more than was the standard season’s effort. Similarly, all birds that lost their partners and tended their broods single-handedly were included, no matter what the final outcome of their efforts, as they had to work much harder than usual for several days at least.

As we were able to find practically all (see above) surviving birds in the following season, and we were interested only in comparing the survival rates (to the next season) of groups of birds that had invested varying levels of effort in reproduction in a given year, there was no need to use sophisticated capture-re-sighting statistical models; thus, we expressed survival rates directly as percentages of birds re-sighted in the following year. We calculated survival rates for both males and females, but compared dates of egg-laying commencement and number of eggs laid only for females. This was because Marsh Tit males have almost no influence on the egg-laying dates and clutch size of their mates (Smith 1993, Wesolowski 1998).
Sample sizes varied across analyses because it was not always possible to gather a complete set of measurements. All statistical procedures follow the formulae given in Simstat for Windows (Anon. 1996). All probability values shown in the text are two-tailed.

**RESULTS**

The successful and unsuccessful Marsh Tit first broods did not differ significantly in their first egg dates or clutch sizes (Table 1). This indicates that, at the outset, the two respective groups of birds did not differ intrinsically in quality or the amount of work that they had been ‘prepared’ to invest in rearing young. It was only the extrinsic factors (mostly predators) that differentiated the birds and prevented some of them from spending the amount of effort for which they had prepared.

Contrary to expectations, the birds whose effort had been reduced did not survive better than those that had reared young (53–54% vs. 57–63%, respectively, Table 2). Indeed, there was an opposite tendency for the successful males to survive better (Table 2). Similarly, the survival rate of overworked birds, those that had commenced replacement broods (54%, $n = 13$) or had consisted of single parents (71%, $n = 7$), was not lower than that of the control birds, and thus provided no evidence for the existence of any costs. Similarly, the successful females laid neither later nor smaller clutches in a subsequent year than did the females that had lost broods in the previous year (Table 3).

The successful rearing of broods must have been especially difficult in the cold and rainy spring of 1999, when Marsh Tits mistimed their reproduction in relation to the availability of leaf-eating caterpillars (Rowiński & Wesołowski 1999, our unpubl. data). In such conditions any costs of reproduction should have been especially pronounced. We therefore carried out all the calculations separately for the 1999/2000 season. These results also did not fit our expectations. The survival of the birds that lost broods (52%, $n = 29$) was no better than that of the successful birds (58%, $n = 50$; $\chi^2 = 0.29$, $P = 0.59$, power = 0.11). The surviving females commenced their broods in 2000 at the same time (in both groups the mean relative laying date was –1.8 days), and laid an equal number of eggs. The mean relative clutch sizes in 2000 were 0.3 ($n = 13$) and 0.4 ($n = 8$) eggs in females that had reared or had failed to rear broods in 1999, respectively (Mann–Whitney U-test, $Z = 0.04$, $P = 0.97$).

| Table 1. Clutch size and the first egg date of fledged and destroyed Marsh Tit broods. |
|---|---|---|---|
| **Outcome** | **No. of eggs laid** | **Laying date (days)** |
| | $n$ | Mean (sd) | $n$ | Mean (sd) |
| Success | 257 | 0.1 (0.99) | 309 | –0.3 (2.87) |
| Failure | 42 | –0.1 (0.97) | 51 | –0.5 (2.63) |
| **Mann–Whitney $U$-test** | $Z = 1.45$, $P = 0.15$ | $Z = 0.34$, $P = 0.73$ |
| **Power** | Power = 0.29 | Power = 0.05 |

Note: To remove the effect of year, data on the number of eggs laid and laying dates were standardized – they are expressed as deviations from medians of the absolute values (set 0) of respective years. Statistical power for $\alpha = 0.05$ was estimated by bootstrapping with 10 000 replacements.

| Table 2. Survival rate of Marsh Tits in relation to the outcome of the previous year’s brood. |
|---|---|---|---|
| **Outcome** | **Females** | **Males** |
| | $n$ | Survival (%) | $n$ | Survival (%) |
| Successful | 319 | 56.7 | 306 | 63.1 |
| Lost, not replaced | 57 | 52.6 | 69 | 53.6 |
| $\chi^2$ test | $\chi^2 = 0.331$, $P = 0.564$, power = 0.11 | $\chi^2 = 2.12$, $P = 0.145$, power = 0.34 |

Note: Statistical power for $\alpha = 0.05$ was estimated by bootstrapping with 2000 replacements.
DISCUSSION

Pairs that we identified later to be successful or unsuccessful did not differ in their laying dates or clutch sizes, thus confirming our assumption that the two groups of birds did not differ intrinsically in quality, and justifying their treatment as ‘control’ and ‘experimental’ (reduced costs) groups, respectively.

We have failed to demonstrate the existence of a demographic cost of reproduction in Marsh Tits living under natural conditions. Neither survival, laying date nor the clutch size of birds was influenced detrimentally by an increase in effort put into brood rearing in the previous season, despite the data having been gathered in conditions conducive to the detection of cost. The observations covered many years, including those with extremely strenuous conditions. Through breeding in natural holes, Marsh Tits were endangered by a diverse set of predators able not only to rob a nest but also to kill the parents. In such a situation the cost, if it existed at all, should have been detectable. Studying the closely related Willow Tit *Parus montanus* breeding in natural holes over a period of 6 years, Orell *et al.* (1996) also found no trace of survival or fecundity cost in subsequent years, although they detected a long-term, delayed survival cost (Orell & Belda 2002), and hence paid the ultimate price. However, before one can treat this as a demographic cost of reproduction, one should also be able to show that the mortality of the breeding females was higher than the mortality of non-breeding females in the same period. Unfortunately, we have no data to address this question. Although Marsh Tits at the BNP did not always commence egg-laying or start incubation, this was probably caused most often by some physiological deficiency or disease (Wesołowski 2002), and not by a tactical decision to miss a season. However, Orell and Belda (2002) found no differences in the year-to-year survival of breeding and non-breeding male and female Willow Tits, but females that bred every year had a lower probability of surviving for more than 5 years than females that had skipped some breeding seasons earlier in life. Hence, there was a postponed survival cost.

Another possible explanation of the apparent lack of a reproduction cost in Marsh Tits could be that the parental cost would appear only after some threshold level of reproductive investment had been exceeded, and birds should have been selected so as to invest only that amount of effort that would keep them below that threshold, a relationship already postulated by Svärdson (1949), Lack (1954) and Jönsson and Tuomi (1994). If the most severe costs arise under conditions in which increased reproductive effort reduces not only future but also current success, there will be strong selection against life histories that express the costs (Jönsson & Tuomi 1994).

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**Table 3.** Clutch size and the first egg date of Marsh Tit females in relation to the outcome of the previous year’s broods.

<table>
<thead>
<tr>
<th>Outcome</th>
<th>No. of eggs laid</th>
<th>Laying date (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>Mean (sd)</td>
</tr>
<tr>
<td>Successful</td>
<td>136</td>
<td>0.4 (0.96)</td>
</tr>
<tr>
<td>Lost, not replaced</td>
<td>22</td>
<td>0.1 (0.93)</td>
</tr>
<tr>
<td>Mann–Whitney <em>U</em>-test</td>
<td></td>
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<tr>
<td></td>
<td>Z = 1.28, P = 0.20</td>
<td>Z = −1.04, P = 0.30</td>
</tr>
<tr>
<td></td>
<td>Power = 0.24</td>
<td>Power = 0.18</td>
</tr>
</tbody>
</table>

Note: To remove the effect of year, data on number of eggs laid and laying dates were standardized — they are expressed as deviations from medians of the absolute values (set 0) of respective years. Statistical power for $\alpha = 0.05$ was estimated by bootstrapping with 10 000 replacements.
If this is the case, then reproductive costs would be difficult to detect and the actual reproductive rates would not be maintained by the demographic trade-offs.

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