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Response of Great Tits *Parus major* to an irruption of a Pine Processionary Moth *Thaumetopoea pityocampa* population with a shifted phenology

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Since 1997, a population of the Pine Processionary Moth *Thaumetopoea pityocampa* exhibited a shifted life cycle in a restricted area of a managed pine forest, at the central west coast of Portugal. Rather than during the regular winter period, larval development of this novel population occurs during the summer. We indicate the populations accordingly as the Winter Population (WP) and the Summer Population (SP). We quantified the numerical response of Great Tits *Parus major* to irruptions of the SP. In the years following an irruption, Great Tits were more abundant in the SP area, than in two similar non-infested forest areas. This was particularly pronounced during summer and autumn, at the time when moths, eggs and larvae of the SP were available for bird predation. A nestbox study allowed us to verify that the SP moth emergence period coincided with egg laying and raising of second broods in Great Tits, and higher reproductive rates were recorded in the SP than in the WP area. To our knowledge, this is the first study to document a response of a bird predator to a local *T. pityocampa* irruption, which was even more special as it concerned an insect population with a large shift in its life cycle. Our results show that the Great Tit is able to respond to local outbreaks of forest defoliator insects, and we suggest a potential impact of Great Tit predation on the population dynamics of the SP.

Key words: Great Tit, Pine Processionary Moth, shifted life cycle, numerical response, second brood, food-dependent breeding success

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INTRODUCTION

The study of seasonal and annual fluctuations in food resources has a long history in bird ecology, due to its impact on life history traits, population abundances, and community structure (Martin 1987, Newton 1998). In temperate forest ecosystems, folivorous Lepidoptera species form an important food resource for breeding birds and some of these folivorous insects reach cyclic outbreak numbers causing extensive defoliation (Myers 1988). These outbreaks constitute a superabundant supply of food for birds and they can have, therefore, a major impact on bird populations (Holmes *et al.* 1986, Hogstad 2005).

The Pine Processionary Moth *Thaumetopoea pityocampa* is an important pine defoliator in the Mediterranean region, known to cause frequent outbreaks (OEPP/EPPO 2004). This univoltine species is inactive during spring when it occurs in the pupal stage below ground. Adults emerge in the summer and live for a few days when they reproduce. Larvae are gregarious throughout their development, which occurs during the winter (between September to March). However, in 1997 a population of *T. pityocampa* with a shifted life cycle was recorded for the first time in a restricted area of the oldest National Forest of Portugal – the National Pine Forest of Leiria. Larval development of this novel population occurred during the summer instead of winter, and so this population will be referred to as the Summer Population (SP). Since its discovery, the SP has been observed every year in the same restricted area, causing high levels of defoliation. It attains higher densities than the Winter Population (WP) in any other part of the Leiria Forest (Pimentel *et al.* 2006). The establishment of the SP, and its higher population densities, leads to the questions whether this might have been due to an escape in time from their predators, and how predators responded to the appearance of this new source of food.

The Great Tit *Parus major* is considered to be the most important predator of *T. pityocampa* larvae (Gonzalez-Cano 1981, Halperin 1990). Tits are able to prey on hairy, urticating, gregarious caterpillars (Royama 1970), and can use all instars of *T. pityocampa* caterpillars as a food source during winter (Gonzalez-Cano 1981). However responses of this bird predator to densities of the defoliator have never been studied. The relation between life history traits and food abundance of this largely insectivorous passerine has been intensively studied during the last 50 years. Food supplementation studies and studies of the phenology of prey abundance have shown that food limitation can have an important impact on different stages of the tits' life history. First, abundance of food during the winter determines survival and breeding density during the next spring (Perrins 1965, Källander 1981); secondly, the amount of food available just prior to the onset of the breeding season determines the timing of egg laying (Perrins 1970, Källander 1974, Seki & Takano 1998); thirdly, food abundance during nestling feeding is critical for reproductive success (van Balen 1973, Verboven *et al.* 2001).

Breeding Great Tits in deciduous woodlands of northern and central Europe, rely heavily on Lepidoptera larvae for feeding nestlings (Betts 1955, Royama 1970). Synchronizing nestling feeding with the peak of caterpillar abundance is crucial for successful reproduction and the evolution of timing of breeding (van Noordwijk *et al.* 1995, Naef-Daenzer & Keller 1999). However, such synchronization is not possible in all habitats inhabited by the Great Tits (Barba *et al.* 1994, Eeva *et al.* 2000). For example, when adult moths are numerous, this food source can replace much of the larvae during the breeding season (Barba & Gil-Delgado 1990). The extensive knowledge about the biology of this forest bird, the facility to manipulate its population density by placing nestboxes (Perrins 1965), its feeding plasticity, and the fact that it is a known predator on *T. pityocampa*, make Great Tits an interesting object for studying the response of a predator to the irruption of the SP.

In the present paper we investigated if Great Tits responded numerically to the irruption of the shifted population of *T. pityocampa*. Numerical responses include changes in density when birds aggregate near insect outbreaks, as well as increase in clutch size and breeding productivity (Otvos 1979). Thus, in the years immediately after the detection of the SP, we compared the seasonal variation of Great Tit abundances in the area of the irruption of the SP with similar forest areas where only the WP was present. Later, nestboxes were erected, and the breeding biology of Great Tits was studied inside and outside the SP distribution area.

MATERIALS AND METHODS

National Pine Forest of Leiria is located 150 km north of Lisbon, covering 11 023 ha in a coastal

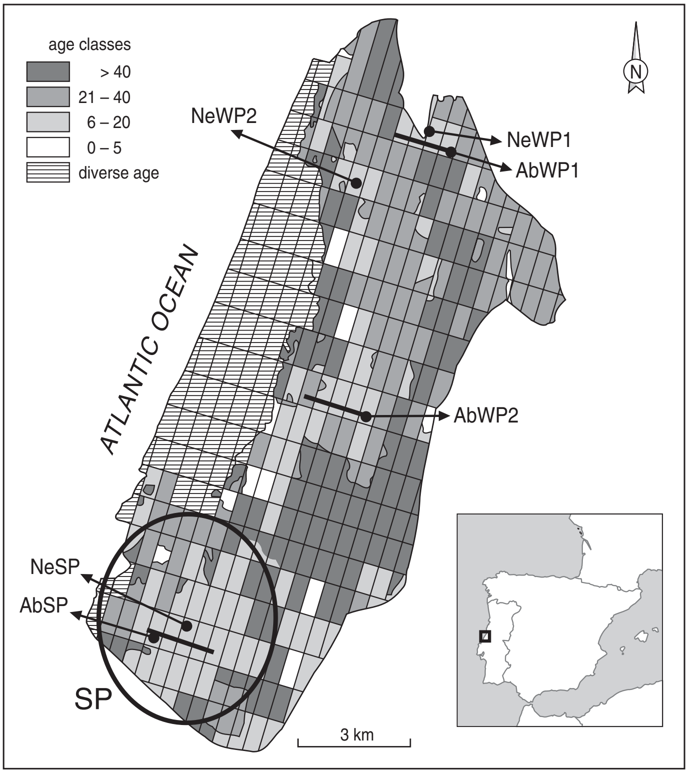

Figure 1. Management units (plots) and age of trees in the National Pine Forest of Leiria, 2001–2002, and location of the Forest within Portugal. Data were supplied by the National Forest Service and the map was obtained through ArcView 3.2. The circle indicates the area of establishment of *T. pityocampa* Summer Population (SP). Transects, along which bird density was assessed through point counting stations are indicated as AbWP1, AbWP2, and AbSP. The location of the nestbox plots are indicated as NeWP1, NeWP2, and NeSP.

dune system (39º50'N, 8º57'W, 30–50 m a.s.l.). About 80% of this area is managed to produce high quality timber. The pinewood is divided into 334 rectangular plots (management units) of 30 to 40 ha each covered mostly by even-aged monocultures of maritime pine *Pinus pinaster*. The establishment of the SP occurred in a large continuous area of homogeneous stands of young trees at high density (1000 to 2000 trees/ha), located at the south end of the Leiria Forest (Pimentel *et al.* 2006; Fig. 1).

Great Tit abundance was compared between the area of SP establishment (AbSP) and two other similar areas of young plots, located at the Centre (AbWP2) and North (AbWP1) of the Forest (Fig. 1). Abundances were estimated through 10 min, 50 m radius point counts (Bibby *et al.* 1992). In each of the areas, 12 point count stations were located along a transect of about 2000 m, separated by a distance of 150–200 m (Fig. 1). Each of these stations was located at least 100 m inside the plot. Abundances of Great Tits were estimated in two time periods: between March 1998 – January 1999, and between October 1999 – June 2000. In each of the periods, visits to the point count stations were made in four distinct seasons: early March (Spring); late June (Summer); late October – early November (Autumn); January (Winter). Visits to the stations of each transect were made at the same day at dawn. Days with strong winds and rain were avoided. In order to test for spatial and temporal differences in bird abundance, a repeated measures ANOVA model was used with two grouping factors – area and season and with bird counts from the two years (i.e. the repeated measure) as the dependent variable. To account for the non-continuous integers and some zero counts, values of the dependent variable (bird counts x) were transformed by $(x+1)^{0.5}$ (Snedecor & Cochran 1980).

Nestboxes were erected in the winter 2000/2001 in two similar plots of young trees located at the north of the Forest (NeWP1 and NeWP2, Fig. 1). In the winter 2001/2002 another similar plot was created, at the south of the Forest, in the area of SP establishment (NeSP, Fig. 1). Nestboxes were placed at a density of one per ha, at equal distances from each other, resulting in a total of 90 nestboxes.

The nestboxes were checked at least once a week to determine the number of breeding pairs, laying date, clutch size, number of fledglings and frequency of second clutches. Laying date was calculated assuming one egg was laid per day. Since adults were not ringed, second clutches were assumed to be produced by females, who had completed a first clutch of eggs in the same or a nearby box (less than 100 m away). The Great Tit is highly territorial with a high degree of breeding area fidelity. The median distance moved between nesting attempts within years by females has been shown to be below 100 m (Harvey *et al.* 1979), which validates our assumption about the identity of females producing a second clutch. We reserve the term 'second clutch' for clutches produced following a successful first brood (defined as a brood producing at least one fledgling).

To calculate changes in breeding density and proportion of pairs producing a second clutch, the breeding seasons between 2001 and 2003 were used for NeWP1 and NeWP2 (after the breeding season of 2003 these two plots were destroyed by fire) and 2002–2004 for NeSP. For comparisons of other breeding parameters between the three plots, we restricted our analyses to data from 2002–2003. For analyses of the variation in breeding parameters between the three areas, we used ANCOVA models with area and year as fixed factors and breeding density as covariate.

Abundance of moth males were monitored during the years 2002 and 2003, using funnel traps (AgriSense^{TM}), baited with one synthetic *T. pityocampa* pheromone dispenser (AgriSense-BCS Ltd; TP058A140; BFL072) and a killing agent (DDVP strip). All traps were placed at a height of 2.5–3.0 m in mid April and checked weekly until October of each year, chemicals being replaced at 30-day intervals. Three traps were located in the SP establishment area and one trap was placed in each of NeWP1 and NeWP2. Furthermore, we made observations on hatching dates and larval development of caterpillars of the SP and WP.

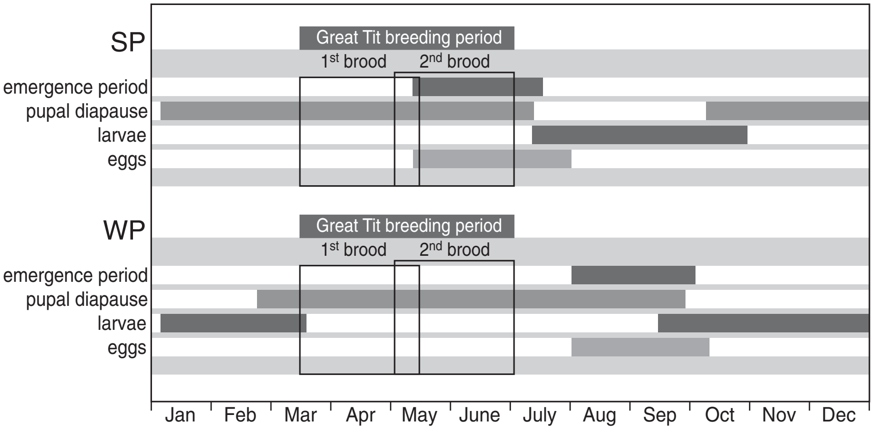

Figure 2. Timing of the life cycle of the two populations of *T. pityocampa*, SP and WP, in relation to breeding in the multiple brooded Great Tit in the Leiria Forest.

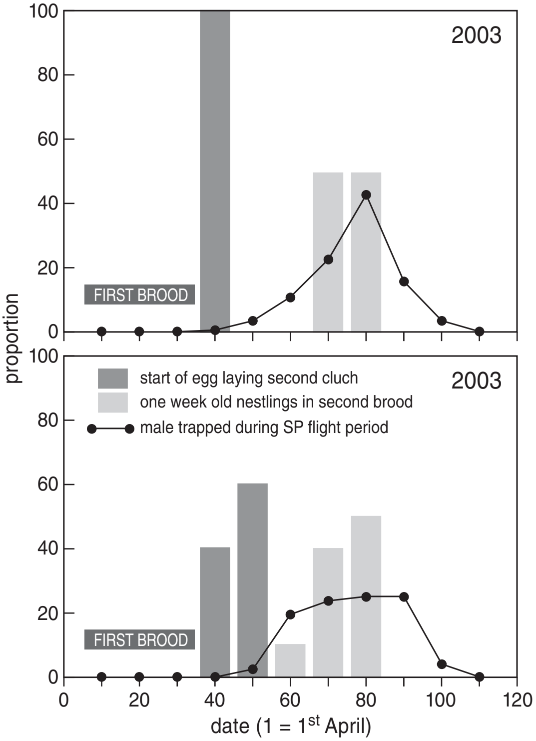

Figure 3. Relation between breeding phenology of Great Tits in NeSP, and abundance of SP imagos during 2002 and 2003. Indicated is the period of time in which nestlings of the first brood are in the nestboxes. Shown is also timing of the start of egg laying in second clutches, of one week old nestlings in second broods and of male *T. pityocampa* trapped during the SP flight period, as proportion of the total.

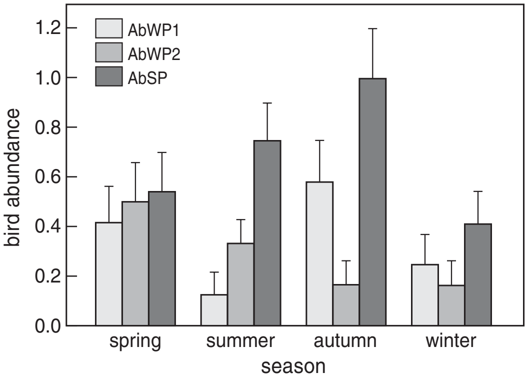

Figure 4. Average (± SE) number of Great Tits per count point in three different locations of the National Pine Forest of Leiria, obtained during four different seasons in each of two years (between March 1998 – January 1999; and October 1999 – June 2000).

RESULTS

A main difference between the WP and SP life cycles was the emergence of adult moths of the SP during rearing of second broods of Great Tits (Figs. 2 and 3). On average 120 ± 54.0 and 80 ± 77.9 SP male moths were captured per trap in 2002 and 2003, respectively, from mid May through mid July. Most adults emerged during mid June, corresponding to the period when Great Tit second brood nestlings were about one week old (Fig. 3). In the two traps placed in AbWP1 and AbWP2, only 0–8 males were trapped in each trap during the flight period of SP. Between mid-July and October, corresponding to the WP flight period, 0–3 males were captured in each trap, indicating a low density of this *T. pityocampa* population. The first instar larval nests of SP were observed between mid to end July, and pupation occurred at mid October–early November, while first instar larval nests of the WP were observed in September followed by pupation in February–March (Fig. 2).

Overall, Great Tit abundances differed between areas with a season effect which was close to significance (repeated measures ANOVA: area $F_{2,132} = 9.71$; $P < 0.001$; season $F_{3,132} = 2.59$; $P = 0.056$; area x season $F_{6,132} = 2.22$; $P = 0.045$; Fig. 4). Differences between areas were due to a higher abundance in the SP area as compared to the other two areas (Tukey post-hoc test: $P < 0.001$ for both comparisons). Differences between seasons were due to a decrease in abundance in winter in relation to autumn (Tukey post-hoc test: $P = 0.051$). The significant interaction between area and season indicates that the differences in abundance between the areas were largest in summer and autumn (Fig. 4). During the three years when nestboxes were available, densities increased 2-fold, 3-fold and 5-fold in NeWP1, NeWP2 and NeSP, respectively (Fig. 5A).

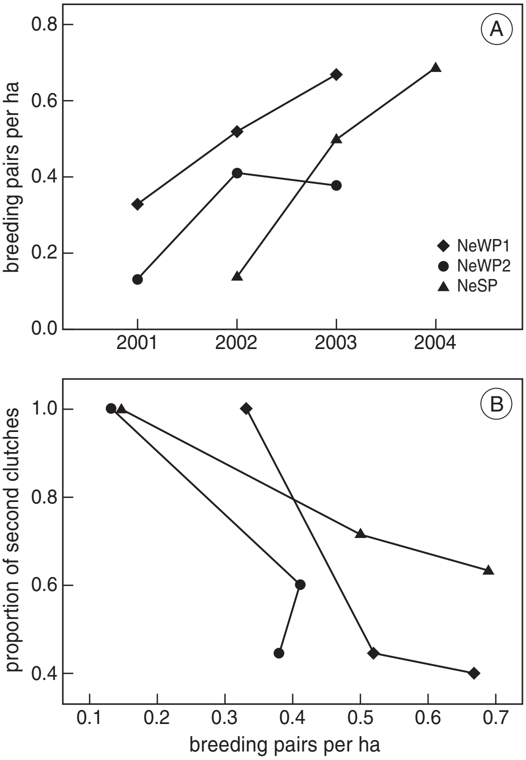

Figure 5. Changes in the number of breeding pairs of Great Tits per ha (A) and proportion of pairs with a second breeding attempt in relation to density (B), in the three years following the setting up of the nestboxes in each plot (2001–2003 in NeWP1 and NeWP2; 2002–2004 in NeSP).

As is commonly observed in Great Tits (e.g. Both 1998), breeding density negatively affected the proportion of second clutches in all the three plots (ANOVA: area $F_{2,5} = 1.81$; $P = 0.26$; density $F_{1,5} = 17.68$; $P = 0.008$; Fig. 5B). In the first year after setting up the nestboxes, all pairs produced a second clutch, however this proportion had decreased to 63 % in the SP area and 40–44 % in NeWP1 and NeWP2 three years later (Fig. 5B).

The onset of egg laying of both the first and second clutch was similar in all the study areas (Table 1), with the median date 24 March and 14 May, respectively. The size of the first clutch did not differ between the areas, whereas second clutch sizes did (Table 1). This variation depended on females in NeSP producing significantly larger second clutches than females in NeWP1 (Tukey HSD test: $P = 0.006$; $P > 0.2$ for the other comparisons, Fig. 6A). The variation between areas in the number of fledglings produced in first broods was not quite significant, which contrasted the highly significant variation in the number of fledglings produced from second broods (Table 1). Second broods in NeSP produced more fledged young than second broods in both NeWP1 and NeWP2 (Tukey HSD test: $P < 0.001$ and $P = 0.005$, respectively) with no difference between the two WP areas (Tukey HSD test: $P = 0.26$, Fig. 6B).

Table 1. Results of ANCOVAs testing for differences between three nestbox plots (NeWP1, NeWP2, and NeSP; Fig. 1) in start of laying, clutch size and number of fledglings in first and second broods of Great Tits. Year (2002 and 2003) and breeding density were dropped from full models if not significant.

Breeding attempt	Parameter	ANOVA		
		df	*F*	*P*
First broods	Start of laying	2,61	0.53	0.59
	Clutch size	2,61	2.12	0.13
	Number of fledglings	2,61	2.57	0.084
Second broods	Start of laying	2,35	0.25	0.78
	Clutch size	2,35	5.60	0.008
	Number of fledglings	2,34	14.92	<0.001[a]

[a] Year included in the final model $F_{1,34} = 5.98$; $P = 0.020$

DISCUSSION

We found that the abundance of Great Tits was significantly higher in an area with a sudden appearance of a *T. pityocampa* population with a shifted life cycle (SP) than in areas with *T. pityocampa* maintaining the normal life cycle (WP). The SP reached much higher densities than the WP in the same or other parts of the forest (Pimentel *et al.* 2006). The increase in Great Tit abundance was

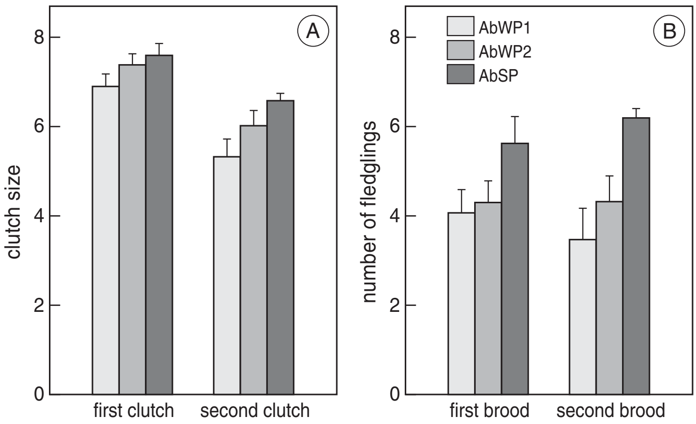

Figure 6. Mean (± SE) clutch size of first and second clutches (A), mean (± SE) number of fledglings in first and second broods (B), in Great Tits breeding in nestboxes during 2002 and 2003 in the Leiria Forest.

most pronounced during summer and autumn, at the time when imagos and larvae of the shifted moth are available (Fig. 2). Great Tits breeding in the area with SP also had a higher reproductive output than Great Tits breeding in the area with WP, mainly due to a higher production of fledglings in second broods, a period that coincides with the availability of imagoes in the field. To our knowledge, this is the first study to document a response of a bird predator to a local *T. pityocampa* irruption. Furthermore this is the first study to report the response of a bird predator to an insect population with a large shift in its life cycle.

Great Tits disperse primarily during their first year of life (Greenwood *et al.* 1979, Delestrade *et al.* 1996, Andreu & Barba 2006). Thus, the high Great Tit abundances recorded in the SP distribution area, in the years immediately following the irruption of the moth, were probably due to both a high local production and to young birds being attracted from nearby areas by the local abundance of food. Both the gregarious caterpillars and the adult moths are life stages that are potentially predated upon by Great Tits (Betts 1955, Royama 1970, Gonzalez-Cano 1981, Barba & Gil-Delgado 1990). At the end of the summer, signs of bird predation on SP caterpillars were observed as holes apparently made by birds were found in some of the larval nests (own observations). However, the increase in Great Tit abundance in the infested area was limited in time to the availability of food provided by the SP. Abundances were similar inside and outside the SP area during winter and spring. Furthermore, in the first year after setting up nestboxes, the breeding density in the SP area was not higher than in the other two nestbox areas, indicating that the primary determinant of breeding density was nest hole availability rather than local food abundance during summer and autumn.

Great Tits in the SP area had a higher success of second broods compared to birds breeding within two similar forest areas only harbouring the WP. The start of egg-laying of second clutches, coincided with the beginning of the emergence period of SP imagos (Fig. 3). The peak of this emergence period occurred when second brood nestlings were about one week old, an age when they require maximum amounts of energy (Perrins 1965). Although, Great Tits in deciduous woods generally rely on Lepidoptera larvae for provisioning nestlings (Betts 1955, Gibb & Betts 1963), adult moths can constitute an alternative food source when larvae are scarce in Mediterranean ecosystems (Barba & Gil-Delgado 1990, Barba *et al.* 1994). Thus, the additional food supply constituted by SP imagos, might have accounted for the higher reproductive rates. The Great Tit population of the Leiria Forest is characterized by a long breeding season, lasting four months (Fig. 2). At low densities all breeding pairs, both inside and outside the SP distribution area, produce a second brood. The Great Tit is considered a facultative double brooded passerine, however several populations seem to be single brooded (Perrins 1965, van Balen 1973, Eeva *et al.* 2000). Although, the relation between seasonal variation in food supply and multiple breeding in this species is not totally clear (Verboven *et al.* 2001), the possibility of producing a second brood and reproductive allocation between two breeding attempts may play an important role as an adaptation to different habitats (Mägi & Mänd 2004, Pimentel & Nilsson 2007). Our results indicate that the possibility to produce a second brood among Great Tits in the Leiria Forest, allowed them to take advantage of a new natural food supply and to increase annual reproductive rates.

In conclusion, our results indicate that the increase of a Great Tit breeding population may exert a strong predation pressure on both adults and larvae of this novel Lepidoptera population. Especially predation on adult moths may be important due to the overlap between the nestling period of second broods and the moth peak of emergence. Predation pressure on adult moths may be even higher considering that the Great Tit population during this time increases due to first brood fledglings that can predate heavily on moths when they are abundant (Betts 1955). High rates of predation on adults in a forest outbreaking insect, can have a potentially higher impact on insect dynamics than the removal of larvae (Buckner & Turnock 1965, Otvos 1979).

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SAMENVATTING

Normaal gesproken komt de mediterrane Dennenprocessierups *Thaumetopoea pityocampa* in de winter voor, maar in een klein gebied aan de westkust van Portugal verschijnen deze rupsen sinds 1997 een aantal maanden eerder in het seizoen. In het hier beschreven onderzoek is nagegaan hoe Koolmezen *Parus major* op uitbraken van deze zogenaamde 'zomerpopulatie' hebben gereageerd. In jaren na een uitbraak waren de mezen talrijker dan in twee vergelijkbare gebieden zonder uitbraak. Dit was het meest duidelijk in de zomer en herfst wanneer de vlinders, eieren en rupsen beschikbaar waren voor de mezen. Het verschijnen van de vlinders van de nieuwe zomerpopulatie viel samen met het moment waarop de Koolmezen hun tweede broedsel hadden, waardoor de mezen een hoger broedsucces hadden dan in gebieden met een winterpopulatie van de processierups. Dit is voor het eerst dat de respons van vogels op een uitbraak van de Dennenprocessierups wordt aangetoond, wat te meer bijzonder is omdat het een populatie rupsen betrof met een verschoven jaarcyclus. Dit onderzoek laat zien dat Koolmezen snel reageren op lokale uitbraken van rupsen. De auteurs veronderstellen dat de mezen mogelijk een groot effect hebben op de talrijkheid van de insecten van de zomerpopulatie. (CB)

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