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Research article

The influence of soil temperature on the nesting cycle of the halictid bee *Lasioglossum malachurum*

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Abstract. The physiology and behavior of ectothermic organisms is strongly influenced by temperature. For ground nesting species like the primitively eusocial halictid bee, *Lasioglossum malachurum*, soil temperature might influence the life cycle as well as the complexity of the social group since the number of broods that can be fitted into the flight season might increase with increasing temperature. Our study population of *L. malachurum* at Wuerzburg exhibits a remarkable variability with respect to the number of broods and the pattern of sexual production. Broods are separated by activity pauses during which the larvae develop. In this study we investigate the influence of soil temperature on the pattern of nesting activity (duration of broods and pauses) and on the number of broods in *L. malachurum*. We observed a total of 1138 nests in 13 aggregations near Wuerzburg. As expected, soil temperature shortened the duration of the pauses, resulting in an overall shortening of the nesting cycle. This is most probably due to a physiological effect of soil temperature on the development of the larvae. With regard to the nesting strategies, we hypothesized that a shortening of the nesting cycle within the limited flight season should enhance the success of a strategy with more worker broods. In fact, patches with higher soil temperature showed more broods. However, this effect was rather weak, suggesting that other factors might have a stronger impact on the variability in nesting strategy within our study population of *L. malachurum*.

Keywords: Activity pattern, life-history strategy, Halictidae, primitively eusocial.

Introduction

Temperature strongly affects the life of insects including numerous behavioral and physiological processes such as flying ability, mating behavior, and especially the duration of development and survival of larvae (Borrell and Medeiros, 2004; Grafton-Cardwell et al., 2005; Larsson, 1991; Woods et al., 2005). Ground nesting insects like many wasp, bee, and ant species probably depend more on soil temperature than on air temperature with regard to nest-site selection, daily activity patterns, as well as foraging success and sex allocation (e.g., Cameron et al., 1996; Crist and Williams, 1999; Potts and Willmer, 1997; Strohm and Linsenmair, 1998; Vogt et al., 2003; Wuellner, 1999).

Social ground nesting Hymenoptera with an annual life cycle might be particularly dependent on soil temperature since it might influence the duration of development of helpers and the rate of provisioning. This in turn would affect the number of broods that can be produced during the limited flight season and, thus, the colony size and the level of social complexity. Here we focus on the influence of soil temperature on the nesting cycle of a ground nesting social halictid bee, *Lasioglossum (Evy-laeus) malachurum* (Kirby, 1802). We investigate how temperature affects the different nesting phases and whether it has an influence on the pattern of broods of workers and sexuals.

Bees of the family Halictidae exhibit a great variability with respect to social organization, both within and among species (Hirata et al., 2005; Packer, 1998; Plateaux-Quénu, 1993; Richards et al., 2003; Yanega, 1988). This extreme social diversity seems to be strongly affected by environmental conditions (for review, see

Wcislo, 1997; Yanega, 1997), although a genetic influence on the life strategy is sometimes involved as well (Danforth et al., 2003; Plateaux-Quénu et al., 2000; Soucy and Danforth, 2002). Our study population of *L. malachurum* at Wuerzburg shows a remarkable plasticity with respect to the pattern of worker and sexual production even within individual nest aggregations (Strohm and Bordon-Hauser, 2003). Mated females hibernate, solitarily found a nest in early spring, and provision a first brood of about four to six workers. After emergence, these workers take over foraging and provision a second brood that consists of either sexuals or workers. Only, if workers are produced, the brood cycle continues with the production of sexuals in the third brood. A third group of nests produces a mixed second brood that consists of both workers and sexuals that is followed by a third brood of only sexuals. There are pauses of mostly one to three weeks between the provisioning of a brood and the emergence of the first individuals. During these pauses, there is no activity outside the nests and nest entrances are usually closed.

We investigated the influence of soil temperature on the duration of the activity phases as well as the pauses of a population of *L. malachurum* at Wuerzburg. We hypothesized that due to the well known effect of temperatures on biological processes (Cossins and Bowler, 1987; Gilbert and Raworth, 1996; Howe, 1967), higher temperatures will shorten the different phases of the nesting cycle of *L. malachurum*. We expected this effect to be strongest during the early stages of the flight season, when weather conditions are cooler and less predictable. A shortening of the nesting cycle in turn is likely to improve the prospects of a strategy with more worker broods. Taking also into account the known clinal variation in the social behavior of *L. malachurum*, with more worker broods produced in warmer climates (Knerer, 1992; Richards, 2000), we hypothesized a higher percentage of colonies with three broods at nesting aggregations with higher soil temperature. To test these hypotheses we investigated different nesting aggregations at Wuerzburg. Some of our nest aggregations were located above subterranean heating pipes at the campus of the University of Wuerzburg. The inclusion of these aggregations considerably increased the available range of temperatures and should make any effect of temperature easier to detect.

Materials and methods

Study species and nest cycle

The ground nesting halictid bee *L. malachurum* is widely distributed in the Western Palaearctic region and can be found from northern Europe to North Africa and from Iberia to the Caucasus (Amiet et al., 2001; Knerer, 1992; Michener, 1979). Detailed information on the nesting biology of the species can be found in Knerer (1992) and Richards (2000).

In the following, the solitary nest founding phase is abbreviated by NF, the different broods are B1 (workers only), B2 (workers, or sexuals, or workers and sexuals), and B3 (sexuals only). The three pauses between the activity periods are abbreviated by P1 (NF-B1), P2 (B1-B2), and P3 (B2-B3).

Study site

We investigated 13 nesting aggregations of *L. malachurum* in the vicinity of the Biocenter of the University of Wuerzburg and in the rural environment in the south of the University in 2004. Within each of these aggregations we selected one observation patch at random leading to 13 observation patches in total. Patches on the university campus were numbered from 1 to 7 and those at the other nesting sites from 8 to 13. All 13 patches were located in an area with a radius of 1 km (Fig. 1). All nests of the aggregations at the Biocenter (patches 1–7) were located on densely overgrown sandy soil and right above subterranean heating pipes. These pipes run in a depth of two to five meters and constantly transport 140°C hot pressurized water, thereby heating up the surrounding soil. The nesting sites in the rural environment (patches 8–13) in the south of the Biocenter were located on sandy or silty soil with very little vegetation. Patches on top of the subterranean heating pipes (1–7) are referred to as “heated” patches; those in the rural environment (8–13) are called “unheated” patches.

Figure 1. Map of the study area showing the location of the 13 observation patches (* heated patches) in the vicinity of the Biocenter of the University of Wuerzburg (1–7) and in the rural environment in the south of the University (8–13).

Each of the 13 observation patches measured 0.25 m², with a nest density between 96 and 852 nests / m² during NF (Table 1). To facilitate the monitoring of the nest cycle, all nests of an observation patch were marked with numbered nails and the exact position of each nest was mapped. Furthermore, vegetation was cut every two weeks.

Table 1. Summary for the 13 observation patches (* heated patches). The number of nests during NF, the failure rates between NF and B1 as well as B1 and B2, the proportion of nests with B3, and the mean soil temperature (season mean $\pm$ SD) at a depth of 20 and 40 cm are given.

Patch number	Number of nests (NF)	Failure rate (%)		Proportion of nests with B3	Soil temperature (°C)	
		NF-B1	B1-B2		20 cm	40 cm
1*	99	23.2	10.5	89.7	19.4 $\pm$ 4.0	18.1 $\pm$ 3.5
2*	99	30.3	18.8	85.7	20.6 $\pm$ 4.0	19.6 $\pm$ 3.8
3*	101	30.7	11.4	83.9	20.4 $\pm$ 4.0	21.3 $\pm$ 3.8
4*	77	32.5	9.6	78.7	21.7 $\pm$ 3.9	25.2 $\pm$ 3.5
5*	50	32.0	5.9	71.9	21.9 $\pm$ 3.9	21.1 $\pm$ 3.6
6*	32	37.5	15.0	76.5	22.0 $\pm$ 4.2	26.2 $\pm$ 4.0
7*	213	37.6	13.5	89.6	19.2 $\pm$ 3.9	19.0 $\pm$ 3.7
8	72	23.6	20.0	52.3	18.1 $\pm$ 4.0	–
9	158	45.6	88.4	40.0	17.9 $\pm$ 4.2	17.5 $\pm$ 3.9
10	70	22.9	3.7	90.4	18.1 $\pm$ 3.8	16.9 $\pm$ 3.1
11	77	15.6	6.2	60.7	18.0 $\pm$ 3.9	17.6 $\pm$ 3.9
12	24	29.2	5.9	43.8	18.6 $\pm$ 4.4	17.6 $\pm$ 3.9
13	66	25.8	14.3	81.0	19.0 $\pm$ 4.7	17.7 $\pm$ 4.2

Soil temperature

Soil temperature of all 13 patches was recorded during the whole observation period from the beginning of April until the end of September using thermo-loggers (iButton DS1921G-F5, Dallas Semiconductor). In the immediate vicinity of each patch (approx. 10 cm from the edge of a patch) two loggers were buried in depths of 20 and 40 cm. They were programmed to measure the temperature every three hours. One of the 26 thermo-loggers could not be recovered at the end of the observation period, so the temperature data for patch 8 at a depth of 40 cm is missing. A nest may range between depths of 10–15 cm during NF, 25–30 cm during B1, and up to 50 cm or more at the end of B2 (Knerer 1992; Legewie 1925; Noll 1931). Thus, the measurements reflect a relevant area with regard to the location of the brood cells.

For all subsequent analyses we use the mean soil temperature for each patch at a depth of 20 and 40 cm over the whole flight season of *L. malachurum* in Würzburg (April 09 – September 19). The mean temperature is a suitable measure since it represents the progression and differences that occur over the season very well.

Nesting activity

In the 13 patches, a total of 1138 nests was checked every other day for nesting activity from the beginning of April until the end of September. We recorded open nest entrances, burrowing activity, and/or the presence of a guarding bee and regarded these as reliable signs for nesting activity. Based on these observations, data on the beginning, end, and duration of the activity periods of the different broods and the respective pauses are available. However, the very first days of the nest founding phase (starting in mid March) were not observed. Therefore, we do not have exact data on the founding of each nest. Some colonies showed no nest closure between B1 and B2 (9 out of 622) or B2 and B3 (24 out of 489), so some data on the end of B1/B2 and the beginning of B2/B3 are missing.

It should be noted that the duration of the nesting activity during B1 depends only on the duration of the foraging activity of workers, whereas during B2 duration of nesting activity means foraging of workers, or the emergence of sexuals, or both. In contrast, duration of activity of B3 exclusively refers to the emergence of sexuals.

Nesting strategy

As a measure of the incidence of either a two or a three brood nesting strategy we calculated the proportion of colonies that showed B3 in relation to the number of active colonies during B2 in a patch. To determine which nests with three broods produced either exclusively workers or workers and sexuals during B2 would have required prolonged observations of the B2 phase as well as catching the emerging bees of B2. The latter might have undesirably affected the nesting cycle. Thus, we only differentiated between nests that showed activity during two or three broods. This procedure has, however, the consequence that colonies that actually had workers in B2 and “tried” to produce a third brood but failed due to whatever reason were counted as nests with a two brood strategy. Therefore, we might somewhat overestimate the number of nests with a two brood strategy.

This procedure might cause biases since patches with low overall success would have a low estimated proportion of a three brood strategy. To check for such a bias we calculated the failure rates between NF and B1 (proportion of B1 nests divided by the number of NF nests) as well as between B1 and B2 (proportion of B2 nests divided by the number of B1 nests) for each patch. Then we tested whether these failure rates correlate with the proportion of nests that show a three brood strategy. No correlation indicates that failure rates do not affect our measure of the nesting strategy.

Data analysis

We checked for normal distributions of our data by histogram plots. All samples showed reasonable approximation to normality. Samples that differed in variance (according to a Levene test) were compared using Welch tests that correct for unequal variances. The data on the proportion of nests with B3 and the failure rates between NF and B1 as well as B1 and B2 of the different patches were arcsine-transformed. Data are presented as means $\pm$ 1 SD.

A One-way ANOVA was calculated to test for differences between the 13 observation patches with regard to soil temperature. We tested whether the patches differed in the timing of nesting activities (beginning, end, and duration of the broods; duration of the pauses) using a One-way ANOVA with Welch correction for inhomogeneous variances. We used *t* tests or Welch tests to compare means of soil temperature, nesting activity, and nesting strategy of the “unheated” and “heated” patches. A Spearman rank correlation procedure was

Figure 2. Mean temperature (season means) in a patch and position of the activity periods (patch means) within the flight season of *L. malachurum* for the 13 observation patches (* heated patches) ordered according to their mean temperatures 20 cm below surface. The bars mark the position of NF, B1, B2, and B3.

used to test for a correlation between the failure rates between NF and B1 as well as B1 and B2 and the proportion of nests with B3. We tested whether soil temperature at depths of 20 and 40 cm had an effect on the duration of different phases of the nesting cycle using Pearson correlation analyses. Since it is reasonable to assume that there can only be an effect of soil temperature on the nesting activity and not vice versa we assume a causal effect of temperature on nesting activity. A chi-square test was calculated to test whether the patches differed in the proportion of nests with a two versus a three brood strategy. Logistic regression analyses were used to test for an influence of the different measures of nesting activity on the nesting strategy of the colonies. Logistic regression analysis was also used to test for an effect of soil temperature on the proportion of colonies in a patch that produced B3. Nagelkerke's r^2 as well as the area-under-curve (AUC) from a receiver-operating characteristic (ROC curve) are used for validation of the calculated logistic regression tests. AUC values range from 0.5 (randomly guessing) to 1.0 (perfect test accuracy). Tests were calculated using either SPSS 12.0, BiAS 8.10, or R 2.1.1.

Results

Soil temperature

During the flight season of *L. malachurum* we measured an overall mean soil temperature of $19.6 \pm 1.5^\circ\text{C}$ (range: $17.9 - 22.0^\circ\text{C}$, $n = 13$, Table 1, Fig. 2) 20 cm below surface and $19.8 \pm 3.1^\circ\text{C}$ (range: $16.9 - 26.2^\circ\text{C}$, $n = 12$, Table 1) 40 cm below surface. The 13 observation patches differed significantly in soil temperature at a depth of 20 (One-way ANOVA: $F_{12,299} = 3.72$, $p < 0.001$) as well as 40 cm ($F_{11,276} = 16.9$, $p < 0.001$). The relatively high temperatures at some patches and the large SD in a depth of 40 cm are caused by the heating pipes. The mean soil temperature 20 cm below surface of the “heated” patches was significantly higher ($20.7 \pm 1.2^\circ\text{C}$, $n = 7$) compared to the “unheated” patches ($18.3 \pm 0.4^\circ\text{C}$, $n = 6$, Welch test: $t = 5.19$, $df = 7.78$, $p < 0.001$). This difference was even more pronounced in 40 cm (“heated”: $21.5 \pm 3.1^\circ\text{C}$, $n = 7$; “unheated”: $17.5 \pm 0.3^\circ\text{C}$, $n = 5$; Welch test: $t = 3.43$,

$df = 6.18$, $p = 0.013$). Thus, the heating pipes on the campus of the University significantly increased the temperature of the surrounding ground by $2-4^\circ\text{C}$.

Nesting activity

The first queens started nest founding in the middle of March, but provisioning of brood cells did not start until the beginning of April. The duration of P1 (NF-B1) was 43 ± 4 days, whereas P2 (B1-B2) lasted for only 19 ± 5 and P3 (B2-B3) for 13 ± 5 days (means $\pm$ SD for 13 patches). Activity of B1 lasted for 16 ± 2 , for B2: 18 ± 2 , and for B3: 21 ± 6 days (means $\pm$ SD for 13 patches). The flight season ceased at the end of September with the last sexuals of B3 emerging on September 19.

Comparing the 13 different patches of *L. malachurum*, there was a great variability with regard to the activity pattern of the different broods despite their spatial proximity (Fig. 1 and 2). The 13 observation patches differed significantly in the beginning, end, and duration of the different broods as well as in the duration of the pauses (One-way ANOVA with Welch correction: $p < 0.05$ for all comparisons, Table 2). For example, we observed a maximum difference of 18 days between the 13 different patches with respect to the beginning of B1 (range: May 26 – June 13, 2004, $n = 13$). These differences add up in the course of the season resulting in a maximum difference of 35 days for the beginning of B2 (range: June 20 – July 25, 2004, $n = 13$) and 42 days for the beginning of B3 (range: July 17 – August 28, 2004, $n = 13$).

Table 2. Results of the One-way ANOVA with Welch correction testing for significant differences among the 13 observation patches with regard to the different measures of nesting activity (beginning, end, and duration of the broods; duration of the pauses). The test statistic *F*, the degrees of freedom *df*, and the probability *p* are given.

One-way ANOVA	<i>F</i>	<i>df</i>	<i>p</i>
End of NF	21.1	12, 301	<0.001
Duration of P1	71.9	12, 209	<0.001
Beginning of B1	278.0	12, 210	<0.001
End of B1	111.4	12, 206	<0.001
Duration of B1	7.5	12, 206	<0.001
Duration of P2	16.2	12, 138	<0.001
Beginning of B2	246.4	12, 136	<0.001
End of B2	157.0	12, 115	<0.001
Duration of B2	2.0	12, 115	0.028
Duration of P3	10.3	12, 53	<0.001
Beginning of B3	156.1	12, 53	<0.001
End of B3	216.0	12, 71	<0.001
Duration of B3	21.6	12, 54	<0.001

Influence of soil temperature on nesting activity

The mean soil temperature 20 and 40 cm below surface had a strong negative effect on the end of NF and on the beginning and end of B1-B3 (Pearson correlation: $p < 0.05$ for all correlations, $n_{20\text{ cm}} = 13$, $n_{40\text{ cm}} = 12$). Both temperature measures were significantly negatively correlated with the duration of all three pauses as well as the

duration of B1 (Fig. 3, Table 3). However, soil temperature at a depth of 20 and 40 cm had no effect on the duration of B2 and B3 (Table 3). The large coefficients for some correlations between temperature and the duration of pauses indicate that soil temperature had a strong effect on the shift in the position of the different broods (earlier beginning and end of B1-B3, Fig. 2).

In “heated” patches activity of the different broods started and ended earlier and showed a reduced duration of P1, P2, and B1 in comparison to the “unheated” patches (*t* test: $p < 0.05$ for all comparisons, $n_1 = 7$, $n_2 = 6$). The duration of P3, B2, and B3 did not differ significantly between the two groups of patches (*t* test: $p > 0.05$ for all comparisons, $n_1 = 7$, $n_2 = 6$).

Nesting strategy

In the 13 observation patches we observed NF for 1138 nests; $70.3 \pm 7.8\%$ of these showed activity in B1, $59.2 \pm 17.5\%$ in B2, and $44.2 \pm 16.2\%$ in B3 (means across 13 patches). A total proportion of $72.6 \pm 17.7\%$ (range: 40 – 90.4%; $n = 13$, Table 1) of the nests that were active during B2 showed activity during B3. The 13 patches differed significantly in the proportion of nests with three broods (chi-square test: $\chi^2 = 71.6$, $df = 12$, $p_{\text{exact}} < 0.001$). The analysis of the failure rates between the different broods (Table 1) revealed no evidence for a correlation between the proportion of nests with B3 and the proportion of colonies that failed between NF and B1 (Spearman rank correlation: $r = -0.201$, $p = 0.509$, $n = 13$)

Figure 3. Duration of P1 (A) and B1 (B) for the 13 observation patches as a function of the mean soil temperature (season means) 20 cm below surface. Linear regression lines are given.

Table 3. Results of the Pearson correlation analyses between the duration of P1-P3 and B1-B3 and the mean soil temperature (season mean) 20 and 40 cm below surface of the 13 observation patches. The correlation coefficient *r*, the sample size *n*, and the probability *p* are given.

Soil temp.		Duration of P1	Duration of P2	Duration of P3	Duration of B1	Duration of B2	Duration of B3
20 cm <i>n</i> = 13	<i>r</i>	−0.895	−0.839	−0.701	−0.644	0.440	0.023
	<i>p</i>	<0.001	<0.001	0.008	0.017	0.133	0.941
40 cm <i>n</i> = 12	<i>r</i>	−0.875	−0.694	−0.590	−0.879	0.344	−0.069
	<i>p</i>	<0.001	0.012	0.043	<0.001	0.274	0.831

Table 4. Results of the logistic regression analyses with the probability of the colonies within a patch to produce B3 as the dependent and the different measures of nesting activity as the independent variables.

independent variable	Wald χ^2	r^2	AUC	effect	p
End of NF	4.93	0.013	0.561	–	0.026
Duration of P1	3.17	0.008	0.549	–	0.075
Beginning of B1	8.90	0.024	0.598	–	0.003
End of B1	0.43	0.001	0.528	–	0.512
Duration of B1	6.58	0.017	0.569	+	0.01
Duration of P2	62.45	0.178	0.737	–	<0.001
Beginning of B2	37.11	0.109	0.681	–	<0.001
End of B2	6.28	0.017	0.578	–	0.012
Duration of B2	28.02	0.075	0.636	+	<0.001

as well as B1 and B2 ($r = -0.223$, $p = 0.464$, $n = 13$). Thus, the difference in the proportion of nests with a three brood strategy was not the result of differences in failure rate.

Influence of nesting activity pattern on nesting strategy

The proportion of the nests that exhibited B3 was significantly influenced by the beginning of B1 and B2, the end of NF and B2, and the duration of B1, B2, and P2 (Table 4). Of these, the durations of B1 and B2 were positively correlated whereas the beginning of B1 (Fig. 4) and B2, the end of NF and B2, and the duration of P2 were negatively correlated with the proportion of a three brood strategy.

Figure 4. The number of broods (2 or 3) as a function of the beginning of B1 (in days since 31.12.03). The logistic fit is shown. The frequency of the combinations of x and y values that occur more than once are indicated by the size of the circles (2–123 nests per data point).

Influence of soil temperature on nesting strategy

There was a marginally non significant difference in the proportion of a three brood strategy between the “heated” and “unheated” patches: $82.3 \pm 6.8\%$ of the B2 nests at the “heated” patches and $61.4 \pm 20.4\%$ of the B2 nests at the “unheated” patches had B3 (Welch test: $t = 2.27$, $df = 6.49$, $p = 0.06$, $n_1 = 7$, $n_2 = 6$). Variation in the nesting strategies was significantly higher among the “unheated” as compared to the “heated” patches (Levene test: $F_{5,6} = 5.66$, $p = 0.037$).

Overall, we found a significant effect of the mean temperature 20 cm below surface on the nesting strategy (logistic regression: Wald $\chi^2 = 5.75$, $p = 0.016$, Fig. 5). Nests at patches with a higher soil temperature showed a

Figure 5. The number of broods (2 or 3) as a function of the mean soil temperature (season mean) at a depth of 20 cm. The logistic fit is shown. The frequency of the combinations of x and y values that occur more than once are indicated by the size of the data points (4–103 nests per data point).

higher probability of producing three instead of two broods. However, the effect of soil temperature on the number of broods was rather small ($AUC=0.599$, $r^2=0.015$). The odds that the colonies produced three instead of two broods increased by 21.3% with a temperature increase of 1°C ($odds\ ratio=1.21$). Soil temperature 40 cm below surface had no significant effect on the nesting strategies of the nests (logistic regression: Wald $\chi^2=0.053$, $AUC=0.554$, $p=0.82$, $r^2=0.0001$).

Discussion

Influence of soil temperature on nesting activity

Soil temperature mainly affected the duration of the different pauses in the nest cycle of *L. malachurum* in the population at Wuerzburg. Pauses at patches with higher soil temperature were shorter, resulting in an earlier initiation and termination of provisioning activity of the different broods within the flight season. These results are confirmed by the comparison of nesting activities of “heated” and “unheated” patches and provide clear evidence for an accelerating, physiological effect of higher soil temperature on the development of the larvae. This is consistent with numerous studies on the effect of temperature on development (Eliopoulos and Stathas, 2003; Gilbert and Raworth, 1996; Grafton-Cardwell et al., 2005; Howe, 1967; Kamm, 1974; Melville and Schulte, 2001; Porter, 1988; Whitfield and Richards, 1992).

The negative correlation of soil temperature with the duration of provisioning of B1 workers might be due to a longer daily activity of workers at warmer patches, thereby reducing the number of days needed to provision the next brood. Additionally, soil temperature might also accelerate ageing of the workers (Cossins and Bowler, 1987). This might lead to a reduced life span of the bees and, thus, a shorter duration of the foraging activity. Soil temperature had an effect on the duration of B1 but not on B2 and B3. In early spring when weather conditions are less predictable and colder on average soil temperature might be more important than during summer. Then other factors like air temperature, solar radiation, and resource availability might have a larger influence than soil temperature (Richards, 2004).

Influence of nesting activity pattern on nesting strategy

Nearly all measured aspects of nesting activity were significantly negatively correlated with the proportion of nests with B3. However, these effects were rather small with r^2 values ranging from 1 to 19%. Actually, whether a nest produces a third brood depends on whether it had (enough) workers in the second brood, which in turn depends on whether workers were produced during the activity of B1. Thus, whether there is a two or three brood nest cycle can only be influenced during or prior to B1: the

end of NF, the duration of P1, and the beginning of B1. Of these three variables, only the end of NF and the beginning of B1 (Fig. 4) had a significant and negative influence (the earlier, the more) on the proportion of colonies with B3. Both effects were rather small, however, and can not explain the considerable variability with respect to the different nesting strategies among patches (Table 1).

All the other measures of nesting activity that were significantly correlated with the proportion of B3 nests have to be interpreted as non-causal relationships. For example, in colonies with a three brood strategy, B2 consists of only workers or workers and sexuals whereas in colonies with a two brood strategy, B2 consists of exclusively sexuals. Since workers are smaller than sexuals (Strohm and Bordon-Hauser, 2003), they develop faster and emerge earlier. Thus, a three brood strategy may result in a reduced duration of P2 and an earlier beginning of B2, which in turn leads to a strong negative correlation between the duration of P2 and the proportion of B3 nests. These considerations show that the duration of P2 does not directly affect the probability of B3, but that both are correlated due to an underlying pattern.

Influence of soil temperature on nesting strategy

We predicted that a reduction in the length of the nesting cycle (maximum difference in the onset of B3: 42 days) would improve the prospects of a strategy with more worker broods. We know that sexuals of *L. malachurum* need at least 22 days for egg to adult development (Weissel and Strohm, unpubl. data). Additionally, for sexuals of *L. zephyrum* reared in artificial colonies in the laboratory at a temperature of 26°C Kamm (1974) reports a development time of at least 21 days. Therefore, taking time for provisioning into account colonies should need at least four weeks to produce a brood of sexuals. In accordance with the clinal variation in the social behavior of *L. malachurum*, with more worker broods in warmer climates (Knerer, 1992; Richards, 2000), we found a higher percentage of colonies with a three brood strategy at patches with a higher soil temperature 20 cm below surface. Yet the effect of temperature on the number of broods was rather small. Less than 2% ($r^2=0.015$) of the variation in the number of broods could be explained by the influence of soil temperature. The probability for a three brood strategy increased only by 13% over the total range of measured temperatures. Moreover, comparing “heated” and “unheated” patches we found no significant difference in the proportion of nests with B3. Why only the temperature in a depth of 20 cm had a significant effect on the nest strategy is not clear. As explained above, the nest strategy is determined prior to or during B1. The depth of the nest might be around 20 cm at that time. Thus, the temperature at 40 cm might not have a strong influence on B1.

In conclusion, soil temperature strongly affected the temporal pattern of the nesting activity at different patches of *L. malachurum* at Wuerzburg. However, although the nests under study experienced a much larger range of soil temperatures than would have been available under natural conditions, temperature does not satisfactorily explain the differences in the proportion of a three as opposed to a two brood nesting strategy. Even though there are various examples for the influence of environmental conditions like photoperiod, altitude, or climate on the variability in social behavior (Eickwort et al., 1996; Knerer, 1992; Miyanaga et al., 1999; Soucy, 2002; Yanega, 1997), at a local scale other extrinsic or intrinsic factors like resource availability, queen quality, or genetic components might have a greater impact on the number of broods in the flight season.

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