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Objekttyp: **Article**

Zeitschrift: **Mitteilungen der Schweizerischen Entomologischen Gesellschaft = Bulletin de la Société Entomologique Suisse = Journal of the Swiss Entomological Society**

Band (Jahr): **64 (1991)**

Heft 1-2

PDF erstellt am: **22.07.2024**

Persistenter Link: https://doi.org/10.5169/seals-402434

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MITTEILUNGEN DER SCHWEIZERISCHEN ENTOMOLOGISCHEN GESELLSCHAFT
BULLETIN DE LA SOCIÉTÉ ENTOMOLOGIQUE SUISSE
64, 93–108, 1991

Worker mortality and colony development in bumblebees, *Bombus lucorum* (L.) (Hymenoptera, Apidae)

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The effect of worker mortality rate on growth and reproduction of colonies of *Bombus lucorum* (L.) was experimentally investigated under field conditions. In the experimental colonies, an extra weekly mortality rate of 10–15% for workers was imposed and the resulting developmental and reproductive performance compared to control colonies. This extra mortality corresponds to approximately half of the naturally occurring background mortality rate and is to be expected when colonies are infested by conopid flies (Diptera, Conopidae), which are endoparasitic on adults and abundant in the study areas. The number of newly hatching workers was positively correlated with number of adult workers present, while per capita growth rate correlated negatively (one-tailed significance) with worker mortality rate. However, extra mortality had little effect on development (i. e. colony growth rate, maximum worker numbers, or worker body size) and reproduction (i. e. timing and number of sexuals produced). There may be a tendency of stressed colonies to produce smaller workers, release relatively earlier and more males, and to produce fewer sexuals altogether, but the effects were statistically not significant. A large amount of unexplained variation in the observed traits existed among colonies, which may suggest intrinsic differences in colony vigor. Because experimentally induced extra mortality was undeniably present, we tentatively interprete our results, together with evidence from the literature, to indicate that colonies of bumblebees are remarkably resilient against moderate rates of worker mortality.

INTRODUCTION

Organisms have to grow and develop before reproduction becomes possible. During this period, a number of largely unavoidable adverse factors may interfere with the unfolding of this process, e. g. shortage of food, inclement weather, or interruptions of normal behaviour by predators. In a number of cases, it has been shown that such unavoidable stress results in variation of the subsequent pattern of reproduction. For example, slower growing fish may become mature later and at smaller size than those growing fast, as do laboratory rats (see STEARNS & KOELLA, 1986, and references therein). How the organism is adapted to cope with stress during growth and development is thus critically important for the pattern of reproduction. In turn, efficient coping strategies may limit the impact of unavoidable stress factors on reproductive success of the affected organism.

A similar situation exists in social insects where entire colonies grow in numbers of (non-reproductive) workers over the course of a seasonal cycle until sexual forms are produced and released. As in an individual organism, growth and development thus precede reproduction, although eusociality adds to the complexity of the system (for a review of social insect biology, see WILSON, 1971; BRIAN, 1983). Furthermore, because up to a point large colonies can normally produce more offspring (e. g. POMEROY & PLOWRIGHT, 1982), rapid growth and thus large eventual numerical size of the colony is likely to be crucially important in the ergonomics of social insects (HOUSTON *et al.,* 1988). The importance of growth and size is also suggested in various other contexts, such as colony defence against conspecific take-overs (HOELLDOBLER & LUMSDEN, 1980), colony fission (LEE & WINSTON, 1985; FRANKS, 1985), redundancy in task organization (HERBERS, 1981), or variation in caste structure (WILSON, 1983).

Among other things, the development of the colony depends onthe continued effort of workers that collect resources and subsequently convert them into new colony members. To collect these resources, workers have to leave the relative safety of their nest and become exposed to a number of risks and physiological stress factors that may affect their chances of future survival or foraging efficiency. Mortality risks are indeed known in theory (e. g. HOUSTON & McNAMARA, 1987) and from empirical tests (MILINSKI & HELLER, 1978) to affect individual foraging behaviours. Also for social insects, mortality rate of workers appears to be an important constraint on individual behaviours (STRASSMANN & MEYER, 1983; SCHMID-HEMPEL & SCHMID-HEMPEL, 1984; SCHMID-HEMPEL *et al.,* 1985).

Bumblebee workers leave the nest to forage for nectar and pollen that is needed both for colony maintenance and to raise new brood. Foraging bumblebees may become victims of predators such as crab spiders that are lurking on flowers (FRITZ & MORSE, 1985; MORSE, 1986). In addition, parasitic conopid flies (Diptera, Conopidae; SCHMID-HEMPEL & SCHMID-HEMPEL, 1988; SCHMID-HEMPEL *et al.* 1990) attack foraging bees and deposit an egg inside the abdomen. Conopid parasitization then leads to premature host death within about 8–10 days (R. SCHMID-HEMPEL, in prep.). Previous studies have shown that frequency of parasitization is rather high (up to 70%), and may vary with time of year, site, host species and sex (SCHMID-HEMPEL *et al.,* 1990). For many populations of bumblebees, mortality induced by the parasitic flies appears to be substantial.

An increase in mortality rate of workers in turn should mean a considerable drain on the available work capacity of a colony. We would expect this to be reflected in a decrease in the rate of colony growth and, consequently, smaller colony size at maturity and thus in a loss of reproductive output, i. e. a smaller number of sexuals produced by a colony (MICHENER, 1964; FREE & WILLIAMS, 1975; POMEROY & PLOWRIGHT, 1982; COLE, 1984; LEE & WINSTON, 1985). However, affected colonies may cope with increased worker mortality by adaptively varying the pattern of further development and reproduction to minimize fitness loss (see MINCHELLA, 1985). This could be achieved by shifting the pattern of reproduction in time and/or a shift in the allocation of resources to male or female offspring.

We will not discuss the theory of this problem here, as some models have already been proposed (e. g. MACEVICZ & OSTER, 1976; SEGER, 1983; GRAFEN, 1986). Under reasonable assumptions, theory suggests that stressed colonies should reproduce earlier and with a male-biased investment in reproductives. However, the situation is more complex than that encompassed by these models and more detailed theoretical work is clearly required. In fact, the expectation of earlier reproduction is at variance with empirical results (BOWERS, 1986), although this evidence relates to entire populations rather than to individual colonies within populations.

Previously recorded natural mortality rates of adult bumblebees in temperate areas are around 4–6% per day or 25–35% per week (BRIAN, 1952; RODD *et* *al.*, 1980; GOLDBLATT & FELL, 1987). Mortality appears to be approximately constant over the first 10 to 14 days of individual life but thereafter increases. Here, we report on a field experiment in which workers of bumblebee colonies were experimentally subjected to extra mortality rates of approximately 10–15% per week. We tested the idea that such an increase in worker mortality would decrease rate of colony growth and cause correlated shifts in the timing and investment of reproduction. Additionally, we collected data to detect possible correlated reponses, such as shifts in worker body size. The aim was to learn how colonies of social insects cope with environmental stress.

MATERIAL AND METHODS

From a large number of queens of *Bombus lucorum* (L.), collected during April 1988 from the study area, 21 were successfully induced to start a colony in one of our nest boxes. These incipient nests were then transferred to wooden boxes (supplied by Schwegler AG; box "Münden") in the field site. The colonies were kept in close proximity to one another to balance environmental conditions for all units. Only data from a core of 12 colonies could finally be used for the present analysis, since many of the initial colonies perished, probably due to prolonged periods of bad weather during that season.

Colonies were assigned arbitrarily to one of two groups – CONTROL (5 colonies) and STRESS (7 colonies), but so that an important confounding factor, date of emergence of first brood, was balanced across both treatments. Each week, we censused the development of all colonies by removing and counting all of the workers, individually marking and photographing the newly emerged ones, and reintroducing all animals after completion of the census. Treatment STRESS involved removal of a random sample of 10% (on the first two occasions) to 15% (afterwards) of the workers present at each census. We did apply the same procedures but not remove workers in CONTROL colonies. Treatments started as soon as the colony had passed the arbitrarily set treshold size of ten bees (mature colonies of *B. lucorum* may contain dozens to hundreds of workers). Mortality rates of workers are likely to vary according to task and age schedules. For practical reasons, when removing workers from stressed colonies, such subtle differences could not be taken into account to match mortality schedules of controls and experimental colonies. The censuses were carried out during night hours under red light to ensure that virtually all workers were inside the nest. Census intervals were shortened to five days towards the end of the colony cycle to increase the chances of finding drones or queens before they had left the nest. No attempt was made to distinguish between queen and worker derived males. Although this neglect was motivated by practical limitations, the distinction is also not of prime importance for the question posed here, i. e. how variation in worker mortality affects development and reproductive performance of the colony as a whole. Furthermore, since the nightly inspections involved considerable disturbance to the colonies, the length of the interval was chosen to balance the need for accurate data and minimization of disturbance.

As natural mortality rates of bumblebee workers are approximately 25–35% per week, our treatment mimicked an additional rate of mortality equivalent to about half of the naturally occurring "background" mortality. Furthermore, straightforward calculations suggest this extra mortality corresponds to the extra drain in excess of natural mortality experienced by colonies moderately affected by the parasitic conopid flies (as estimated from SCHMID-HEMPEL & SCHMID-HEMPEL, 1988; SCHMID-HEMPEL *et al.*, 1990).

In each nest, all animals were individually marked on the census days, their presence noted and body size measured. The latter was done by photographing the animals against a standard background during the nightly censuses. From this material, total wing length (TWL, from tegula to outer edge) and radial wing length (RWL, tegula to distal end of subcostal cell) was obtained. In addition, for those animals that died in the nest and could thus be recovered, the length of the cubital cell #2 on the rostral side (LCC), and width of the medial cell #3 (WMC), between knots M3M4Cu3 and R2R3M3 (see WOLF, 1972; BRÜCKNER, 1976) was measured with a stereo microscope. Both kinds of measurements proved to be highly correlated, so that the photographic measurements can be considered to be a reliable measure of body size.

The censuses additionally provided regular estimates of the number of workers and sexuals in the colony, approximate birth and mortality rate over the census intervals, and body size of the workers present. To test for the effect of STRESS treatment on colony development, the following parameters were calculated (c.f. Fig. 1). (1) W_{SEX}: the number of workers present when the first sexuals emerged; (2) W_{MAX}: the maximum workers ever present in the colony; (3) W_{VOL}, the number of worker-days spent in the colony ("work-volume"); (4) Parameters K, r and t_{50} from the cumulative growth curves. For the latter quantities, cumulative colony growth in worker numbers was used as a basis (i. e. the total number of workers produced until time t). A logistic growth curve was then fitted according to the equation:

$$CW(t) = K/[1 + e^{r(t-t_{50})}],$$

where CW(t) = the cumulative number of workers until time t. K is an estimate of the total number of workers produced over the season. The number and position of empty brood cells at the end of the experiment were matched with census data to provide a rough confirmation of the worker counts, although worker and male cells are often difficult to distinguish. Fitting of the equation finally estimated parameters r (instantaneous rate of cumulative colony growth) and t_{50} (time to production of half of all workers in the season). Statistical calculations were done with procedures from the SAS-package (SAS Inc 1985).

RESULTS

Effects on colony growth

Colony growth results from the queen laying fertilized eggs and workers tending and raising brood that develop into pupae and finally emerge as adult workers. In bumblebees, egg-laying rate or sperm supply of the queen is not a limiting factor for colony growth, certainly over the major part of the colony cycle, while the size of the worker force has been shown to be an important ergonomic parameter in various contexts (MICHENER, 1964; ROESELER, 1970, 1973; ALFORD, 1975; DONOVAN & WEIR, 1978; POMEROY, 1979; POMEROY & PLOWRIGHT, 1982). Regardless of the detailed causal mechanisms involved in determining growth rate, it is therefore to be expected that the number of newly emerging workers is positively related to the number of workers already present. We have verified this assumption with pooled data for all colonies, by plotting the number

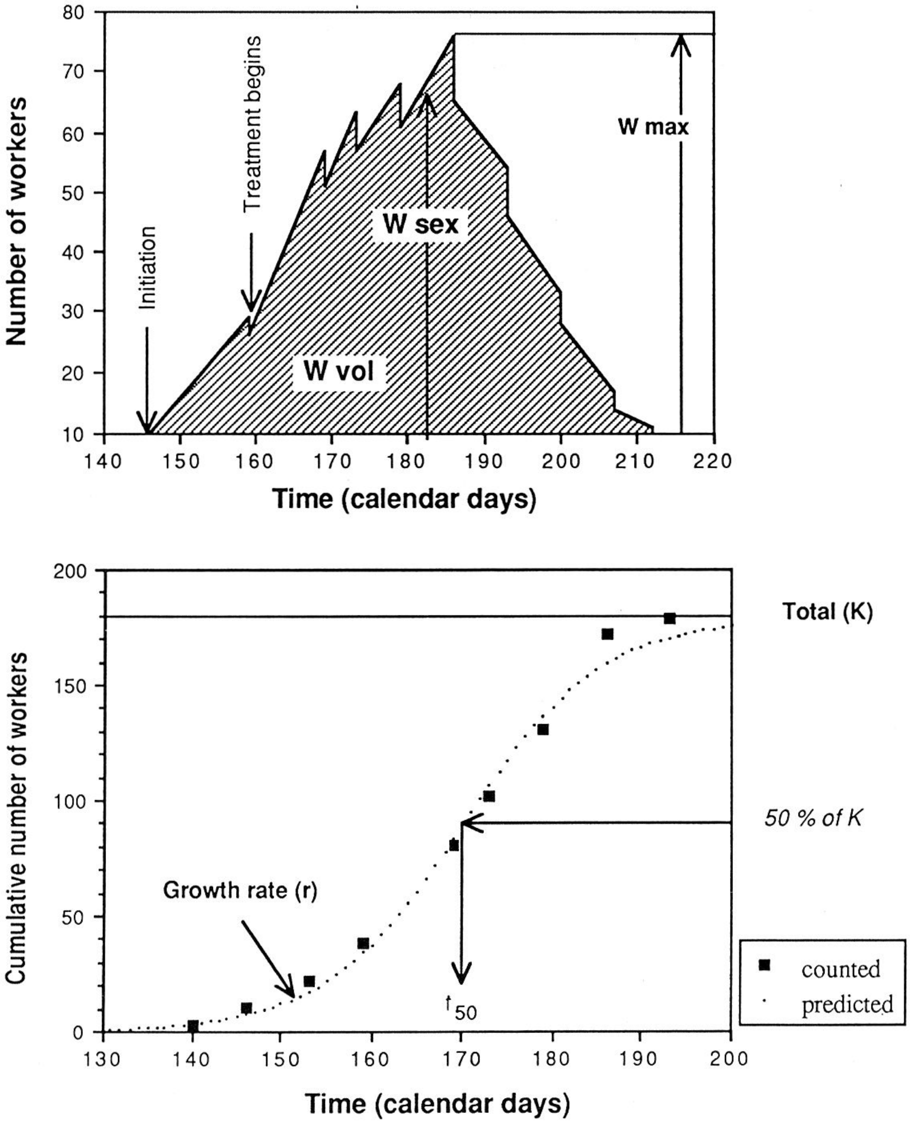

Fig. 1. (a) Example of colony development in our study (STRESSed colony # 12). Initiation is the day when the first batch of eggs are laid. Removal of workers starts at the end of the census interval when the colony has passed the lower threshold size of ten animals. The staggered increase indicates repeated experimental removal of workers. W_{MAX} is the maximal number of workers present, W_{SEX} the number of workers present when the first eggs of sexuals are laid, W_{VOL} is the available work effort, i. e. the area under the curve. Time axis (calendar days) starts on January 1st. (b) Cumulative growth curve, as calculated from the same data as in Fig. 1a (colony # 12). Predicted line is best fit logistic regression line.

of newly produced workers during a census interval against the number of adult workers present in the colony during the interval when the newborns were still in their egg, larval, or pupal stage. Since all three measures are, by virtue of their mutual dependence, correlated to one another, only data for the larval stage are shown here (Fig. 2). The larval stage precedes emergence by approximately two weeks (ROESELER, 1970; DUCHATEAU & VELTHUIS, 1988) hence with the weekly censuses used here, the number of new workers is plotted against the worker force present two weeks earlier. The analysis suggested a significant relation of number of newly emerged workers on the size of the operating worker force

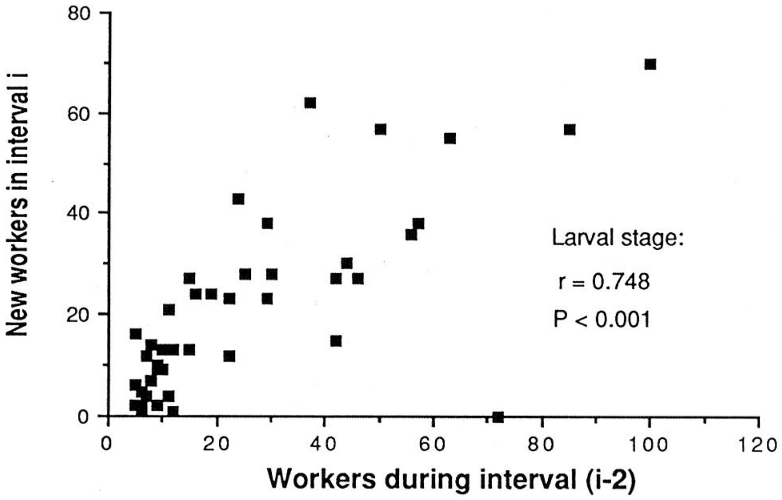

Fig. 2. Relationship between the worker force caring for larvae during census interval i-2 and the number of newly emerging workers in the present interval i. Pooled data for all colonies. The correlation is significant (Pearson's r = 0.748, F = 54.7, $P < 0.001$, n = 45; Kendall's $\tau = 0.225$, z = 2.18, $P = 0.029$). Development from larva to adult takes about two census intervals.

Tab. 1. Raw observations on colony growth and reproduction in control and stressed colonies. No differences between treatments are found (median-tests: $P > 0.2$ in all cases). For definitions, see Fig. 1 and text. Estimates of W_{VOL}, K,r, and t_{50} for colony #32 are not given because of missing values for some colony workers.

Colony #	W_{SEX}	W_{MAX}	W_{VOL} (days)	K	r (day^{-1})	t_{50} (days)	Males (N_M)	Queens (N_Q)
Controls:								
23	37	51	1242	103	0.099	170.3	14	1
32	118	136	-	-	-	-	14	16
36	-	12	41	22	0.117	185.0	0	0
41	63	71	2253	155	0.103	169.7	3	1
43	24	36	527	63	0.083	173.6	1	5
Median	50	51	885	91	0.094	172.6	3	0
Mean	60.1	61.2	815.9	99.3	0.099	174.3	6.4	4.6
S.E.	20.7	21.0	480.6	30.5	0.011	3.8	3.1	3.0
Stressed:								
12	15	76	2001	163	0.120	172.2	11	2
22	96	124	4432	289	0.119	166.8	9	1
30	88	100	2830	204	0.112	172.5	0	3
33	3	13	11	21	0.068	157.1	2	0
34	-	16	33	28	0.111	195.0	0	0
39	11	23	167	35	0.136	184.1	1	0
49	23	23	131	37	0.127	169.9	0	0
Median	15	23	167	62	0.127	172.5	1	0
Mean	42.3	53.6	1372.2	126.1	0.125	176.4	3.3	0.9
S.E.	20.2	17.3	664.1	41.9	0.009	5.1	1.8	0.5

(Fig. 2). Therefore, extra mortality as induced to STRESS colonies is expected to reduce colony growth potential by causing a drain on the available work force.

Variation in the colony growth patterns among treatments was tested by comparing CONTROL and STRESS colonies. Table 1 summarizes the raw observations for W_{SEX}, W_{MAX}, W_{VOL}, number of males and queens produced, and estimated parameters K, r, and t_{50}. None of these measures proved to be different in pairwise comparisons between treatments.

Worker size

Since there was little effect of extra mortality on the pattern of colony growth, we hypothesized that stressed colonies might have been able to compensate for a loss in available work force (and consequently available work volume, Table 1) by producing the same number of workers but at smaller body sizes. But this hypothesis was not supported by the observations on morphological parameters (Table 2): sizes of workers proved to be similar among treatments, but significantly different among colonies. Hence, colonies did not compensate by producing smaller workers if stressed.

Pattern of reproduction

Both males and females were produced in the colonies. These sexuals could have emerged and left the colony during a census interval and thus not all were in

Tab. 2. Measures of worker body size: TWL = total wing length, RWL = radial wing length, LCC = length of cubital cell, WMC = width of medial cell (see text). Average for each colony entered in the analysis (n = number of colonies). The random factor "colony" is nested within fixed factor "treatment". Means (S.D.) in mm.

Treatment		TWL	RWL	LCC	WMC
CONTROL (n=5)		10.576 ± 0.54	8.848 ± 0.29	1.440 ± 0.04	0.665 ± 0.04
STRESS (n=7)		10.205 ± 1.07	8.625 ± 0.89	1.437 ± 0.15	0.660 ± 0.07
Source of variation :					
"Treatment"	*F*	0.46	0.93	1.47	1.73
	P	0.51	0.36	0.25	0.22
"Colony "	*F*	33.17	24.37	12.17	9.71
	P	< 0.001	< 0.001	< 0.001	< 0.001

fact detected. This limitation is reflected in the generally low counts for sexuals. In particular, since males leave earlier than queens, male production is more likely to be systematically underestimated. Hence, the figures given here can only be taken as estimates used in the comparison between treatments, rather than as absolute estimates of reproduction. Furthermore, workers are known to be responsible for some of the produced males (OWEN *et al.,* 1980), but we here do not distinguish between queen and worker derived eggs. With this in mind, STRESSed colonies (n = 7) tended to have fewer males (median: 1, range 0–11) than CONTROLs (n = 5) (median: 3, range 0–14), and also fewer females (STRESS: median 1, range 0–3; CONTROL: median 1, range 0–16). The biomass of sexuals produced, expressed as drone units (1 drone ≈ 54 mg dry weight; MUELLER, 1988) was somewhat larger in CONTROL colonies (median: 12 units, range 0–49.2) than in STRESSed ones (median: 2, range 0–15.4). Again, none of these differences was significant (median tests, $P > 0.5$ in all cases).

From the above data and the measurements of dry weights for queens and drones, we could gain a rough estimate of the ratio of biomasses invested in the two sexes, at least for some of the colonies (i. e. male biomass/total biomass of reproductives). STRESSed colonies invested an average ratio of 0.804 into drones (range 0–1.0; n = 5 colonies) and CONTROLs a ratio of 0.431 (range 0.08–0.86; n = 4 colonies); a difference could not be detected with our limited sample. The same pattern existed for the numerical ratio of the sexes. For all colonies, the average percentage of biomass contained in males was r = 0.46 (95%– confidence interval: 0.37–0.55).

The timing of reproduction, i. e. when resources are shunted towards production of sexuals rather than towards production of new workers, was estimated by the time when half of the sexuals had been counted. For males in CONTROL colonies this was 51.3 ± 9.5 days (S.D.; n = 4 colonies) after initiation of the colony, while in STRESSed colonies it was 43.2 ± 12.5 days (n = 4) (t = 1.03, N.S.). Half of the queens in CONTROL had emerged 52.1 ± 6.2 days (n = 4), and in STRESSed 59.2 ± 9.6 days (n = 3) after colony initiation (t = 1.20, N.S.). Thus, queen delay, i. e. the time between male and female emergence, was somewhat larger for STRESSed colonies (6.3 ± 8.8 days) than for CONTROL colonies (0.8 ± 8.5 days) (t = 0.74, N.S.), but our data did not allow us to detect significant differences attributable to treatment.

Mortality rates of workers

The censuses provided estimates of net worker mortality rates, i. e. the rate of disappearance of the individually marked workers between censuses. Of course, workers could have emerged and already died within the same census interval. This would not have been detected with our method. However, the empty brood cells at the end of the season could be matched with our counts of workers and males obtained during the censuses. This comparison suggested that the error introduced with the weekly censuses was probably small with no systematic bias between treatments.

The observed natural ("background") mortality rates ranged from 30 to 40% per week during the experiment (Fig. 3). Rates were suspected to increase with time in the season. Thus, the appropriate regression lines were first fitted to the observations for each colony. ANCOVA then tested for sources of variation among the regression lines, both for natural mortality and total mortality rates,

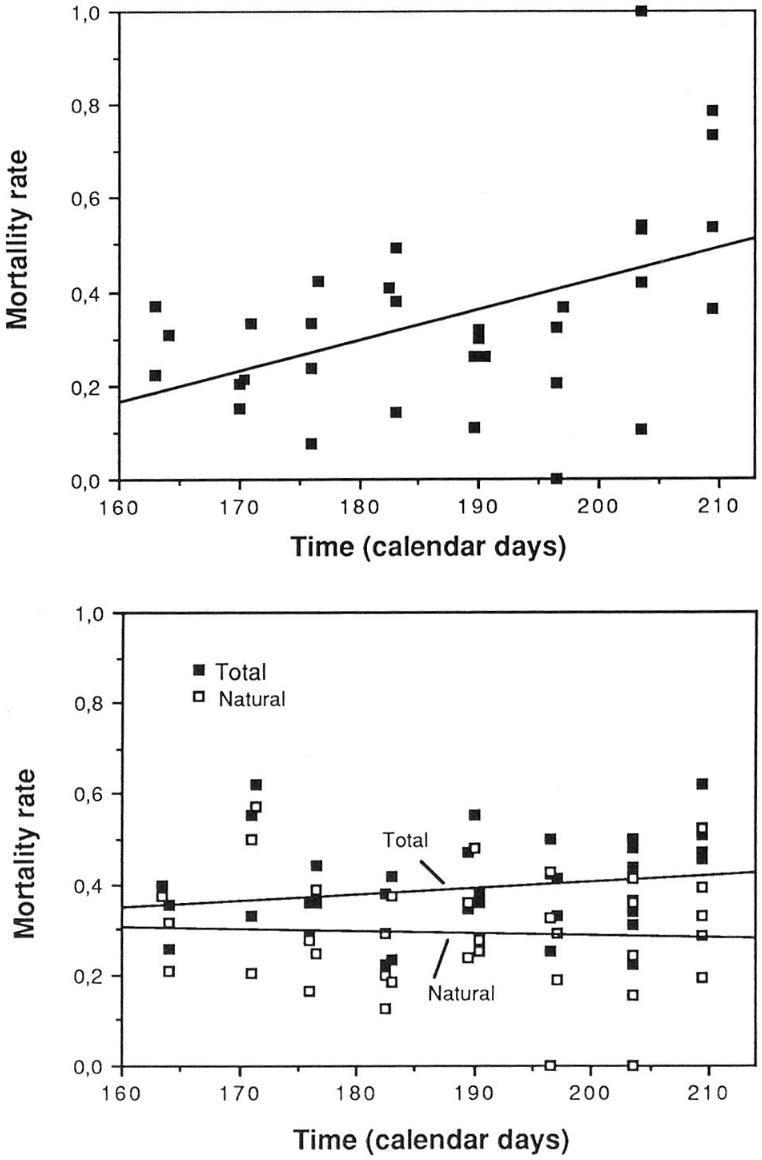

Fig. 3. (a) Mortality rates (μ, per week) for CONTROL colonies estimated from weekly cenuses during the experiment was related to time (Kendall's $\tau = 0.30$, $z = 2.46$, $P = 0.14$). Fitted regression line is $\mu = -0.873 + 0.00649\,T$ ($r^2 = 0.213$; $F = 8.40$, $P = 0.007$, $n = 33$). T = calendar days (c. f. Fig. 1). No extra experimental mortality is induced. (b) Natural (μ_0) and total (i. e. natural plus extra) mortality rates (μ_1) for STRESSed colonies during the experiment. No effect of season was found (μ_0: Kendall's $\tau = 0.006$, N.S.; $r^2 = 0.001$, $F = 0.119$, $P = 0.7$, $n = 36$) (μ_1: $\tau = 0.165$, N.S.; $r^2 = 0.038$, $F = 1.330$, $P = 0.25$, $n = 36$). The (non-significant) regression lines are: $\mu_0 = 0.393\text{–}0.0005\,T$ and $\mu_1 = 0.113 + 0.0015\,T$.

respectively (ZAR, 1984, p. 300 ff; no test is available for nested data: STEEL & TORRIE, 1981).

Within CONTROL colonies, natural mortality rate equals total mortality rate. A significant increase with season was found, although this effect seems to come from higher mortalities late in the season (Fig. 3a). Natural mortality rates of STRESSed colonies, in contrast, remained more or less constant (Fig. 3b). This difference in slope between treatments is significant ($F = 6.84$, $P = 0.01$, $n = 67$). On average, natural mortality rates in STRESSed colonies were similar

(28.6 ± 4.9% per week, n = 5 colonies) to those of CONTROL (31.1 ± 6.6%, n = 5) (arcsin-transformed percentages: t = 0.69, $P = 0.5$; comparison of regression elevations: F = 2.56, df = 1.66; $P = 0.12$). As expected, total mortality rates (i. e. natural plus extra removed) differed between treatments (arcsin-transformed percentages: t = 2.41, $P = 0.043$), with STRESSed (average: 39.3 ± 3.8%, n = 5 colonies) higher than CONTROL (31.1 ± 6.6%, n = 4). In contrast to CONTROLs, no seasonal effect for STRESSed colonies was found (Fig. 3b) (comparison of slopes: F = 3.92, $P = 0.052$, n = 67).

Worker mortality and colony ergonomics

Here, we summarize observations on all colonies, irrespective of treatment, to substantiate the importance of worker mortality and available work effort for the development of the colony in our field experiment.

Firstly, we investigated the relationship between mortality rate of workers and productivity, i. e. the number of new workers produced per capita of the operating worker force. Both quantities could be calculated on the basis of censuses of the individually marked individuals. The operating worker force was assumed to be the number of workers present when the newly produced workers were in their egg, larval, or pupal stage (as before). Again, all these measures were found to be highly correlated with one another. Therefore, only data for the larval stage are discussed here. Fig. 4 suggests a negative, but only marginally significant, correlation between mortality and productivity.

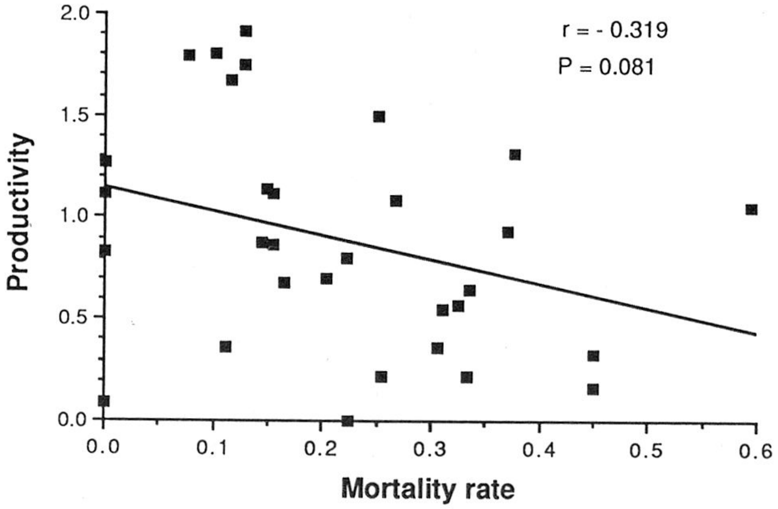

Fig. 4. Relationship between number of new workers having hatched since the last inspection (W, *ordinate)* and mortality rate (μ, per week, *abscissa)* that was experienced by adult workers during the interval when the newly hatched ones were still in their larval stage (i. e. two weeks earlier). Regression line is: $W = 1.15\text{–}1.20\ \mu$ ($r = -0.319$; one-tailed $P = 0.04$, $n = 31$).

Nevertheless, the importance of a large worker force is also suggested when the total volume of work effort available in the colonies is compared with their respective reproductive performances (Table 3). Two measures of available work effort were included in the analysis: W_{VOL}, the number of worker-days available in the colony over the season, and W_{MAX}, the maximum number of workers pre-

Tab. 3. Regression of indicators of reproductive performance (T_M, T_Q = time since colony initiation for 50% of all males, queens, to have appeared; N_M, N_Q = lower limit to number of sexuals produced, see text) on parameters characterizing ergonomic performance W_{VOL}, W_{MAX}, see Fig. 1).

Ergonomic parameter		Reproductive performance			
		N_M	N_Q	T_M (days)	T_Q (days)
W_{VOL}	Slope (10^{-3})	1.613	0.1554	3.181	6.602
	(S.D., 10^{-3})	(2.16)	(1.46)	(9.36)	(2.54)
	n	11	11	7	6
	t	2.48	0.35	0.90	6.36
	P	0.016	0.37	0.20	< 0.001
W_{MAX}	Slope	0.084	0.069	0.119	0.145
	(S.D.)	(0.09)	(0.20)	(0.27)	(0.30)
	n	12	12	8	7
	t	3.05	1.17	1.27	1.27
	P	0.006	0.13	0.12	0.13

sent (c.f. Fig. 1). W_{VOL} and W_{MAX} had a significant influence on male production, but time of emergence of queens was correlated only with W_{VOL}.

Our data also showed a significant positive relationship between available work effort of the colony (W_{VOL}) and the average size of individual workers (RWL, mm), such that strong colonies also tended to produce larger workers with $RWL = 0.216 + 0.484\, W_{VOL}$ ($t = 7.07$, $P < 0.001$; n = 11 colonies).

DISCUSSION

Resilience against external disturbances has often been considered an advantage of the ergonomic organization of social insects (e. g. the idea of a reserve worker force: LINDAUER, 1961; MICHENER, 1964). When workers are experimentally removed, individual activities of the remaining ones have indeed often been reported to increase or shift to compensate for the loss (e. g. WILSON, 1983, 1984; KOLMES, 1985; GORDON, 1987; WINSTON & FERGUSSON, 1985). Thus, redundant task organization and large numbers of individuals present in a colony may have opened new ways of coping with environmental stress (see OSTER & WILSON, 1978). There are, however, few studies that further clarify how colonies adapt by varying their life history pattern, or studies that estimate the magnitude of fitness loss (e. g. GENTRY, 1974).

In this study, we have adopted the view that in social insects large colony size at reproduction is advantageous, although large size may also be associated with adverse effects, such as vulnerability to predation or parasitization (STRASSMANN, 1981) or decreasing per-capita efficiency of brood rearing (MICHENER, 1964; COLE, 1984). Growth curves of social insect colonies are often exponential over at least part of the cycle (see BRIAN, 1965, 1983; WILSON, 1971), suggesting that rate of growth often depends primarily on the number of workers already present. This pattern was also observed in our study (Fig. 2). The size of the operating worker force, i. e. the number of (active) workers present at any one time, is in turn determined by the current size of the worker force and the difference between the per-capita rates at which new workers emerge and at which they die. Mortality rate should thus be important for colony development and eventual reproduction. This is also indicated by our observations (Fig. 4).

Despite these relationships, we were not able to find significant differences among treatments (Tables 1 and 2). Such differences may of course have gone undetected with our limited sample size. Nevertheless, the sample allowed to detect significant variation among colonies (Table 2), and, in addition, experimentally imposed extra mortality rate added about half of the natural background mortality rate. It therefore remains a surprising fact that the effect of intrinsic variation among colonies seems to override this substantial manipulation and hence stressed colonies were on average not different from the controls. It also is clear that stressed colonies did not simply compensate for numerical loss by a decrease in worker body size. While keeping in mind the limitations of our data set, we conclude that our observations could not support the theoretical expectation of earlier and male-biased reproduction in reponse to increased worker mortality (MACEVICZ & OSTER, 1976).

It appears from Fig. 3b that natural background mortality rates were marginally smaller for STRESSed colonies than for CONTROLs. In addition, natural mortality rates for STRESSed colonies did not vary over time, whereas they increased in CONTROL colonies (Fig. 3). Such a pattern might have been the result of changes in risk-prone behaviours of individual workers, e. g. with workers of STRESSed colonies less profligate in the allocation of their work capacity (WOLF & SCHMID-HEMPEL, 1989) in response to increased mortality risks. If this were the case, it would however leave open the question why this was achieved at negligible costs for colony development. We have actually observed the behaviour of individual workers and colony activities at the hive entrances over several periods of time. But none of the observed parameters, such as number of foraging trips, activity patterns in terms of bees leaving or entering the nest, and so forth, were found to be different between the two treatments (HEEB, unpubl. MS).

On the other hand, our findings are surprisingly well in line with reports of studies where colonies of social insects were stressed in various ways. For example, GENTRY (1974) found that moderate removal of workers from colonies of the harvester ant *Pogonomyrmex badius* had little effect on further colony development, worker body size and frequency of swarming. Effects were observed, however, if five times as many workers were removed and thus stress level considerably increased. Similar findings were reported by HERBERS (1980) who found no drastic effect of either food shortage or artificial predation on caste ratios in *Formica obscuripes,* although reduced fecundity is mentioned (see also FOWLER, 1984). Similarly, POMEROY & PLOWRIGHT (1982) observed that colonies of *Bom-*

bus perplexus which were experimentally kept small tended to produce queens and males later than controls, but again the effects were marginal, and the difference was significant only for very small colonies but not for moderate-sized ones. SUTCLIFFE (1987; SUTCLIFFE & PLOWRIGHT, 1988) applied different levels of food stress to colonies of *B. terricola* and reported that moderate food shortage did not affect colony development to a great extent. Only substantial shortage, such that food was available for only 8 hrs rather than 14 or 24 hrs a day, could produce significant differences. In general therefore, it appears that moderate stress on colonies does not result in significant negative effects, although heavy predation of parasitism will of course eventually lead to fitness losses (GIBO, 1978; LITTE, 1979).

In all of these studies, a large amount of scatter is present, as in our own observations. Moreover, it seems often the case that traits, such as number of queens emerging per day and the length of time over which they are produced, do not show a simple trade-off structure, but, quite to the contrary, are positively correlated to one another (e. g. POMEROY & PLOWRIGHT, 1982). This suggest intrinsic differences in the "quality" of colonies. In our study we found a positive correlation between worker body size and size of the worker force.

Our failure of demonstrating substantial differences among treatments can of course by simply explained away with limited sample size. However, as just discussed, the results could reflect a deeper property of the ergonomics of social insects colonies. This is supported by the fact that negative effects of excessive mortality rates existed in our experiments (e. g. Figs. 2, 4). Thus, despite the lack of a clear cut difference we feel encouraged to report our findings: Together with those reported in the literature, we suggest that colonies of social insects may be remarkably well buffered against external perturbation (such as imposed here by extra mortality rates). It is less clear what mechanisms, e. g. differences in the behaviours of individuals or their activity budgets, actually would ensure such resilience. Furthermore, a large amount of intrinsic variance in the ergonomic capacity among colonies appears to exist. Unfortunatley, these aspects are little studied but would be crucially important for understanding the evolution of colony-level characteristics. Furthermore, between-colony variance may normally go unnoticed and is only expressed when environmental conditions deteriorate.

Our study was initially motivated by the high frequency of conopid attacks and the resulting decreased life spans of infested workers (SCHMID-HEMPEL & SCHMID-HEMPEL, 1988; SCHMID-HEMPEL *et al.,* 1990). If the extra mortality induced in our experiment is a fair simulation of the impact of conopids under normal conditions, the fitness cost of conopid parasitization would seem to be small. But such costs must be studied and substantiated if variation in growth and development are to be interpreted in adaptive terms. In addition, by seeing how a highly social life affects the coping strategies of the developing colony, a better appreciation of the alternatives available to solitary organisms can be obtained.

ACKNOWLEDGEMENTS

We thank C. MÜLLER, J. SHYKOFF, R. SCHMID-HEMPEL and many other friends for help in the field censuses. M. FLÜCKIGER of the Institute for Applied Plant Biology at Schönenbuch generously provided the facilities for the field work. V. MISLIN and P. WEHRLI assisted with technical help. Financial supported was given by grants from the Schweizerischer Nationalfonds (nos. 3.017–0.87 and 3.074–0.87 to PSH). The Freiwillige Akademische Gesellschaft helped with supplying field equipment.

ZUSAMMENFASSUNG

Mortalität von Arbeiterinnen und Kolonieentwicklung bei der Hellen Erdhummel Bombus lucorum (L.). – Die Wirkung der Mortalitätsrate von Arbeiterinnen auf das Wachstum und die Reproduktion von Kolonien von *Bombus lucorum* (L.) wurde experimentell unter Feldbedingungen untersucht. In den Versuchskolonien wurde eine Mortalitätsrate von 10–15% erzeugt (gestresste Kolonien) und die resultierende Entwicklung und Reproduktionsleistung mit Kontroll-Kolonien verglichen. Diese Zusatzmortalität entspricht etwa der Hälfte der natürlicherweise vorkommenden «Hintergrund»-Mortalität. Diese Extra-Rate ist zu erwarten, falls adulte Arbeiterinnen durch endoparasitische Larven von Dickkopffliegen (Conopidae, Diptera) befallen werden, welche in unseren Studiengebieten häufig sind. Die Anzahl neuschlüpfender Arbeiterinnen war positiv mit der Anzahl vorhandener Arbeiterinnen, die Pro-Kopf-Wachstumsrate der Kolonie negativ (einseitig signifikant) mit der Mortalitätsrate korreliert. Die experimentell induzierte Extra-Mortalität hatte jedoch wenig Auswirkungen auf Kolonieentwicklung (d. h. auf Wachstumsrate, maximale Arbeiterinnenzahl, Körpergrösse der Tiere) und Reproduktion (d. h. Zeitpunkt und Anzahl produzierter Geschlechtstiere). In der Tendenz scheinen gestresste Kolonien kleinere Arbeiterinnen zu haben, früher und relativ mehr Männchen sowie gesamthaft weniger Geschlechtstiere zu produzieren. Die Effekte waren allerdings statistisch nicht abzusichern. Zwischen den Kolonien gab es eine beträchtliche, unerklärte Varianz in den gemessenen Merkmalen, welche inhärente Qualitätsunterschiede vermuten lassen. Weil die Zusatzmortalität trotzdem beträchtlich war, vermuten wir auf Grund unserer Resultate und der Evidenz aus der Literatur, dass Kolonien von Hummeln erstaunlich elastisch sind gegenüber mässig hohen Mortalitätsraten von Arbeiterinnen.

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(received September 24, 1990)