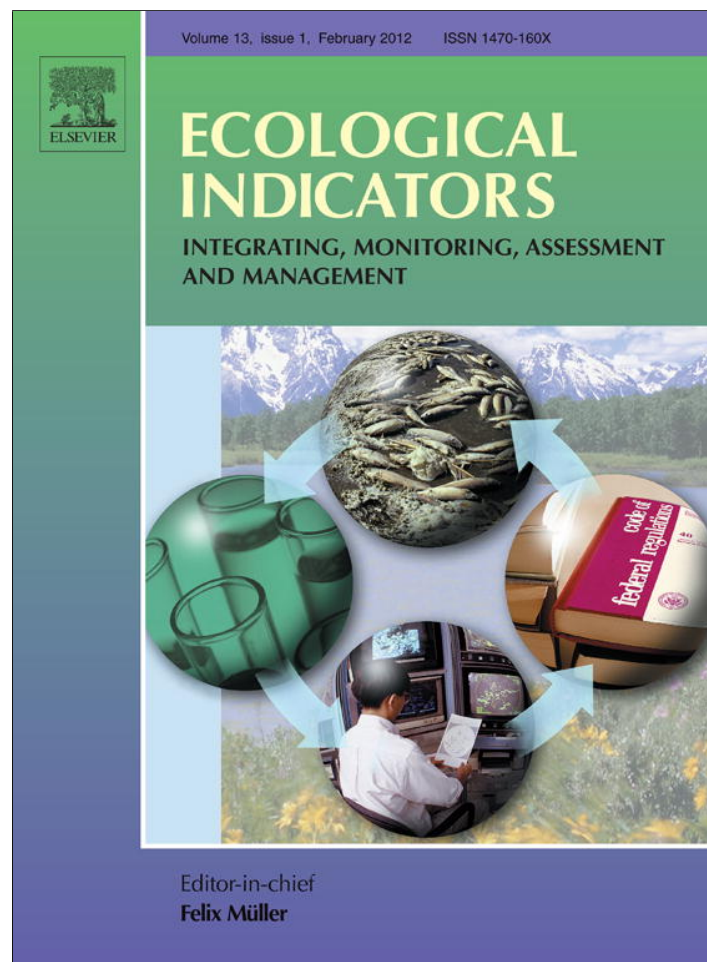


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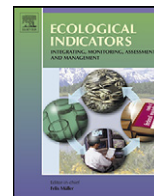
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Life-history strategies as a tool to identify conservation constraints: A case-study on ants in chalk grasslands[☆]

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ABSTRACT

Species' life-history traits underlie species–environment relationships. Therefore, analysis of species traits, combined into life-history strategies, can be used to identify key factors shaping the local species composition. This is demonstrated in a case-study on ants in chalk grasslands. We developed four life-history strategies based on traits related to reproduction, development, dispersal and synchronization that are documented in the literature. These theoretical strategies reflect different responses to certain environmental conditions. They can be characterized as generalists (G), poor dispersers (D), species whose distribution is limited to sites with high food availability (F) and species that are restricted to sites with high soil temperatures during nest founding (T). Next, we tested whether the occurrence of these strategies differed between six Dutch chalk grasslands and four reference sites situated in Germany and Belgium. We found significant differences in species numbers between sites for strategies D and T but not for strategies F and G. The differences could be explained by differences in connectivity and microhabitat conditions; species richness of strategy D decreased exponentially with increasing distance to the next nearest chalk grassland, while summer soil temperature strongly affected species richness of strategy T. From these relationships we could successfully identify the most relevant bottlenecks for the occurrence of both of these strategies in Dutch chalk grasslands. Management recommendations resulting from this analysis include adapting the management timing in Dutch chalk grasslands and focussing on counter-acting habitat isolation. With this case-study we demonstrate that the life-history strategy approach is a valuable alternative to approaches that try to identify key factors by analysing the variation in environmental parameters. The main advantage of the presented alternative is the focus on mechanistically understanding species responses, allowing a comparison of processes rather than occurrences of single species.

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1. Introduction

To assess the success rate of restoration and conservation projects, restored sites are frequently compared to more pristine reference sites, either in space or time (White and Walker, 1997). In this way the extent to which the target sites differ from

reference sites can be determined, for example in terms of species richness or abundance of characteristic species. To define successful management measures it is essential to establish which factor is key in explaining these differences between target sites and reference sites. The most common method to get insight in these species–environment relationships is a top-down approach in which the variation in environmental parameters is analysed and correlated to differences in species composition by use of multivariate statistics. Such top-down approaches have been proven to be a valuable tool to explore which factors out of the multitude of measured ones could potentially be causing the observed difference. However, they present two major problems. First, such correlations cannot be used to establish causality (Verberk, 2010; Michener, 1997), while causal understanding is essential to predict which actions will be most effective for reaching management targets (Bradshaw, 1996; Hobbs and Norton, 1996). Secondly when

[☆] Nomenclature follows Seifert (2007).

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using these top-down approaches researchers have to decide in advance which factors they will measure. Especially in complex restoration situations, the number of possible factors to measure is overwhelming. Many general factors like microclimate, fragmentation and management practice can be measured in different ways and at different levels of detail, all with a (slightly) different outcome as a result. Selecting in advance which factors to measure essentially prevents the discovery of new key factors. This limits the value of applied restoration and conservation ecology to advance our understanding regarding more fundamental aspects of community ecology.

In recent years a growing number of studies have demonstrated that species' life-history traits can successfully be used to gain insight in species–environment relationships (Bremner et al., 2006; Cristofoli et al., 2010; McGill et al., 2006). This provides a bottom-up (starting at the species end of species–environment relationships) alternative to traditional top-down approaches (Verberk et al., 2008b). Species traits include any morphological, physiological or phenological feature without reference to the environment (Violle et al., 2007). The attractiveness of trait-based approaches is rooted in the promise of traits potentially providing mechanistic understanding of species–environment relationships. This makes them especially appealing to explain and predict species responses to changes in their environment (e.g. Van Kleef et al., 2006; Verberk et al., 2010a; Williams et al., 2010). Previous trait-based approaches have mostly tried to link individual traits to species' responses. However, within species, traits are not independent but are linked to form an integrated response to particular ecological problems (Siepel, 1994, 1995; Stearns, 1976). Traits are interconnected through trade-offs and different traits may act in concert (Siepel, 1994; Verberk et al., 2008a). Therefore a specific trait may have very different ecological implications depending on the remainder of the traits possessed by the species. E.g. wings generally make an ant species more mobile, but if flight is used only to find mates while the founding of a new nest occurs by nest-splitting (walking to a new site accompanied by workers), the presence of wings is of no value to the species' colonization ability. The importance of these linkages between traits is widely acknowledged, however, only few studies have found a way to deal with them. Siepel (1994), Verberk et al. (2008a) and Van Turnhout et al. (2011) have found an alternative by operationalising species traits through life-history strategies (called tactics in Siepel, 1994). They focused on trait combinations rather than single traits allowing to evaluate the relative importance of traits and to weight traits in an informed way depending on the remainder of a species' biology. In this way they assigned species to different life-history strategies that respond in a uniform way to changes in their environment.

In this paper we develop such life-history strategies for ants in chalk grasslands and demonstrate that life-history strategies can be used as indicators for specific ecological processes within a conservation context. In line with the components of life-history strategies identified by Siepel (1994) and Verberk et al. (2008a) we focus on traits related to development, reproduction, dispersal and synchronization to build life-history strategies. Since ants live in eusocial colonies which act as single reproductive units (Hölldobler and Wilson, 1990) we focus on colony development and colony reproductive effort rather than individual development and reproduction. Ants are especially suitable for a life-history strategy approach as both the general life-cycle and deviations from it are well documented (Hölldobler and Wilson, 1990; Seifert, 2007). In addition species traits of ants are strongly interrelated (Bourke and Franks, 1995; Tschinkel, 1991) and especially the mode of nest founding is connected to numerous other traits (Bourke and Franks, 1995; Johnson, 2006). Nest founding is also widely recognized to be the most vulnerable and critical period in the life-cycle of an ant colony (Hölldobler and Wilson, 1990; Johnson, 2006). Therefore, it

is reasonable to assume that the combination of life-history traits related to the nest founding phase most strongly determine under which conditions species can survive. This makes the nest founding mode a good starting point when exploring the differences in life-history strategy between ant species.

Chalk grasslands in North-Western Europe are potentially very rich in flora and fauna (WallisDeVries et al., 2002) including ants (Dekoninck et al., 2007; Seifert, 2007). Over the past century however, the number, size and quality of these grasslands have declined strongly (WallisDeVries et al., 2002). This decline has been especially severe in the Netherlands, where only 20 chalk grassland sites remain with a combined surface area of no more than 30 ha (Willems, 2001). These sites are highly isolated and have suffered from eutrophication from both adjacent agricultural areas and airborne nitrogen pollution. Together with the cessation of traditional land use, this has resulted in severe grass- and shrub encroachment by the early 1980s (Bobbink and Willems, 1993; Willems, 2001). At this point populations of characteristic ant species had also declined in the Dutch chalk grasslands (De Boer, 1983; Mabelis, 1983). In the ensuing decades restoration management has been implemented or improved, focusing primarily on removing excess primary production through grazing, mowing or both. To evaluate the current status of the ant assemblages in these habitats, we sampled ants in six of the largest Dutch chalk grasslands and four reference sites in Belgium and Germany. Specifically, the aim of this study is to: 1) develop life-history strategies for ants based on literature data to predict which environmental factors are of key importance; 2) test whether these predictions correspond to observed differences in environmental conditions between sampling locations using independent field data and; 3) use this mechanistic understanding of species–environment relationships to formulate management recommendations to improve the status of the ant fauna in the study sites.

2. Methods

2.1. Study sites

Ants were sampled in six Dutch chalk grasslands and in one Belgian and three German reference sites (Fig. 1). The German and Belgian sites were selected because they were expected to host more ant species that are characteristic for chalk grasslands and are thus presumably more intact with respect to factors that are important for these ant species. In general the reference sites are either less isolated or have been less degraded due to a shorter period of abandonment, lower atmospheric nitrogen levels or more effective restoration management. However, both among and between the Dutch sites and the reference sites there are considerable differences with respect to size, slope, aspect, degree of isolation and current and past management type and timing (Table 1). In addition, management history was not known in great detail for all sites. To quantify the combined effect of slope, aspect and management on the soil temperature we used Askey Keytag data loggers (model KTL-108). Due to logistical reasons no loggers were placed in the German sites. Soil temperature was measured at 30 min intervals at all sampled locations (see Section 2.2) in the Netherlands and Belgium throughout the year. Loggers were sealed in a plastic bag and buried at a depth of 5 cm (sensor depth). These measurements were conducted in 2008, while ant sampling took place in 2005 and 2006. However, as the management regime in all sites follows a strict yearly cycle the relative differences between sites should correspond well between years. Two sampling locations where the management in 2008 differed from previous years were excluded from the temperature data analysis. Unfortunately there was considerable drop out of data loggers as a result of management activity, failing loggers and logger disappearance. This

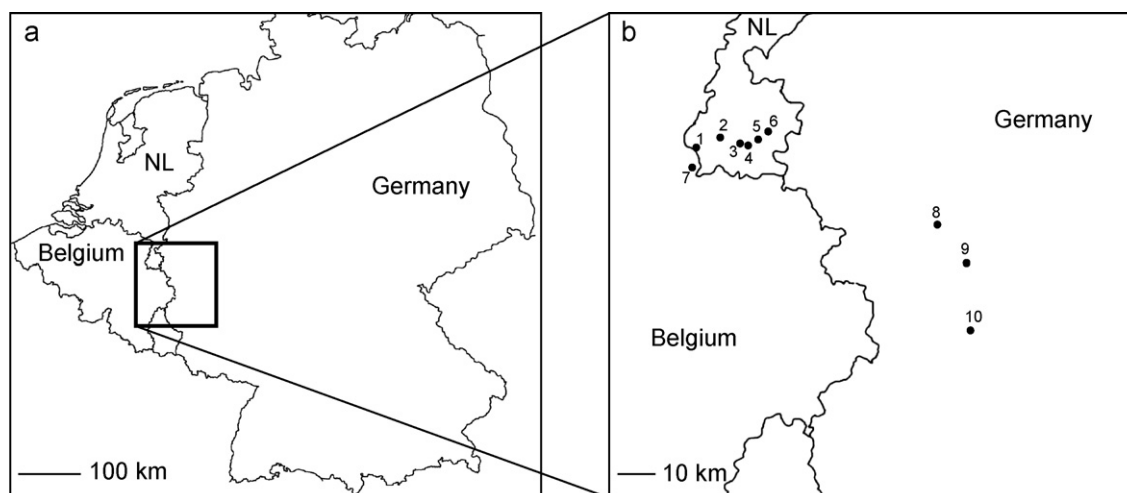


Fig. 1. Location of the study area in North-Western Europa (a) and the study sites within this region (b). 1 Sint Pietersberg (SP), 2 Bemelerberg (Bem), 3 Laamhei (Laam), 4 Berghofweide (Bh), 5 Wrakelberg (Wra), 6 Kunderberg (Kun), 7 Thier de Lanaye (Th), 8 Bürvenicherberg (Bu), 9 Halsberg (Ha), 10 Ahrhütte (Ah).

made it impossible to compare large periods of time between sites. As an alternative we selected five warm days between May and November with maximum logger data availability to compare soil temperatures between sites. To select these warm days we used weather data from the Maastricht weather station published at www.meteomaastricht.nl. All selected days were (almost) dry with a minimum of cloud cover and an average and maximum daily temperature well above the long-term monthly average (derived from the Dutch Meteorological Institute KNMI available at www.knmi.nl). We selected warm days as the differences in soil temperature between sites are most pronounced on these days.

2.2. Field sampling

Ant sampling was conducted using four series of pitfall traps per site. Each series consisted of five traps with an 8.5 cm diameter which were placed approximately 5 m apart. Each trap was covered with a 10 cm by 10 cm wooden plate placed at a height of about 2 cm above the ground to reduce evaporation and to prevent

small rodents from entering the traps. Traps were filled with 0.1 L of formaldehyde solution (5%) to which a few drops of liquid soap were added to reduce surface tension. The four pitfall trap series per site were placed at least 25 m (but mostly more) apart and together sampled the main variation in aspect, inclination and vegetation structure within each chalk grassland. In general, this within-site variation was rather limited. At Bemelerberg, Laamhei, Kunderberg, Wrakelberg, Ahrhütte, Halsberg and Thier de Lanaye sampling was carried out from the beginning of July 2005 until the end of October 2005. Sint Pietersberg, Berghofweide and Bürvenicherberg were sampled from the beginning of July 2006 until the end of October 2006. Traps were serviced every three weeks during the sampling period. Ant nests usually exist for several years (Seifert, 2007) and as there were no recent management changes within sites, no difference is expected between consecutive years. Ants were identified to the species level by the second author, using Boer (2010) and Seifert (2007). Pitfall trap data are not suitable to measure local nest density in ants, as the number of individuals caught is strongly influenced by the proximity of the nest

Table 1
Main characteristics of the sampling locations in the Netherlands (NL), Belgium (BE) and Germany (GER). The degree of isolation is defined as the distance to the next nearest chalk grassland. The management period is depicted as the months from January to December in which management is executed (white).

Site	Country	Size (ha.)	Aspect	Inclination(°)	Isolation (km)	Management	Management period
Bemelerberg (Bem)	NL	5.2	SSW-SSE	20-30	0.3	Grazing	■ J ■ A S O N ■
Berghofweide (Bh)	NL	2.6	S	10-15	1.2	Mowing & grazing	J ■ ■ ■ J ■ ■ ■ N D
Laamhei (Laam)	NL	1.3	W-WNW	10-15	1.2	Grazing	■ ■ ■ ■ ■ O N ■
Kunderberg (Kun)	NL	2.9	SW	15-20	3.0	Grazing	■ ■ ■ ■ ■ O N ■
Sint Pietersberg (SP)	NL	3.2	S/W	15-25	1.0	Grazing	■ F M A M J ■ S O ■ D
Wrakelberg (Wra)	NL	4.7	S	15-20	1.0	Mowing	■ ■ ■ ■ ■ O ■
Thier de Lanaye (Th)	BE	4.0	S-SE-ENE	20-30	0.8	Grazing	■ ■ ■ A M J A S O N D
Bürvenicherberg (Bu)	GER	2.6	SSW-SE	15-25	0.3	Grazing	■ ■ ■ A M J J ■ ■ ■ ■
Ahrhütte (Ah)	GER	4.3	NW-S-SE	15-25	0.1	Grazing	■ ■ ■ A M J J ■ ■ ■ ■
Halsberg (Ha)	GER	11.2	SSE	15-25	0.5	Grazing	■ ■ ■ A M J J ■ ■ ■ ■

Table 2
Traits and their consequences for survival used to build-up life-history strategies. Traits between brackets are strongly linked to the trait above. References to the main literature sources are given as footnotes.

Trait	Description	Consequences and preconditions for survival
Nest founding mode (Mature nest size) ^{a,b} (Number of males and gynes) ^{a,c} (Costs of producing a single gyne) ^{d,e} (Mode of dispersal prior to nest foundation) ^{a,b}	Nest splitting	Limited dispersal distance ^{a,b}
	Social parasitism	Distribution limited to sites large enough for stable host populations ^{g,h}
Additional founding modes	Semi-claustral	High food availability needed during nest founding ⁱ
	Claustral	Initial development time during nest founding restricted ^l causing high temperature dependence in species with slow larval development ^{k,l}
Mode of colony growth (Colony age) ^{a,b}	Additional nest-splitting	Promotes expansion within already colonised sites ^a
	Pleometrosis	Speeds up initial development ^{m,n}
Development speed of worker-larvae	Independent	Long colony life-span ^b
	Dependent	Short colony life-span ^b
Development stages capable of overwintering (Period of initial larval development) ^f	Fast	Short initial development time during colony founding ^l
	Slow	Long initial development time during colony founding ^{l,o}
Timing of the nuptial flight	Only adults	Determines time-window for colony founding
	Adults and larvae	
Period of initial egg-laying (Period of initial larval development) ^{a,f}	Early season	Determines time-window for colony founding
	Late season	
Period of initial egg-laying (Period of initial larval development) ^{a,f}	Before winter	Determines time-window for colony founding
	After winter	

^a Hölldobler and Wilson (1990).

^b Seifert (2007).

^c Bourke (1999).

^d Keller and Passera (1989).

^e Stille (1996).

^f Kipyatkov (2001).

^g Holt et al. (1999).

^h Mabelis and Chardon (2006).

ⁱ Johnson (2006).

^j Andrasfalvy (1961).

^k Wagner et al. (1984).

^l Kipyatkov (1993).

^m Waloff (1957).

ⁿ Sommer and Hölldobler (1995).

^o Kipyatkov et al. (2004).

(Schlick-Steiner et al., 2006). Therefore, only species presence and absence per pitfall trap series was recorded.

2.3. Trait selection

Traits were obtained from published literature for all species found in our study. All species traits falling within the four domains (reproduction, development, synchronization and dispersal) defined by Stearns (1976) and Siepel (1994) that were reported by (Hölldobler and Wilson, 1990) to play a role in the life-cycle of ants were considered. Selecting for traits that play a role at the population level and that actually differed between the species in our study, the following life-history traits were incorporated: main mode of nest founding, additional nest founding modes, mode of colony growth, mature nest size, maximum colony age, development speed of worker larvae, development stages capable of overwintering, number of males and gynes produced, costs of producing a single gyne, mode of dispersal prior to nest foundation, timing of the nuptial flight, period of initial egg-laying and period of larval development. Feeding niche was not considered separately as the differences in diet choice and diet breadth were very limited among the studied species (Seifert, 2007).

2.4. Life-history strategies

Life-history strategies were derived by starting with the main nest founding mode. For all nest founding modes represented by species in our study it was deduced from literature what the ecological consequences are and thus under which environmental conditions species with this trait are favoured or selected against.

Next, it was analysed for each nest founding mode which other traits co-occur and what the consequences of these trait combinations are. Specifically it was analysed what combinations of traits could counter or amplify the ecological consequences of the main nest founding mode and what new limitations arise from these additional traits. At the end of this exercise all species with similar ecological responses were grouped into the same life-history strategy, thus partially grouping species differing in some single traits. In this way we created a limited number of functionally different life-history strategies with clear predictions with respect to their response to specific environmental factors.

2.5. Data analysis

For each of the identified strategies we tested whether the number of species per pitfall trap series differed between sites using a Kruskal–Wallis test. For each strategy that showed a significant difference in the number of species per site we best fitted regression curves between the number of species and specific environmental factors, using the Akaike information criterion (AIC). The choice for environmental factors to be included followed the species–environment relationships predicted from the theoretically derived life-history strategies. In addition we explored the effect of the management regime on the changes in soil temperature during the summer season. Using an ANOVA we tested whether the soil temperature on a warm day in spring (May 12) and summer (August 6) differed between sites where vegetation was removed in summer (summer management; Table 1) and sites where management was only executed in autumn and winter. Likewise we tested whether the change in soil temperature between

these dates differed between sites with and without summer management.

3. Results

3.1. Life-history strategies

In total 35 ant species were caught. The life-history traits of these species are listed in Appendix A. There were four main modes of colony founding: (i) nest-splitting, (ii) social parasitism, (iii) semi-claustal founding (queens forage during nest foundation) and (iv) claustal founding (queens feed their first batch of workers by metabolizing their own nutritional reserves). The consequences of these nest founding modes described in literature are given in Table 2, along with the consequences of all co-occurring traits. The ecological background to these consequences is further explained in Appendix B. Ecological consequences of the nest founding modes and co-occurring traits were found to revolve around the time-window for initial colony founding, food availability during founding and dispersal limitations. The time-window for initial colony founding is strongly linked to site temperature as the time ant larvae need to develop increases greatly with decreasing temperature (Kipyatkov, 1993; Kipyatkov et al., 2004; Wagner et al., 1984). This means that species with a narrow time-window for initial development are restricted to nest founding locations that are relatively warm to ensure the completion of the development of the first worker batch before the onset of winter.

Based on the ecological consequences of the occurring trait combinations we arrived at four functionally different life-history strategies. All species with nest-splitting or parasitic founding as main nest founding mode are poor dispersers between habitats and were therefore grouped to form strategy D (13 species). Due to the availability of workers during the nest founding phase they

are much less affected by low food availabilities and low soil temperatures during nest founding. All semi-claustal and claustal species are reasonably good dispersers. The semi-claustal species are limited to sites with high food availability as their queens have to forage by themselves to feed their first batch of workers. They were grouped to form strategy F (11 species). The claustal species are not affected by the food availability during nest founding, as claustal queens feed their first worker batch from their own nutritional reserves. Some claustal species however, have a very narrow time-window for initial colony founding. The time available for development of the first batch of workers is determined by the species' phenology (timing of the nuptial flight and egg laying), its overwintering stages and its development speed. Time-constrained species are restricted to warm locations to complete development of the first worker batch before winter. All claustal species with a narrow time window were grouped to form strategy T (seven species). The fourth strategy, G (four species), consists of species which are all claustal, but with a broader time-window for initial development. These are more generalist species that are well adapted to cope with both low food availability and low temperature and are reasonably good dispersers.

3.2. Ant species richness

For strategies F and G the average number of species per pitfall trap series does not differ between sites (strategy F, $\chi^2 = 12.149$, $p = 0.205$, $df = 9$; strategy G, $\chi^2 = 15.038$, $p = 0.090$, $df = 9$; Fig. 2). The number of species from strategy T, which need a high temperature during nest foundation before the onset of winter, does significantly differ between sites ($\chi^2 = 23.403$, $p = 0.005$, $df = 9$). This is also the case for the average number of species from strategy D, which are all limited in their colonization ability ($\chi^2 = 23.019$, $p = 0.005$, $df = 9$).

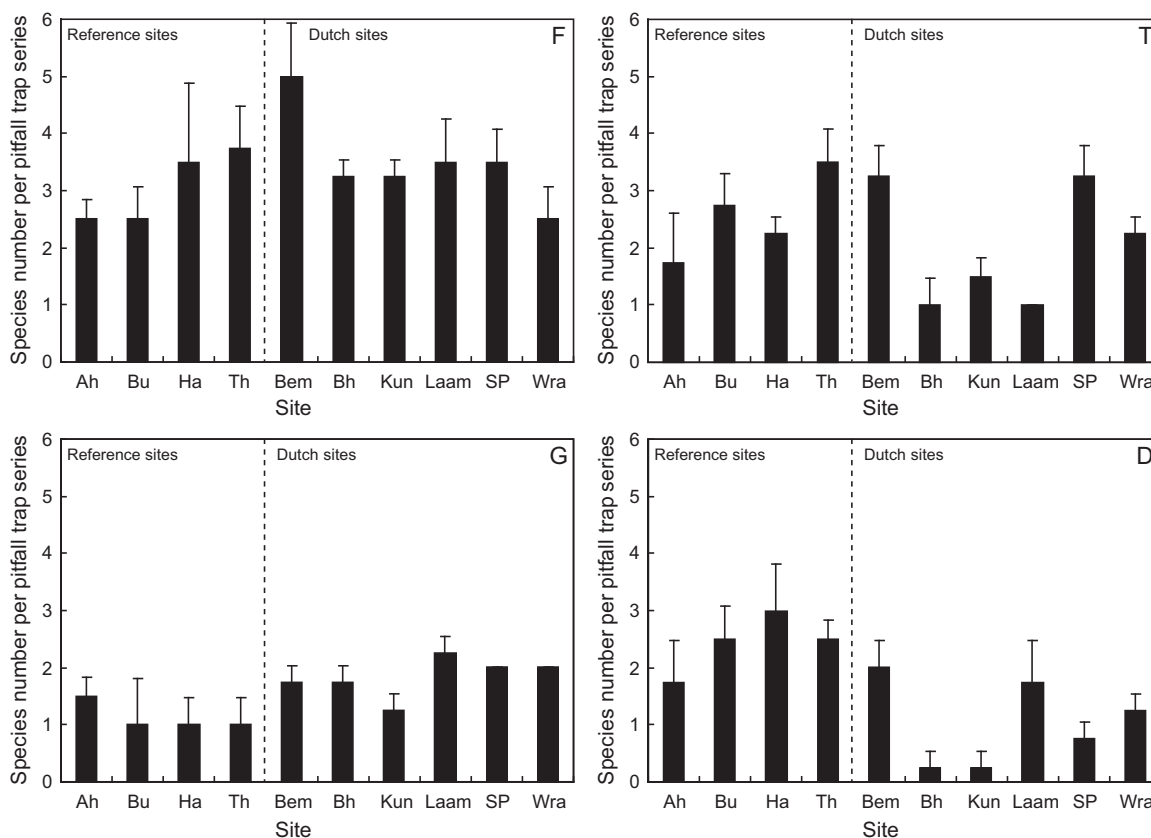


Fig. 2. Mean number of species per site (+SE) for strategy F, T, G and D. Ah, Bu and Ha are German sites, Th is located in Belgium and Bem, Bh, Kun, Laam, SP and Wra are Dutch chalk grasslands.

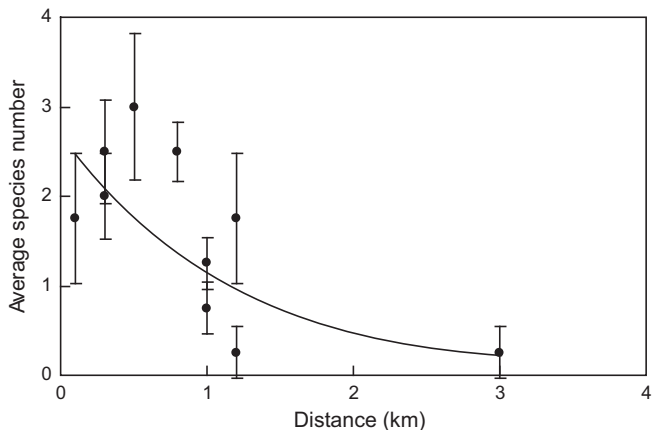


Fig. 3. Relation between the distance to the next nearest chalk grassland site and the mean number of species from strategy D per site (\pm SE). The significant exponential regression is plotted with the data ($R^2 = 0.578$, $p = 0.011$, $df = 9$).

3.3. Site isolation

The degree of isolation, defined as the distance between the study sites and their next nearest chalk grassland, ranges from 0.1 to 3.0 km. The relation between this distance and the average number of species from strategy D per site is best described by an exponential regression (Fig. 3). With increasing distance to the next nearest chalk grassland there is a significant exponential decline in the number of species from strategy D ($R^2 = 0.578$, $p = 0.011$, $df = 9$).

3.4. Temperature

The relations between the soil temperature on five warm days throughout the year and the number of species from strategy T per pitfall trap series are best described by linear regressions (Table 3). In summer and autumn (August 6, September 11 and November 8) there is a strong correlation between the soil temperature and

Table 3
Linear regression results for the relationship between the average daily temperature on five warm days and the number of species from strategy T.

Date	R^2	p	df
May 12, 2008	0.265	0.024	19
June 24, 2008	0.167	0.066	21
August 6, 2008	0.464	0.001	23
September 11, 2008	0.335	0.009	19
November 8, 2008	0.381	0.008	17

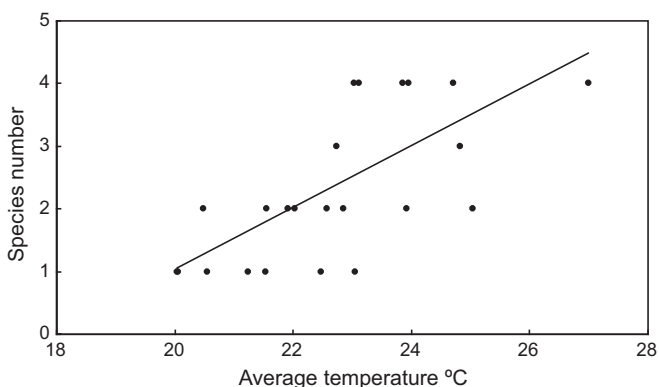


Fig. 4. Relation between the average soil temperature on a warm day in August (August 6, 2008) and the number of species from strategy T per pitfall trap series. The significant linear regression is plotted with the data ($R^2 = 0.464$, $p < 0.001$, $df = 23$).

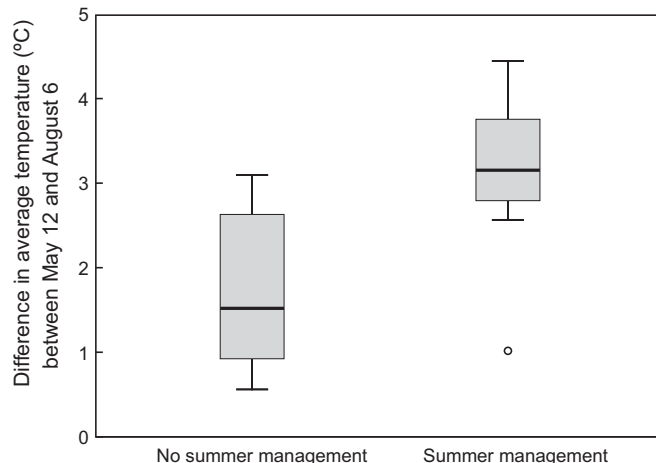


Fig. 5. Boxplot showing the significant difference (ANOVA $F = 6.360$, $p = 0.024$, $df = 15$) in the change in soil temperature between May 12 and August 6, 2008 between sites with and without summer management.

the number of species from strategy T (Fig. 4). In spring the correlation between the soil temperature and the number of species from strategy T is less pronounced (May 12) or not significant (24 June). Within each sampling location soil temperatures throughout the season are strongly autocorrelated (Pearson correlation > 0.75 , $p < 0.003$). There is however a significant effect of management timing on the changes in soil temperature during the summer season (ANOVA $F = 6.360$, $p = 0.024$, $df = 15$; Fig. 5). Sites that are managed in summer are significantly warmer in August than sites that are only grazed or mown in winter (ANOVA $F = 17.342$, $p < 0.001$, $df = 22$), while there is no difference in soil temperature between these sites in May (ANOVA $F = 2.069$, $p = 0.168$, $df = 18$).

4. Discussion

By grouping species according to the ecological consequences of their reproduction, development, synchronization and dispersal traits we could assign the 35 ant species found in our study sites to four functionally different life-history strategies. We identified three main variables which will differently affect ants with different life-history strategies; the degree of isolation of their habitat, the temperature during nest founding before the onset of winter and the food availability during nest founding. Tests of these theoretically predicted responses matched field observations; time constrained species strongly responded to summer soil temperature, whereas dispersal limited species showed a strong relationship with site isolation. While food availability and habitat isolation in relation to a species' dispersal capability are of obvious importance, low temperature has also previously been identified as one of the most critical stress factors for ant communities (Andersen, 1995).

4.1. Bottlenecks for ants in Dutch chalk grasslands

The aim of our study was to use the mechanistic understanding of species–environment relationships to formulate management recommendations to improve the status of the ant fauna in the study sites. From the complex web of environmental factors affecting the study sites (site size, habitat isolation, aspect, inclination, current management, management history, eutrophication and past abandonment) we have identified two main issues affecting the ant fauna; the degree of habitat isolation and the soil

temperature in summer. Both of these issues are connected to different types of management efforts.

4.1.1. Habitat isolation

Our results show that the number of ant species from strategy D decreases exponentially with increasing distance to the next nearest chalk grassland. This implies that at more isolated sites species from strategy D cannot reach these sites once they have disappeared. Whether ant species will actually disappear from a site is related to habitat quality (Dauber et al., 2005, 2006). It is likely that in some or most Dutch sites past degradation has caused local extinctions, while in other sites the habitat quality has always been suitable for these species. Incorporating detailed data on the site history would therefore shed more light on the exact relation between site isolation and recolonization probabilities. It is clear however, that at sites which are more than one kilometre apart from their next nearest chalk grassland, and especially at sites as isolated as Kunderberg, species from strategy D are severely threatened. So far, studies on the effects of isolation and fragmentation on ants in temperate grasslands have mainly focused on fragment size rather than isolation itself (Dauber et al., 2006), although site isolation has previously been suggested to be of importance (Mabelis and Verboom, 2009). Our results show that management actions aimed at counteracting habitat isolation are of prime importance for the conservation of ant communities in these sites. For species from strategy D small steppingstones in the landscape are insufficient (see Appendix B). The most effective management actions are to optimize and enlarge existing chalk grassland sites in order to promote species persistence and to create new nutrient-poor grasslands in close proximity to existing sites.

4.1.2. Summer soil temperature

We successfully tested the prediction that the soil temperature especially in summer and autumn is of great importance to the time-constrained species from strategy T. The soil temperature in chalk grasslands is affected by the aspect and the inclination of the site and by the vegetation structure, higher and denser swards being much cooler than short swards (Stoutjesdijk and Barkman, 1992). Sward height itself is strongly related to the management regime. Accordingly, we demonstrated an effect of management timing on soil temperature, with higher summer soil temperatures in sites that are mown or grazed in summer compared to sites that are only managed in autumn or winter. This temperature difference of about 2 °C in average daily temperature on a warm day is likely to indeed cause a significantly longer development time for worker larvae (Andrasfalvy, 1961; Kipyatkov, 1993; Kipyatkov et al., 2004). Species from strategy T can thus only occupy sites with a suitable aspect and inclination, if the management intensity and timing are sufficient to create an open sward with a sufficiently high soil temperature in summer. It seems that with the present increased nutrient levels in the Dutch chalk grasslands (Smits, 2010) management efforts that are restricted to autumn or winter are insufficient to produce such an open sward, causing the decline in species from strategy T. Previous studies have already shown that ant communities are strongly influenced by sun exposure (Dauber et al., 2005, 2006). Our study demonstrates that specifically the soil temperature in summer, during the period of nest founding before the onset of winter, is a key factor. This is crucial added information for formulating management measures. We would recommend site managers of chalk grasslands with increased nutrient levels to shift the main management period to the summer season (May–June), where necessary combined with low intensity autumn grazing. This is most likely also beneficial for the chalk grassland vegetation (Smits, 2010) as more nutrients are removed in this period. Summer mowing or grazing may however create new problems like insufficient nectar plants for butterflies and bees. Therefore,

sites should be divided into several compartments which are managed separately, with ample time between compartments to allow regrowth and reflowering of food plants. Such compartmentation also allows to tailor the management intensity to the local situation. In this way the negative effects of disturbance caused by management actions can be minimised, while optimising the vegetation structure. The management regime we propose here has already been applied successfully for several years in a number of chalk grasslands in the Viroin region (Belgium), which also tend to be inhabited by higher numbers of characteristic ant species (Dekoninck et al., 2007). This is however no guarantee for success as the nitrogen accumulation in the soil and the landscape configuration differ dramatically from the Dutch sites. Field testing of the proposed management alterations is essential to really improve management for chalk grassland ants.

4.2. Life-history strategies as a tool

The use of life-history traits to analyse species responses to their environment is growing rapidly (e.g. Bremner et al., 2006; Cristofoli et al., 2010; Lambeets et al., 2009). However, only a limited number of studies have incorporated interactions between traits, using aggregated traits (Öckinger et al., 2010) or life-history strategies (Siepel, 1995; Van Turnhout et al., 2011; Verberk et al., 2008a,b). One reason to use traits rather than strategies is that the compilation of meaningful life-history strategies is a very time consuming process. In addition, the compilation of strategies is often termed somewhat arbitrary, even though it is based on logic (Verberk, 2010). From an ecological perspective however, one could argue that ignoring the interactions between traits completely or weighing all traits equally, as is done in multivariate statistical analyses (clustering, ordination), is equally arbitrary if not more so. Within species, traits are not independent, they are linked to form an integrated response to particular ecological problems (Siepel, 1994, 1995; Stearns, 1976). The interactions among life-history traits can be essential to understand species responses to their environment (Davies et al., 2004). Our case study illustrates this. Single traits like the timing of the nuptial flight, the period of initial egg-laying, the development stages capable of overwintering and the development speed of worker larvae did not show clear ecological consequences. Only when taken together, it becomes clear that the time-window for initial colony founding differs between species, causing some species to be restricted to warm habitats.

The explicit incorporation of trait interactions and the deduction of ecological consequences by way of logical reasoning are the main advantage of the life-history strategy approach. It gives insight into the mechanisms underlying species–environment relationships, providing clear testable hypotheses (see also Verberk et al., 2010b). This increases our understanding regarding which conditions are most important for the species group under study. Our case study, for example, revealed that specifically soil temperature in summer and early autumn is an important parameter for ants in chalk grasslands, rather than soil temperature in general. This led to the specific hypothesis that summer management is essential, which is confirmed by our field data. Multivariate top-down approaches and single-trait approaches would likely have overlooked this factor. Without the specific ecological knowledge derived from the combinations of life-history traits, researchers would have measured soil temperature with no specific timing, likely missing the effect of summer management. In addition, the life-history strategy approach enabled us to pinpoint the main factors shaping the ant species composition even though the study sites differed with respect to a large number of environmental factors. Strategies can be represented by different species in different sites making it possible to compare sites with different local species pools, for example located in different geographical regions. The

use of life-history strategies also decreases the biasing effects of stochastic extinction and colonization patterns for single species, which for example, severely hamper the usefulness of single indicator species (Andelman and Fagan, 2000). The mechanistic character of our approach is an essential difference to the earlier classifications of ants by Andersen (1995) based on functional groups, taxonomy and habitat requirements (generalist/specialist).

5. Conclusion

The life-history strategy approach is a valuable tool to get insight in the factors shaping the local species composition. It is especially valuable to disentangle and ascertain the importance of factors related to either local habitat suitability or regional connectivity (Verberk et al., 2010b). Life-history strategies function as indicators for specific ecological processes, focusing on those processes that are most important to the species group under study. The general method here demonstrated on ants in chalk grasslands can be used for all organisms and ecosystems. The life-history strategy approach is a valuable alternative to the use of single indicator species and to top-down approaches that try to identify key factors by analysing the variation in environmental parameters. The most important advantage of this method is that it provides understanding of the underlying mechanisms. In effect, it compares processes rather than the occurrence of single species. These features make this method especially suitable to translate species–environment relationships into practical management measures.

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Appendix A. Life-history traits of captured ant species

Table A1

Appendix B. Theoretical back-ground to the ecological consequences of occurring trait combinations.

B.1. Claustral and semi-claustral (independent) founding

Both claustral and semi-claustral queens feed the first batch of worker larvae by themselves. During the nest founding phase they have no workers to collect food and no large nest with improved microclimatic conditions. In claustral queens the amount of food available for raising the first batch of workers is predetermined at the moment the queens start nest foundation, while in semi-claustral queens food is gathered throughout the nest founding stage. This enables semi-claustral queens to produce more and bigger workers when food is prevalent, but also causes brood failure when food is too scarce (Johnson, 2006). Claustral species are not limited by the food availability during founding, but in these species the founding phase is limited in time, as queens will not be able to survive more than one winter on their nutritional reserves

(Andrasfalvy, 1961). Claustral species thus need to have workers by the end of the second summer to take up foraging tasks, while semi-claustral species are not affected by this time-constraint. The time window for larval development is further determined by whether species start laying eggs directly after their nuptial flight or postpone egg-laying until spring. The development time of ant larvae is strongly temperature dependent (Kipyatkov et al., 2004; Wagner et al., 1984). Therefore, the time window, combined with the rate of larval development and the larval instar capable of overwintering determines to what extent species are constrained to warm nest sites. Claustral and Semi-claustral species which start laying eggs directly after their nuptial flight are restricted to warm nest sites if they have late nuptial flights, slow larval development or larvae that can only overwinter in late instar stages. Claustral species whose queens overwinter once before they start laying eggs are also restricted to warm nest sites if they have slow larval development, as they need to have adult workers within one season. The speed of larval development depends in the first place on intrinsic factors. The duration of ontogenesis from egg to pupa is much shorter for *Formica* species (20–25 days at 25 °C) than for *Myrmica* (e.g. *Myrmica rubra* 35 days at 25 °C) (Kipyatkov, 1993) or *Lasius* species (e.g. *Lasius niger* 40 days at 25 °C) (Kipyatkov et al., 2004). In addition, the speed of development in the founding phase can be enhanced by the presence of several founding queens (Sommer and Hölldobler, 1995; Waloff, 1957). Based on the timing of the first egg-laying period, the timing of the nuptial flight, the larval instar capable of overwintering and the speed of larval development, the claustrally founding ant species in this study could be divided into time-constrained (and thus temperature dependent) and non-time-constrained species. The time-window was defined as constrained if i) species have one season for complete development from egg to adult and have a low intrinsic development speed and no additional traits that speed up development (e.g. pleometrosis or availability of workers), ii) species have a high intrinsic development speed, but only half a season (nuptial flight no earlier than June) for complete development from egg to adult or iii) species have a low intrinsic larval development speed and only half a season for development from egg to last instar larva or an even shorter period for development from egg to first instar larva. By these definitions, a limited time-window and consequent high temperature dependence only occurred in the claustrally founding species in our study, not in semi-claustral species.

B.2. Nest-splitting

Nest-splitting is an effective way to avoid the workerless phase. It provides a queen from the start with an extensive worker force for nest building and food collection. However, in nest-splitting species new nests can only be established close to the old nest, since the whole group of workers and queen(s) needs to reach the new nest site on foot. Although this enhances local population expansion (Hölldobler and Wilson, 1990), it also severely limits the dispersal capabilities of these species between sites (Hölldobler and Wilson, 1990; Seifert, 2007). All mainly nest-splitting species in this study also have an alternative nest founding mode for dispersal over longer distances. *Tapinoma* species can additionally found nests independently and all mainly nest-splitting *Formica* species additionally found nests by social parasitism. As only a small proportion of all nests is founded through these additional strategies, long distance dispersal is still limited making these species especially prone to local extinction following isolation.

B.3. Social parasitism

Nest founding through social parasitism is also an effective way to avoid the workerless phase, supplying the queen not only with

Table A1

Ant species captured and their main traits per life-history strategy (S). The main literature source for each trait is given in every column head, additional sources are given in footnotes. The founding mode is semi-claustral (s-c), claustral (cl), independent claustral or semi-claustral (ind), by nest-splitting (ns) or parasitic (p). In addition founding can be haplometrotic (h) or facultatively pleometrotic (fpl). The colony growth mode is independent (ind) if own workers are produced or parasitic (p) if queens rely on host-workers throughout their life-cycle. The column 'Development speed' depicts the intrinsic speed of larval development. The period of the nuptial flight is given in 0.5 month intervals from April to October where white periods show main swarming periods and grey periods depict that some swarming events may occur. Larval diapause stage lists which larval stages are capable of overwintering. In the column 'first egg laying' '?' indicates that no specific information was found, but that the given 1st egg-laying period for newly mated queens is assumed based on the period of the nuptial flight.

S	Trait →	Founding mode	Growth mode	Development speed	Nuptial flight period	Larval diapause stage	1 st egg laying
	Source →	Seifert, 2007	Seifert, 2007	Kipyatkov, 1993	Seifert, 2007; Boer, 2010	Kipyatkov, 1993, 2001	Seifert, 2007
F	<i>Myrmecina graminicola</i>	s-c	independent	slow	■■■■■AASS■	unknown stage ^f	after diapause ^g
F	<i>Myrmica lobicornis</i>	s-c	independent	slow	■■■■■JAAS■	last	after diapause?
F	<i>Myrmica rubra</i>	s-c, ns	independent	slow	■■■■■AS■	last	after diapause ^g
F	<i>Myrmica ruginodis</i>	s-c, ns	independent	slow	■■■■■JAA■	last	after diapause ^g
F	<i>Myrmica sabuleti</i>	s-c ^a , ns ^d	independent	slow	■■■■■JJAAS■	last	after diapause ^g
F	<i>Myrmica schencki</i>	s-c	independent	slow	■■■■■JAASS■	last	after diapause ^g
F	<i>Myrmica scabrinodis</i>	s-c, ns	independent	slow	■■■■■AAS■	last	after diapause ^g
F	<i>Myrmica specioides</i>	s-c	independent	slow	■■■■■JJAAS■	last	after diapause
F	<i>Ponera coarctata</i>	s-c, fpl	independent	slow	■■■■■AASS■	none	after diapause ^g
F	<i>Stenamma debile</i>	s-c, ns, fpl	independent	slow	■■■■■SSOO	last	after diapause ^g
F	<i>Temnothorax interruptus</i>	s-c	independent	slow	■■■■■JJJAA■	unknown+egg	after diapause?
T	<i>Lasius (Lasius) alienus</i>	cl ^b , fpl ^c	independent	slow	■■■■■JJAAS■	all	directly ^c
T	<i>Solenopsis fugax</i>	cl, ns, h	independent	slow	■■■■■SS■	unknown stage ^f	after diapause ^h
T	<i>Tetramorium caespitum</i>	cl, h ^c	independent	slow	■■■■■JJJ■	last	directly?
T	<i>Tetramorium impurum</i>	cl, h ^c	independent	slow	■■■■■AASSOO	last	after diapause?
T	<i>Formica (Serviformica) cunicularia</i>	cl, ns, fpl	independent	fast	■■■■■JJJ■	none	directly?
T	<i>Formica (Serviformica) lusatica</i>	cl, ns, fpl	independent	fast	■■■■■J■	none	directly?
T	<i>Formica (Serviformica) rufibarbis</i>	cl, ns, fpl	independent	fast	■■■■■JJJ■	none	directly?
G	<i>Formica (Serviformica) fusca</i>	cl, ns, fpl	independent	fast	■■■■■JJJAAS■	none	after diapause
G	<i>Lasius (Cautolasius) flavus</i>	cl ^b , fpl	independent	slow	■■■■■JJA■	all	directly & after diapause
G	<i>Lasius (Lasius) niger</i>	cl ^b , fpl	independent	slow	■■■■■JJA■	all	directly & after diapause
G	<i>Lasius (Lasius) platythorax</i>	cl ^c , fpl	independent	slow	■■■■■JJA■	all	after diapause ^e
D	<i>Anergates atratulus</i>	p	parasitic	?	■MMJJJAA■	last ^c	directly
D	<i>Myrmica karavajevi</i>	p	parasitic	slow	■■■■■JJA■	last	directly?
D	<i>Lasius (Chthonolasius) fuliginosus</i>	p, fpl	independent	slow	■■■■■JJJJAAS■	all	directly
D	<i>Lasius (Chthonolasius) jensi</i>	p	independent	slow	■■■■■JJAASS■	all	directly
D	<i>Lasius (Chthonolasius) meridionalis</i>	p, fpl	independent	slow	■■■■■JJAASSO■	all	directly
D	<i>Lasius (Chthonolasius) mixtus</i>	p, fpl	independent	slow	■■■■■JAASSO■	all	after diapause
D	<i>Lasius (Chthonolasius) sabularum</i>	p	independent	slow	■■■■■ASSO■	all	directly & after diapause
D	<i>Lasius (Chthonolasius) umbratus</i>	p, fpl	independent	slow	■■■■■JJAASS■	all	directly
D	<i>Lasius (Dendrolasius) distinguendus</i>	p	independent	slow	■■■■■JJA■	all	directly?
D	<i>Formica (Formica) polyctena</i>	ns, p	independent	fast	■AMMJ■	none	directly
D	<i>Formica (Formica) pratensis</i>	ns, p	independent	fast	■AMMJJ■	none	directly
D	<i>Formica (Raptiformica) sanguinea</i>	ns, p	independent	fast	■■■■■JJJJA■	none	directly
D	<i>Tapinoma erraticum</i>	ns, ind ^c	independent	?	■■■■■J■	first	directly

^aAll non-parasitic *Myrmica* species exhibit semi-claustral colony founding and nest-splitting (Seifert, 2007).

^bKutter, 1977 and Dumpert, 1978 in Keller and Passera (1989).

^cP. Boer personal observation.

^dSchoeters and Vankerkhoven (2001).

^eStitz (1939).

^fEidmann (1943).

^gUnpublished data of first and second authors suggest queen foraging after diapause.

^hAndrasfalvy (1961).

an extensive worker force, but also with an existing nest with thermoregulation capacities. Parasitic nest founding does not in itself restrict the dispersal capabilities of ant species, but it does limit their distribution. Parasitic species can only inhabit sites with a sufficiently large and stable host population (Holt et al., 1999). Therefore, they are more prone to local extinction (Cronin, 2004) and they cannot use isolated host populations in a landscape as steppingstones from which they could more easily reach suitable habitats (Mabelis, 1994; Mabelis and Chardon, 2006; Mabelis and Korczyńska, 2001). This means that parasitic species will be more susceptible to effects of isolation than independently founding species. This effect will be most pronounced in the permanently parasitic species which do not produce own workers and thus need a steady supply of new host colonies, given the limited life-span of host workers (Seifert, 2007). Colonies of temporarily parasitic species can live-on independently for a substantial period enabling them to survive in sites with a smaller host population or even to overcome a short period of host absence. This is especially true for the temporarily parasitic species that also exhibit nest-splitting as they have an alternative strategy to reproduce locally. However, these species are more limited in their colonization capacity because only a small fraction of the reproductive effort is invested in long-distance nest founding by individual queens.

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