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Life span in the wild: the role of activity and climate in natural populations of bees

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Summary

1. Animal life span is constrained by ecology and physiology. The latter has been studied under controlled conditions, but little is known about determinants of life span under natural conditions.

2. We studied the relationships between length of adult life, magnitude of foraging activity, and environmental abiotic conditions in two bee species: a pollen specialist *Andrena vaga* (Andrenidae) and a pollen generalist *Anthophora plumipes* (Apidae).

3. Our research indicates that life span is driven both directly by climate and indirectly through climate-dependent activity patterns. We found a negative relationship between proportion of active days and length of life; in contrast, a high activity rate within the active days had no negative effect on longevity.

4. Individuals active during warm and/or wet days lived longer, with precipitation being a more important determinant of life span than temperature.

5. Timing of the first appearance at the site was also an important predictor of bee life span. Individuals that first appeared closer to the end of season (critical time horizon) lived a shorter time than individuals observed earlier. The first observed active day in the season was also correlated with seasonal temperature and precipitation.

6. We demonstrate that life span and activity patterns of wild populations of insects are regulated by a tractable interplay of ecological (mostly climatic) variables that were previously studied only in isolation or *in vitro*.

Key-words: behaviour, critical time horizon, foraging, life history, moisture, temperature, weather

Introduction

Life span has traditionally been considered to depend on ecological and physiological constraints (Stearns 1992). The latter has been intensively studied under controlled conditions, with a special emphasis on metabolic rates (Speakman 2005). Metabolic rates depend on the body temperature and activity of individuals (Brown *et al.* 2004), factors that both depend on ambient temperature in insects (Miquel *et al.* 1976; Sohal, Donato & Biehl 1981). Interestingly, effects of activity and temperature on life span have rarely been studied under natural conditions (*in situ*), where they interplay with ecological factors such as

predation, disease, food availability or environmental stochasticity (Stearns 1992; Kawasaki *et al.* 2008; Monaghan *et al.* 2008).

The effect of activity on insect adult life span was documented in laboratory studies where flight activity was manipulated in *Drosophila melanogaster* and *Musca domestica* (Sohal & Buchan 1981; Magwere *et al.* 2006). Intensive flight activity in both species causes oxidative damage to some proteins and lipids, resulting in a shorter life (Yan & Sohal 2000; Magwere *et al.* 2006). Although the influence of metabolic stress is obvious, there is some evidence that even moderately high activity has a positive effect on life span in some vertebrates (Lee, Hsieh & Paffenbarger 1995; Navarro *et al.* 2004) and insects trained for regular activity regimes (Niitepõld & Hanski 2012). Metabolic stress from activity can be the reason why long-lived

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queens of eusocial insects (ants or termites) drop their wings as early as possible or why they reduce flight to a minimum (bees) (Wilson 1971). In contrast, solitary insects cannot avoid the costs of high flight activity, which is necessary for their own feeding or provisioning of a brood. However, they can modulate their behavioural strategy depending on the actual conditions they experience, and they can optimize their behaviour according to an evolutionarily stable strategy (Maynard Smith 1978). Experimental studies show that some bees can individually optimize their own life strategies to forage with maximum efficiency (Schmid-Hempel, Kacelnik & Houston 1985; Schmid-Hempel 1987).

Although there are *in situ* studies on the effects of climate on insect life histories (Vicens & Bosch 2000; Walther *et al.* 2002; Bartomeus *et al.* 2011), these studies do not address the impact of climate on the actual length of life. Yet, it is known that temperature has a characteristic effect on the survival and development of various insect instars (Dixon *et al.* 2009). For example, survival of adult bees was shown to be negatively affected by the temperature and duration of overwintering of larval stages (Bosch & Kemp 2004). It has also been shown that changes in the temperature-dependent activity of predators can cause a shift in the mortality of foraging insect prey (Logan, Wolesensky & Joern 2006). Finally, Tauber *et al.* (1998) noted that broad ignorance and underestimation exists regarding the effect of moisture on insect life. We thus expect that climatic conditions are critical *in situ* determinants of life span and activity patterns of solitary insects.

We present an empirical exploratory analysis of ecological correlates on the length of active life in natural conditions in adults of two solitary bee species. The analysis is based on a large data set consisting of daily observations of hundreds of individual bees of both species over several years. Specifically, we test the prediction that adult bees with high foraging activity should have a shorter life span than bees with low activity. We also investigate how the life span of solitary bees depends on environmental conditions, such as temperature, sunshine, precipitation and pollen availability, as well as on the proportion of active days, foraging time per day or date of first appearance of a bee at the nesting site.

Materials and methods

SPECIES STUDIED

We studied the above-mentioned phenomena *in situ* in two solitary bee species: *Andrena vaga* Panzer (Andrenidae) and *Anthophora plumipes* (Pallas) (Apidae). These species belong to phylogenetically distant bee lineages (Danforth *et al.* 2006).

Andrena vaga (Fig. 1a) is an oligolectic solitary bee that becomes active between mid-March and the beginning of May (Westrich 1990; Rezkova *et al.* 2012). Females (12–15 mm in body length) collect large pollen loads predominantly on *Salix* trees (Bischoff, Feltgen & Breckner 2003). *Andrena vaga* builds about 20–70 cm deep nests in sandy soils in sunny locations and closes the nest entrance with soil every time it leaves (Fig. 1b).

Anthophora plumipes (Fig. 1c, d) is a solitary bee that is active between the end of April and the beginning of June (Westrich 1990). Females (14–15 mm in body length) make short and frequent foraging flights and collect small pollen loads from a wide range of plant species (Westrich 1990). *Anthophora plumipes* builds 5–10 cm deep nests with an open entrance in either horizontally or vertically positioned patches of bare soil (Fig. 1d).

The two species differ in the way they regulate body temperature. Although both species are heterotherms, *Andrena* is able to moderately increase body temperature through active muscle work
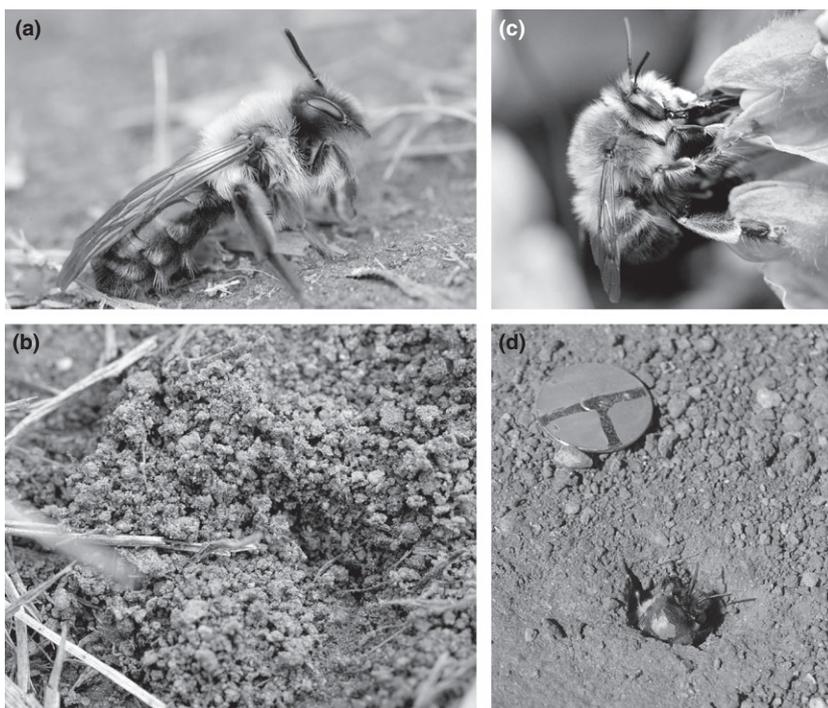

Fig. 1. *Andrena vaga* (a) and its nest entrance covered by soil (b); *Anthophora plumipes* on a flower (c) and an individually marked female sitting in the nest entrance (d). Photograph credits: P, Krásenský (a, b, c) and K, Doležalová (d).

(called endothermic heating or warm-up) (Stone & Willmer 1989). *A. plumipes* is known for its high endothermic warm-up rates (Stone & Willmer 1989; Stone 1993).

FIELD DATA COLLECTION

The observations of *Andrena vaga* females (N = 539) were performed at a nesting site close to the Čelákovice village, Czech Republic (north-eastern periphery of Prague, 50° 10′ N, 14° 45′ E), between the end of March and the end of April in 2007 and 2008 (see Table S1 for details in Supporting Information). The studied nest aggregation is situated on alluvial sand with patches of grass on the margin of a secondary oak and pine forest. The observations of *Anthophora plumipes* females (N = 334) were performed at a nesting site in Praha-Strahov, Czech Republic (50° 05′ N, 14° 24′ E), between early April and early June in 2007, 2008, 2009 and 2010 (see Table S1 for details in Supporting Information). Both species were observed daily except for days with heavy or continuous rains (*c.* >10–20 mm) in the morning. Nesting sites were visited in most days with no rain (0·0–0·4 mm), light rain (*c.* 0·4–20 mm) or rain showers.

We individually marked all females as they gradually appeared at the nesting sites during the season. The first observation of a bee is considered as the first active day, though its exact emergence day and previous activity is not known. The marking was performed using 6–8 different oil-based colours, and every specimen received a unique combination of three coloured spots on the scutum and metasomal terga. We followed the observation methods described previously (Rezkova *et al.* 2012). For each marked female observed on the nesting site, we recorded its colour mark, type of activity (leaving nest or returning) and exact time (in hours and minutes). Bees were usually observed from 9–10:00 a.m. to 5–6:00 p.m., with shorter time on days when few or no bees were active. The resulting variability in the time (in hours and minutes) spent each day observing at the field site is considered in the analysis of the daily activity of bees (Table 1). This method allowed us to monitor bee activities across the whole season as well as within days.

Daily and annual climatic data (Table 1) were acquired from two local meteorological stations of the Czech Hydrometeorological Institute situated within 10 km from the nesting sites. Data on the amounts of pollen grains in the air (per m^3) were acquired from three stations for monitoring of allergens in the air (Praha,

Table 1. Overview of variables that were used in *Andrena vaga* (N = 425) and *Anthophora plumipes* (N = 334) analyses

Variable name	Description	*Andrena*			*Anthophora*		
		Mean	Median	Min–max	Mean	Median	Min–max
Length of life	Number of days between the first and last observation of an individual	15·1	14	4–38	14·01	13	4–41
Number of active days	Number of days, when the bee was observed outside of the nest	6·38	5	2–21	5·48	4	2–29
Relative activity	Number of active days/Length of life	0·44	0·43	0·07–1	0·42	0·4	0·08–1
First active day in year	The day when the animal was first observed as being active; counted as number of days since the 1st of January.	100·2	101	87–123	121·3	119	94–157
Year	Season temperature and season precipitation are coupled in *Andrena* bees to a single variable				Not applicable		
Season temperature		Mean temperature in a given year [°C] (1.iii.–31.v.): 2007: 10·2 °C 2008: 8·6 °C			Mean temperature in season [°C] (1.iv.–15.vi.): 2007: 15·6 2008: 13·3 2009: 14·6 2010: 12·7		
Season precipitation		Sum precipitation in a given year [mm] (1.iii.–31.v.): 2007: 60·1 2008: 134·0			Sum precipitation in season [mm] (1.iv.–15.vi.): 2007: 70·2 2008: 171·8 2009: 140·0 2010: 169·7		
Relative time of activity during active days	Mean proportion of time (within the daily observation period) during which the bee was active and outside of the nest.	0·19	0·18	0–0·56	0·32	0·32	0–0·86
Temperature during active days	Mean daylight temperature during active days [°C]	12·38	12·37	6·2–17·6	14·33	14·26	9·65–21
Precipitation during active days	Sum of precipitation during active days [mm]	2·7	2	0–12·8	8·97	5·9	0–60·7
Sunshine during active days	Mean sunshine during active days [h]	9·15	9·14	1·1–12·7	6·41	6·55	0–13·5
Pollen availability during active days [pollen grains in air]	Mean number of pollen grains from willow trees collected in 1 m^3 of air during active days. Mean from three monitoring stations.	8·67	8·71	1–22	Not applicable		

Plzeň, and Brno). All data used in this study are accessible for the public at www.aculeataresearch.com.

PREPARATION OF DATA ON LIFE SPAN AND RELATIVE ACTIVITY

Our study is specifically focused on explaining variability of two response variables. First, *length of life* (life span), which was measured as the number of days between the first and last observation of the individual during the season. We are aware of a caveat: although *A. vaga* and some other bee species with aggregated nests are known for their philopatry (Rosenheim 1990; Bischoff 2003), we could not rule out that some individuals emerged elsewhere outside of the observed nesting site or that they moved away from the site during the season. For this reason, the observed values of life span (and first active date) are used as approximate estimates of real values and should be interpreted as such. The second response variable was *relative activity* (proportion of active days during life), which could be viewed as 'density' of active days within the whole life span. Bees are generally not active every day of their life regardless of the weather conditions (Minckley *et al.* 1994); thus, the active day was defined simply as a day on which a given individual was observed outside of its nest. Although we collected the activity data at fine temporal scale (i.e. minutes and hours), we decided to aggregate data to days as observation periods. While the observation periods were not exactly constant during each day, we did not discard the fine temporal information entirely and instead used it to create the variable *relative time of activity during active days* (Table 1), which standardizes the time of daily activity (in minutes) by the total length of daily observation period (in minutes). All variables are listed and summarized in Table 1. We included only individuals with a life span longer than 4 days; all of the short-lived individuals were discarded from the data set.

STATISTICAL ANALYSES

Our main focus was to explain variability in observed life span and relative activity in *Andrena* and *Anthophora* bees. We hypothesized that life span can be influenced by environmental conditions, such as temperature; relative foraging activity, which may also be influenced by environmental conditions (Schmid-Hempel & Wolf 1988); or the date of first active day.

To identify which factors might be the most important potential predictors of life span in both species (Table 1), we employed regression trees based on binary recursive partitioning (package 'tree' in R) (Breiman *et al.* 1984). Regression trees are ideal for such purposes as they are simple, they require no assumptions about the distributions of the data, and they provide a good preliminary picture of data structure (Crawley 2012). We set the within-node deviance to be at least 0·03 times that of the root node (the default is 0·01 in function 'tree') so that the tree would not be overly detailed and could be easily plotted.

Following the regression tree analysis, we performed two sets of generalized linear models [GLM; function glm() in R] for each of the species. The first set of models used life span as a response variable (Gaussian family); the second set of models used the relative activity of individual bees as a response variable (binomial family, logit link). Note that the latter model takes into account the total number of trials (i.e. life span) and successful outcomes (i.e. active days) so that 1/2 is treated differently from 10/20 (although the proportion is 0·5 in both cases). We additionally carried out analyses relating the first active day to seasonal variables (year, seasonal temperature, and seasonal precipitation). For *A. vaga*, we performed a Wilcoxon test to compare the first active day between the years 2007 and 2008 (for this species, we only had data from two seasons). For *A. plumipes*, we performed GLM (Gaussian family, identity link) explaining first active day by seasonal temperature and precipitation (four seasons available).

To find a robust minimum adequate model, we used both stepwise backward deletion (predictors are deleted from the full model) and forward addition of predictors (predictors are added to the full model). In both cases, we first fit the full model with all explanatory variables in their linear and polynomial forms. We used AIC both during the selection process and to compare the resulting models. If the two models were indistinguishable during the stepwise procedure (ΔAIC<2), we retained the model with the lower number of predictors. We checked the resulting models to determine whether any of the terms could be replaced by a polynomial or linear form, or by any of the variables that were already deleted. In the case of length of life, we attempted to add interactions between temperature and precipitation during active days and between first active day and precipitation, temperature, precipitation and sunshine during active days. However, none of these interactions considerably reduced the AIC of the minimum adequate models.

Burnham and Anderson (2002) advise reporting not only the minimum adequate models but also other candidate models. However, our best models very clearly outperformed all of the other candidate models (ΔAIC>10). Deletion of the least important variables from the best models did not change the standardized coefficients of the remaining variables substantially. Additionally, the best models were consistent between the two different species and were congruent with results from the regression trees. Finally, the potentially misleading rate of collinearity between predictors was low (see Table S2 for details in Supporting Information). Therefore, we considered our results to be robust (more so given the large *n*), and we only report the best-fitting minimum adequate models in the results section.

We report the best models by plotting the partial residuals for each variable, in addition to reporting the standardized coefficients for each variable (the 'betas' in statistical literature). In addition to the percentage of explained deviance, these results give very detailed insight into the structure of the models and their explanatory power.

Results

LIFE SPAN

Both the regression trees and the best-fitting GLMs using life span data explained a large proportion of the variability in life span within both species (ranging from 57·9 to 72·9%; Figs 2 and 3), indicating that we captured important ecological predictors. In both species, the most important predictors of life span were relative activity (higher activity led to shorter life span), first active day in the year (the later an individual appeared, the shorter it lived), and precipitation during active days (individuals that were active during wet days lived longer than those that were active during dry days) (Figs 2 and 3). This finding was demonstrated independently by both the regression tree analysis (Fig. 2) and the GLMs (Fig. 3). Both species showed annual differences in life span: they lived longer in colder years (Fig. 3).

In *Andrena* bees, we also detected a unimodal effect of temperature during active days, a positive effect of sunshine during active days, and a negative effect of pollen
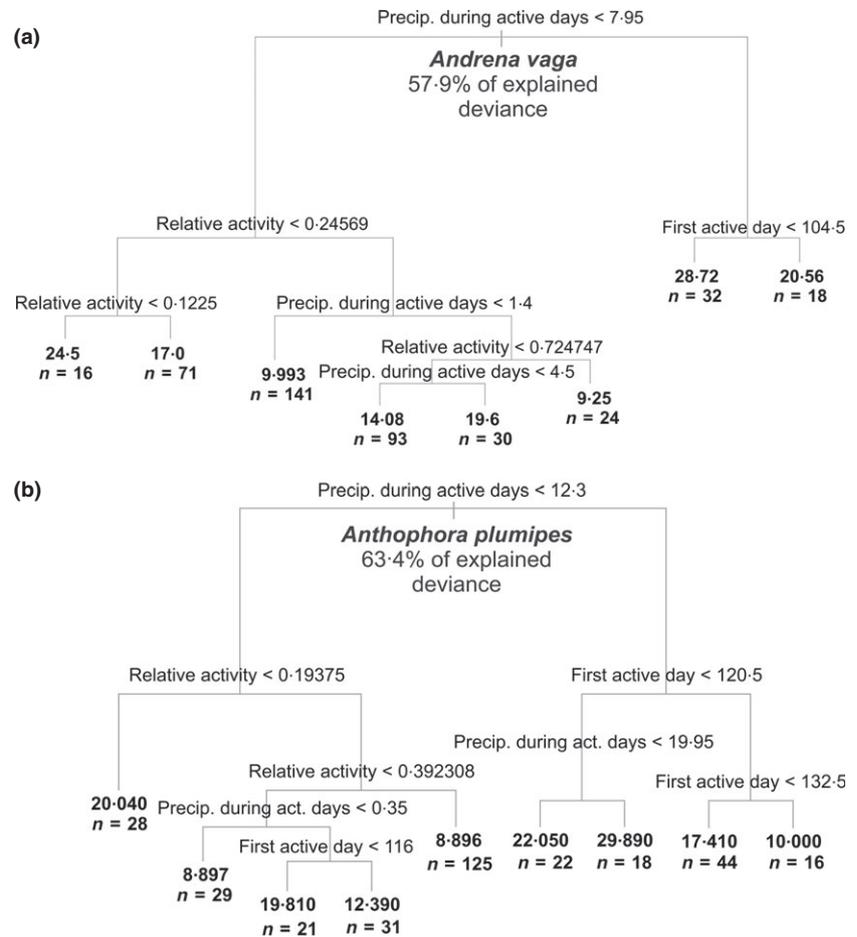
Fig. 2. Regression trees explaining the *life span* of the two bee species; *Andrena vaga* (a) and *Anthophora plumipes* (b). The trees are based on binary recursive variance partitioning. We used all variables from Table 1. Names of the splitter variables and their split values are indicated at each node. Mean values of life span and the number of individual bees (*n*) in each terminal group are given at each terminal branch. For more details on the predictors, see Table 1.

availability on life span. In *Anthophora* bees, the effect of temperature during active days was positive but weak (Fig. 3). We also detected a weak positive effect of relative time of activity during active days on life span.

RELATIVE ACTIVITY

Note that, as we demonstrated above, relative activity was an important predictor of life span. Therefore, any predictors of relative activity also ultimately influence life span. In both species, we found that the most important predictors in the best-fitting GLMs of relative activity (Fig. 4) were the date of the first active day in the year (positive effect), the precipitation during active days (positive effect), and the relative time of activity during active days (positive effect) (Fig. 4). We also detected a negative effect of temperature during active days on relative activity in both species (Fig. 4). Neither year nor the seasonal climatic variables made it to the final best model explaining the relative activity of *A. plumipes*.

In *Andrena* bees, relative activity was higher in the warmer year, 2007, and in bees that became active during days with high pollen availability (Fig. 4). In *Anthophora* bees, none of the seasonal climatic variables or year seem to be an important predictor of relative activity. There was,

however, a striking positive effect of sunshine during active days detected in *A. plumipes*, and the negative effect of temperature on relative activity was much stronger in *A. plumipes* then in *A. vaga* (Fig. 4).

FIRST ACTIVE DAY

The first active day is a nonclimatic variable that was found to have a strong effect on the life span in the previous analyses. Thus, we also checked whether variability in the first active day could be related to some of our seasonal climatic variables. We found that *Andrena* bees became active earlier in the warmer year, 2007 (Fig. 5). Similarly, in *Anthophora* bees, we found that individuals become active earlier in warmer and in wetter years (Fig. 5).

Discussion

As hypothesized earlier, the length of active life should depend on factors such as climatic conditions, food resources, activity regime, predation and parasites. However, such a correlation has rarely been demonstrated using *in situ* data. Our results show that ecological variables do have a detectable effect on the life span
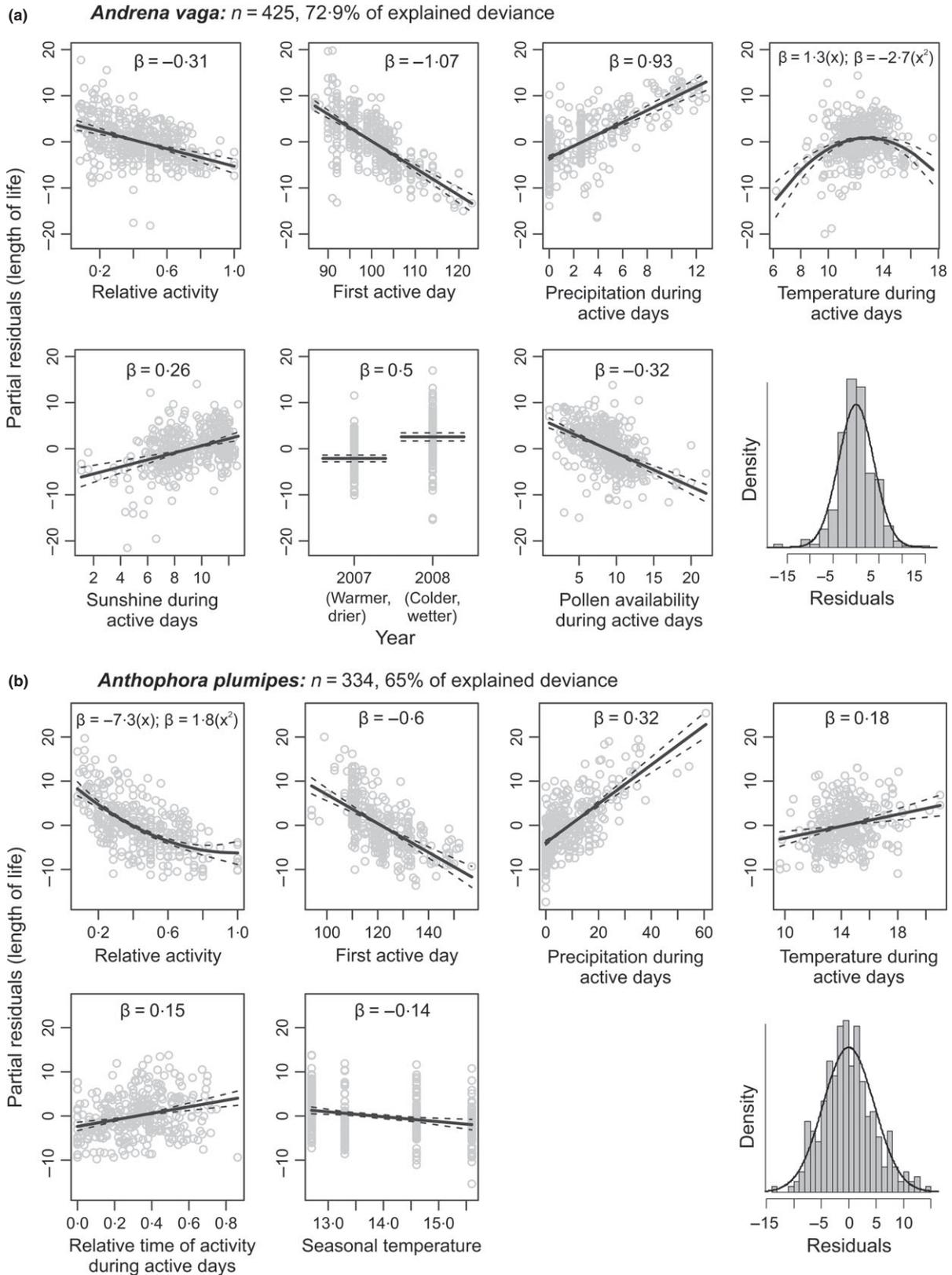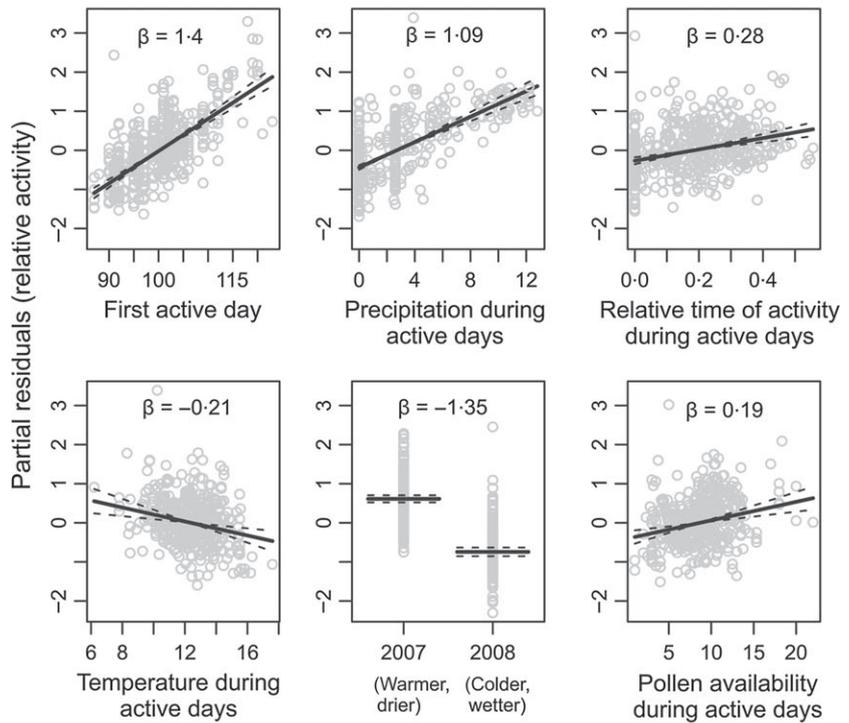
Fig. 3. Partial residual plots of the best-fitting generalized linear models (GLM, Gaussian family) explaining *life span* in the two species; *Andrena vaga (a)* and *Anthophora plumipes (b)*. Partial residuals are those remaining after the effect of all the other variables has been accounted for. Solid lines represent fitted model terms, dashed lines represent standard errors, and grey circles represent partial residuals. The standardized coefficients (β) are provided. The greater the absolute value of β, the more important the variable is in the model (which is roughly equivalent to the steepness of the solid line with steeper lines indicating a stronger effect). For more details on the predictors see Table 1. The histograms show the overall (non-partial) residuals of the best models.

(a) *Andrena vaga:* *n* = 425, 69% of explained deviance

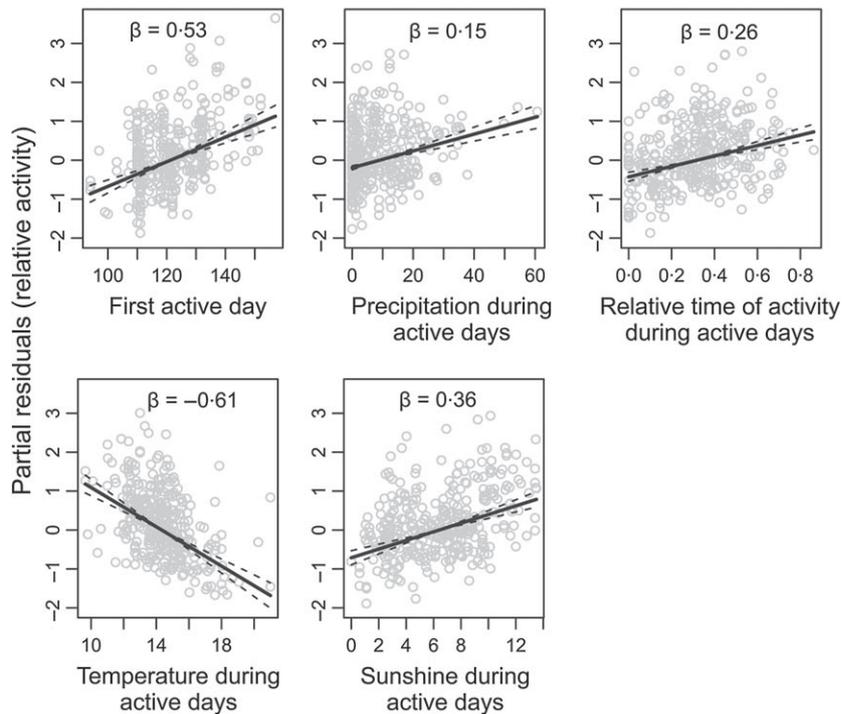**(b)** *Anthophora plumipes:* *n* = 334, 34·1% of explained deviance

Fig. 4. Partial residual plots of the best-fitting generalized linear models (GLM, binomial family) explaining *relative activity* (proportion of active days during the life span) in the two species; *Andrena vaga (a) and Anthophora plumipes (b)*. Partial residuals are those remaining after the effect of all the other variables has been accounted for. Solid lines are fitted model terms, dashed lines are standard errors, and grey circles are partial residuals. The standardized coefficients (β) are provided. The greater the absolute value of β, the more important the variable is in the model (which is roughly equivalent to the steepness of the solid line with steeper lines indicating a stronger effect). The *y*-axis is in logit scale. For more details on the predictors, see Table 1.

of solitary bees, with the prominent variables being moisture (precipitation), magnitude of activity, and timing of the first appearance at the nesting site. Our data led to similar results in both studied species (and also when different analytical techniques were employed), which implies the possible general applicability of our findings.

ACTIVITY INFLUENCES LENGTH OF LIFE

We had expected relative flight activity to be one of the key factors determining life span in the two bee species. The high energetic cost of flight was demonstrated by laboratory experiments (Wolf *et al.* 1989), and the situation in wild populations is unlikely to be different. Accordingly,
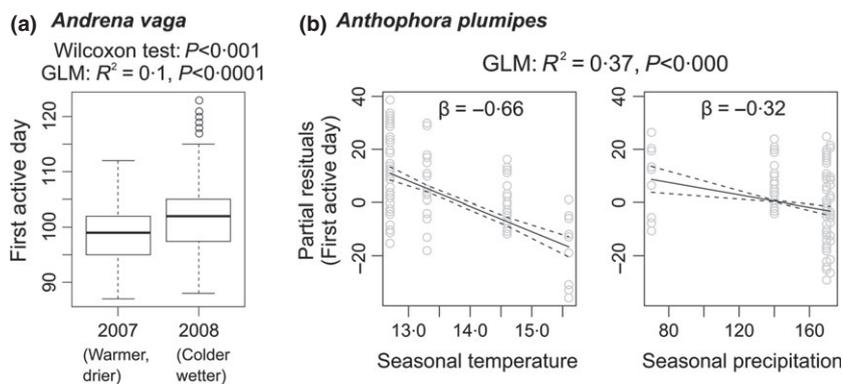
Fig. 5. Variables that correlate with the *first active day*. (a) The relationship between season and first active day, in *Andrena* bees (boxplots show medians, quartiles and outliers). (b) Partial residuals of the generalized linear model explaining first active day in *Anthophora* bees.

we confirmed that there is a strong negative effect of proportion of active days in life on the life span of both species. We further found that when the bees had a higher number of active days during their life span, they tend to be active for slightly longer periods of time within these days. Surprisingly, this longer time of activity during the active days had either no detectable effect on longevity (in *A. vaga*) or even had a weak positive effect (in *A. plumipes*). The high activity during the active days thus does not seem to directly reduce longevity; a similar finding has been demonstrated for some mammals (Lee, Hsieh & Paffenbarger 1995; Navarro *et al.* 2004) and recently also for insects (Niitepõld & Hanski 2012) in laboratory experiments. We suggest that experiments manipulating the magnitude of activity at fine and coarse temporal scales should be conducted to explore this relationship further.

CLIMATE INFLUENCES RELATIVE ACTIVITY AND LIFE SPAN

Our analysis shows that the most active individuals (measured by proportion of active days in their life) are those that are active during relatively high-precipitation and/or low-temperature days. Unsurprisingly, only a minority of individuals prefer to activate in such weather conditions. The question is what causes positive response of bees to rainy and cold weather in their activity. Only behavioural and physiological factors can be taken into account for the explanation because most climatic factors, pollen availability (*A. vaga* only), and time scale were already considered in the analysis. The individuals that are active in colder weather and higher precipitation may receive different costs and benefits from their behaviour in comparison with individuals that are active in 'better' weather. Some of these benefits may be connected with our finding that different bees with comparable relative activity live longer under wet weather than under dry weather. The effect of precipitation is stronger than the effect of temperature, so the fact that the higher relative activity of bees under cold weather has a negative effect on life span is not that important (but significant).

Explanation of the response of life span to temperature during active days can help with understanding the other results from the analysis of climatic variables. This life

span-temperature relationship has a unimodal character in *A. vaga*. The likely explanation of this result is an insufficient thermoregulation ability of bees exposed to full sun (Rezkova *et al.* 2012). Females of *A. vaga* cover the nest entrance with sand prior to each departure (Fig. 1), which protects the nest from parasites, but the bees have to dig through the cover upon return. This digging can be costly, especially in warmest sunny spring days: relatively high temperature and direct sun forces the bee to leave the nesting site after a few minutes of digging, because such bee risk overheating; it takes a few minutes to cool down and continue the digging. Such behaviour is repeated until the bee finally gets into the nest and is typical for hot and sunny days only (Rezkova *et al.* 2012). We could expect relatively high physiological costs of such behaviour that could cause a negative effect on the longevity in *A. vaga*. This could also explain why *A. vaga* tends to be more active on days with colder weather than on warm days. In contrast, *Anthophora* does not cover its nest entrance and does not show the unimodal response. However, *A. plumipes* also prefer cold temperatures over warm temperatures for activity. This result is surprising because, as we have already indicated, higher temperatures have a positive effect on the life span of *A. plumipes*. This discrepancy ceases to be mysterious when we take the effect of cuckoo bee parasites into account. Cuckoo bees prefer higher temperatures for their activity compared to their hosts (Straka & Bogusch 2007; Rozen, Straka & Rezkova 2009), and *Melecta albifrons* (a common cuckoo bee parasite of *A. plumipes*) is not an exception (Stone & Willmer 1989). The risk of parasitism in warmer temperatures might be so high that the bees may prefer to be inactive and stay in the nest to protect it, even though such behaviour could generally result in a decrease in their life span.

OPTIMIZATION OF FORAGING ACTIVITY IS OPTIMIZATION OF LIFE SPAN

As expected, we have shown that a higher relative activity (the proportion of active days) leads to a shorter life span. The question is whether the bees tend to maximize foraging efficiency or food gain (Ydenberg *et al.* 1994). If they maximize gain, then the maximum rate of foraging activity should be maintained at any cost (Werner & Anholt 1993),

especially under strong environmental pressure, such as limited food sources, time or predation. However, we observed that the bee's relative activity is not constant (and thus not maximized), so that observed bees were able to optimize their foraging efficiency. Relative activity depended on pollen availability (data for *A. vaga* only) and, more importantly, on the proximity of the end of the season, which corresponds to the *critical time horizon* (Maynard Smith 1978; Ydenberg *et al.* 1994). Apart from our results, there is little evidence of such a critical time horizon in nature (but see Javoiš & Tammaru (2004) for a rare study of moths).

The existence of strategies dependent on critical time horizon in bees can explain why the early-emerged bees are less active and live longer than the late-emerged bees. The bees, which appeared earlier, are far from the critical time horizon and may have not yet reached an optimum time for foraging (optimal climate, highest pollen availability, etc.). In contrast, the bees that emerge later should be closer to the optimal conditions; however, in unpredictable spring weather, they also risk missing the optimum. In conclusion, life span is regulated by optimization of efficient use of time and activities, such as we found in our bee models.

SEASONAL EFFECTS

In years with warmer early-spring temperatures, animals become active earlier, which is a fact that is frequently discussed in connection to global climate change (Walther *et al.* 2002; Bartomeus *et al.* 2011). Unsurprisingly, our data demonstrated that solitary bees appear earlier in warmer years.

We observed that both *A. vaga* and *A. plumipes* lived longer in colder years and that *A. vaga* also had a generally lower proportion of active days. However, individual bees had a lower proportion of active days and also lived longer when the average temperature during those active days was higher. This discrepancy in sensitivity to temperature between seasonal and daily data could be connected to the different effect of temperature on active and inactive bees. Our daily environmental data were collected only for active bees, which have 'endothermic' thermoregulation physiology (Stone & Willmer 1989), whereas the overall seasonal data included numerous records of inactive days for individual bees. Bees that are inactive (i.e. sitting in nests) are physiologically ectothermic. Because the rate of metabolism changes with the ambient temperature in ectotherms (i.e. temperature in the soil for our bee models), increasing ambient temperatures over long temporal scale (over the whole season) have a negative effect on the life span of inactive bees, as also known for overwintering bee larvae (Bosch & Kemp 2004). We suggest that the soil temperature changes will be important especially in the case of *A. plumipes* which builds shallow nests, not more than 10 cm deep.

We also observed a weak but significant effect of seasonal precipitation on the first date of appearance at the site in *A. plumipes*. The sensitivity of date of emergence to moisture is well known in desert bees (Danforth 1999), and here, we also demonstrate this phenomenon in a region with a less extreme climate. As already suggested (Tauber *et al.* 1998), our results highlight the critical need to consider precipitation in *in situ* ecological studies of longevity, activity, and phenology patterns.

Outlook

As in almost every observational study, there could be factors influencing life span that were not captured. The survival of bees can be influenced, for example, by various pathogens and parasites (Lindberg 1939; Paxton *et al.* 1997; Brødsgaard, Ritter & Hansen 1998; Kathirithamby 2009; Francis, Nielsen & Kryger 2013; Martin *et al.* 2013) or by the size of bee individuals and their size-dependent fecundity (Honěk 1993). These factors can correlate or interact with the variables that we measured in a complex manner, and the only real way to eliminate their effect is a randomized manipulative experiment. However, given that our results are consistent across both species, we are optimistic about the potential of these results to provide a valuable baseline for such experiments.

Acknowledgements

Data accessibility

All primary data are uploaded as online supporting information.

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Table S1. Dates and frequencies of daily field observations of the studied bees.

Table S2. Pearson's correlation coefficients between variables used in this study. Values >0·3 or lower than −0·3 are indicated by bold letters. Asterisks denote correlations significant at $\alpha = 0.01$. For variable description see Table 1.