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Why do we find dead bumblebees under linden trees?

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Abstract

1. Linden trees (*Tilia* spp.) have for a long time been associated with bumblebee (*Bombus* spp.) mortality in Europe and North America. Several explanations have been suggested for this phenomenon. This study aimed to explore to which extent the factors of predation, ageing, starvation, and poisonous nectar serve as explanations for bumblebee mortality in association with linden trees.
2. Starvation, ageing, and predation all contributed to mortality of bumblebees found under flowering linden trees. The mean weight of a dead wild bumblebee found under linden trees was found to be close to the weight of a starved bumblebee of the same size. This indicated that starvation was the main driver for many of the deaths.
3. A significant proportion of the dead bumblebees collected under linden trees had injuries indicating predation. The authors suggest that predation may serve as a secondary explanation for the bumblebee mortality, after weakening by starvation or other factors.
4. A small proportion of the bumblebees may have died from physical degradation or age. The present study did not support the poisonous nectar hypothesis. It is necessary to explore the covariation between the suggested hypotheses more closely, to better understand the interplay between the different factors. In addition, there is a need to investigate alternative hypotheses for the association between bumblebees and linden trees.

KEYWORDS
ageing, *Bombus*, predation, starvation, *Tilia*

INTRODUCTION

Expanding cities change the food supply for bumblebees, and occurrence of good habitats for pollinators in urban areas is important (Baldock et al., 2015; Goulson & Darvil, 2009; Potts et al., 2010). To conserve pollinating insect populations and preserve good habitats in cities, we need knowledge on how pollinating insect species utilize, and are affected by, different nectar-producing plant species (Baldock et al., 2015).

Nectar-producing trees are important food resources for pollinating insects in cities (Somme et al., 2016). Species of linden (*Tilia* spp.) are well adapted to withstand conditions in cities (Håpnes & Hansejordet, 2017). As more and more linden trees are planted in cities, there is increasing attention on the many dead bumblebees found under these trees. The number of dead bumblebees found under linden trees can be so large that the media describes it as a mass death. Observations of dead bumblebees under linden trees have been reported for more than a century (Saunders & Saunders, 1907), and many explanations for the phenomenon have been suggested (Fossen et al., 2019; Illies & Mühlen, 2007; Jacquemart et al., 2018; Koch & Stevenson 2017; Lande et al., 2019). Fossen et al. (2019) focused on the chemical composition of the linden nectar and concluded that ageing was the sole reason for the death of the bumblebees. However, they did not investigate other aspects such as starvation. The Norwegian Scientific Committee for Food and Environment (VKM) stressed the need to look more closely at bumblebee death associated with linden trees and presented four hypotheses that should be studied in this connection (VKM, 2017).

The aim of this study was to test how these hypotheses contribute to the death of the bumblebees observed under linden trees: (i) bumblebees die through predation; (ii) bumblebees die of ageing; (iii) bumblebees die by starvation; and (iv) bumblebees are poisoned by the nectar from the linden tree.

Linden trees

In Norway, we find three types of linden trees, small-leaved lime (*Tilia cordata*), large-leaved lime (*Tilia platyphyllos*), and the hybrid between these two species, the common lime (*Tilia x europea*). Although all three species are native to Europe (Jacquemart et al., 2018), only the small-leaved lime (*Tilia cordata*) occurs naturally in Norway (Håpnes & Hansejordet, 2017). The common lime is abundant in cities and other urban areas in Europe (Sjöman, 2012). Although this is also the case in Norway (Sjöman, 2012), the common lime is not known to reproduce naturally in this country (Grundt et al., 2015).

The flowering period of linden trees normally lasts between 2 and 3 weeks (Kirk & Howes, 2012). Nectar is produced during the whole flowering period, but reaches a maximum towards the end when the flower reaches its female stadium (Kirk & Howes, 2012). The nectar is easily accessible (Anderson, 1976). Studies in England and Germany have shown that the nectar production in linden trees decrease from early morning to the evening (Corbet, S. & Prŷs-Jones 1979; Illies & Mühlen, 2007). We were not able to measure this in our study area.

Bumblebees

The bumblebee species of northern Europe have an annual life-cycle where all individuals except the new queens die at the end of the season. Bumblebees have a small effective population size, which makes them particularly vulnerable to landscape changes (Goulson & Darvil, 2009). Bumblebees feed on nectar, honey dew, and pollen, and depend on continuous access through the whole season (Couvillon et al., 2014; Goulson, 2009). Queens and workers of bumble bees gather nectar for energy supply, whereas they collect pollen to provision protein for the larvae, as well as freshly emerged adults (Konzmann & Lunau, 2014). Bee species carrying nectar back to their nest, like bumble bees, has a large developed honey stomach.

Suggested explanations for bumblebees dying under flowering linden trees

Predation

Great tits (*Parus major*) have been observed eating bumblebees in linden trees (Goulson & Brown, 2009; Saunders & Saunders, 1907). A study of about 3500 bumblebees found dead or dying under linden trees in Germany showed that 54% of them had injuries, one-third of which included loss of the sting, and birds were suggested as the cause of the observed damages (Mühlen et al., 1992). In addition, Mühlen et al. (1994) found that 76.1% of the collected dead bumblebees had injuries that indicated predation, and there was a large variation in the number of damaged bumblebees between seasons and between individual linden trees. Their interpretation was that predators take dying or dead bumblebees, and that predation was a secondary factor (Mühlen et al., 1994). Fossen et al. (2019) found that most of the dead bumblebees collected under common lime trees in Bergen did not have injuries indicating predation.

Ageing

Depending on bumblebee species, each brood of workers can live for 2–6 weeks. Many colonies end their life cycle in July or August (Goulson, 2009). In northern Europe, the life cycle can be extended to September (Ødegaard et al., 2015).

Mortality in bumblebees increases with age (Rodd et al., 1980; Silva-Matos et al., 2000). It has been suggested that wear of the wings and body, that is, general degradation, in old bumblebees is the cause of death (Rodd et al., 1980). Mühlen et al. (1994) assigned 4013 dead bumblebees to five age categories based on wear of wings and body hairs. They found that old bumblebees accounted for a small proportion of the dead.

As pointed out by VKM (2017) and Jacquemart et al. (2018), the bumblebees that die naturally of advanced age will be easier to observe when they have fallen down on asphalt under linden trees compared to vegetated areas.

Starvation

Bumblebees need large amounts of food to maintain normal activity (Goulson & Osborne, 2010). After a few hours without an energy supply, they will not be able to fly. Baal et al. (1994) found that nearly dead bumblebees found under linden trees recovered after being fed with nectar from the same tree, which indicates that the reduced condition was caused by energy deficit.

Poisonous nectar

One of the earliest hypotheses for the bumblebee death was that flowers of linden trees are poisonous (Argoti, 2016; Crane, 1977; Von Frisch 1928, Geissler & Steche, 1962; Madel, 1977; Staudenmayer, 1939, VKM, 2017). It is not unusual that plants produce secondary metabolites that can be poisonous for pollinators (Adler, 2000). Nearly 500 chemical compounds have been found in the nectar of the small-leaved linden (Naef et al., 2004). The biological effects of all these compounds alone or in combination are not well known, but currently no compounds poisonous for bumblebees are known (Fossen et al., 2019; Jacquemart et al., 2018).

No negative effects have been observed when bumblebees were fed on linden nectar (Baal et al., 1994; Jacquemart et al., 2018; Surholt et al., 1992). Feeding experiments using common lime nectar have not, to our knowledge, been performed before.

TABLE 1 Bumblebees found dead under 24 common lime trees (*Tilia x europea*) during the 16 days flowering period in 2018. The indeterminate specimens are specimens that were so damaged that we were not able to determine their cast.

Species	Caste
Bombus s.str.	374 workers 23 males 1 queen 13 indet
Bombus hypnorum	65 workers 2 males 2 queens 1 indet
Bombus pratorum	5 workers 1 queen
Bombus pascuorum	6 workers
Bombus lapidarius	3 workers
Bombus spp.	3 workers 1 indet
Total	500

METHODS

Study area and data collection in the field

The survey was done in Trondheim, Central Norway (63.4 N, 10.4 E). The study area consisted of 41 common linden trees (*Tilia x europaea)* in a car parking area, of which 24 were used in the study. The trees in this area were selected because a large proportion of the coverage area consisted of asphalt (35%) (Aalberg Haugen et al., 2018); it is much easier to observe dead bumblebees on asphalt-covered areas than in vegetated areas.

The location was visited four times a day during 12–27 July 2018, as the trees bloomed on those days. During this period, the temperature was slightly higher than normal (Meteorologisk institutt, 2018). Dead bumblebees found under the trees in the asphalt area were collected and frozen for further investigations. During each visit, the number of living bumblebees in each tree was also estimated by counting them for 1 min from a fixed position. Although this does not give an accurate estimate of the number of bumblebees, it does give a relative density estimate for comparison.

Analysis at lab

Bumblebees collected from the field were sorted into species and caste. Species belonging to *Bombus s.str*. were treated as one group (Table 1), as workers of *Bombus terrestris*, *B. lucorum*, and *B. cryptarum* are especially hard to separate from each other taxonomically without DNA analysis. (Carolan et al., 2012). In this article, *Bombus s.str*. will be termed Earth bumblebee.

Predation analysis

To explore the extent of possible predation, all dead bumblebees from the study area were analysed for injuries and holes in the abdomen. In particular, it was noted when the head of the animal was missing.

Physiological age

Dead bumblebees ($n = 500$) were sorted into five age categories based on the state of wings and hair, following the criteria used by Mühlen et al. (1994). Animals that were damaged in a way that made age categorization impossible were excluded from the ageing analysis ($n = 192$).

Starvation analysis

A random sample of uninjured Earth bumblebees from the field ($n = 95$) was dried, their size measured, and weighed before they were compared with two control groups consisting of bumblebees *(Bombus terrestris)* from artificially reared colonies purchased from the company BOMBUS AS. The first control group consisted of animals starved to death ($n = 34$), while the second group of bumblebees was taken directly from the rearing nest and put to death in a freezer ($n = 49$).

All bumblebees were dried in a drying oven (50°C, >40 h). The mass and the size of the dried bumblebees were then measured. As the length of the wing correlates with body mass in many bumble bee species (Owen, 1988), wing length was used as a size measure. Wing length was, in this study, defined as the distance from the farther end of the first medial cell, point A, to the outermost at the marginal cell, point B (Figure 1).

Feeding experiment

Our feeding experiment investigated how bumblebees responded to an exclusive diet of linden nectar. Bumblebees from commercial nests

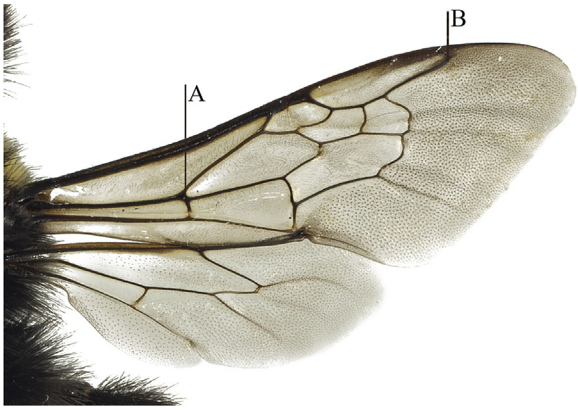

FIGURE 1 Bumblebees front- and hindwing. In this study, the length of the wing was defined as the distance between points a and B at the front of the wing (photo: Arnstein Staverløkk, NINA).

(*Bombus terrestris*) from BOMBUS AS ($n = 10$) were placed in pairs in tents with a volume of 75 × 75 × 115 cm. The two first hours of this stay were without access to nourishment or water. The purpose of this was to make the animals hungry and motivated to eat when nectar was introduced. After 2 h, branches of flowering linden trees (*Tilia x europaea*) were put into the tent, and the bumblebees were observed eating nectar. Bumblebees were further kept in the tent for at least 10.5 h. After this stay, the animals' physical shape was assessed as good, reduced, or dead by observation.

Statistical analysis

To investigate associations between the proportion of dead bumblebees predated and day of the season, we applied a generalized linear model (GLM) with binomial error distribution. The first day of the data collection period was set to day 0, and subsequent days were numbered consecutively.

The relationship between the number of dead bumblebees found under linden trees and daily 1-min counts of living bumblebees was evaluated by a GLM with quasi-Poisson error distribution, to account for overdispersion. Both the total number of dead bumblebees and the number of non-predated dead bumblebees were modelled. Day of season was included in the models for the number of dead bumblebees, to account for seasonal trends.

To test if the proportion of old animals (two oldest age categories) changed between the early (days 0–5), middle (days 6–10), and late (days 11–15) part of the season, we used two-sample binomial proportion tests.

To evaluate how the body mass–size relationship for dead non-predated bumblebees compared with both satiated and starved reared bumblebees, we fitted a linear regression model for body mass with wing length and bumblebee category (wild, satiated reared, and starved reared) as predictors. Body mass was cube root transformed to yield a linear relationship with wing length, since mass is proportional to volume. We found no significant interaction terms, that is, the wing length–mass associations are the same for the three bumblebee categories.

All statistical analyses were carried out in R version 4.0.2 (R Core Team, 2020).

RESULTS

Predation

Of all collected bumblebees ($n = 500$), 51% had abdominal injuries presumably caused by birds. The percentage of injuries among the males ($n = 25$) was 72%, and among the workers ($n = 456$) was 49%.

Day of the season was found to have importance for the portion of bumblebees predated (Figure 2). There was a significant positive association between the proportion of dead bumblebees predated and day of season ($z = 10.8$, $p < 0.001$). The expected proportion of the dead bumblebees that are predated increased from 0.02 on the first day of the season to 0.88 for the last 15 days later.

The relationship between the number of dead and the number of living bumblebees

There was a positive association between the number of dead and the 1-min count of living bumblebees ($t = 2.82$, $p = 0.007$) when the increase in dead bumblebee numbers through the season was accounted for (Figure 3a; $t = 5.95$, $p < 0.001$). If the bumblebees with injuries that indicated predation were excluded from the data set, the 1-min count of living bumblebees had still a significant positive association with dead bumblebees ($t = 6.10$, $p < 0.001$). However, day of season had no longer any significant effect on the number of non-predated dead bumblebees (Figure 3b; $t = 1.38$, $p = 0.17$).

Physical age

The age distribution among dead wild bumblebees that were in a condition allowing age determination is shown in Figure 4. In total, 10% of the animals were categorized as very young (A), 20% as young (B), 35% as intermediate (C), 24% as old (D), and 12% as very old (E).

The proportion of old animals (D and E) was not found to change significantly between the early (day 0–day 5) and middle (day 6–day 10) part of the season, nor between the middle and late (day 11–day 15) part of the season (all $p > 0.05$).

Starvation

Starvation experiment

The expected body mass of dead wild non-predated bumblebees was much lower than the body mass of satiated reared bumblebees

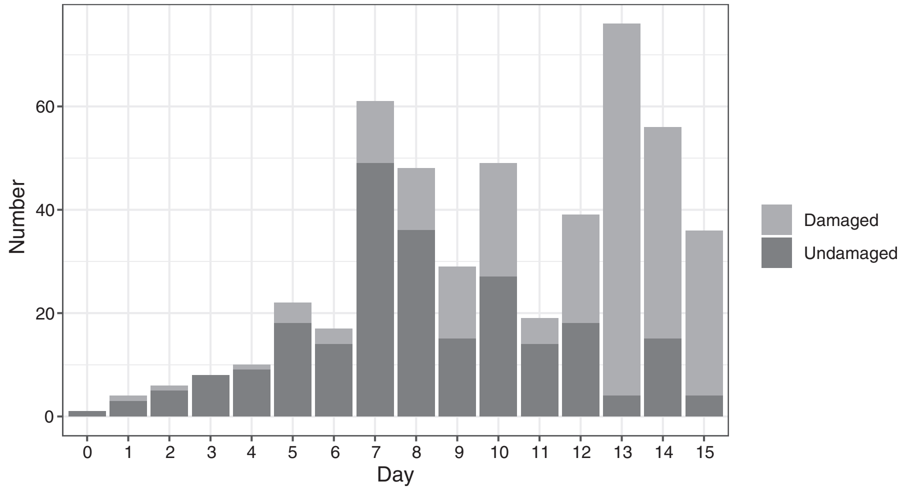

FIGURE 2 Number of all dead bumblebees found under linden trees during the flowering period

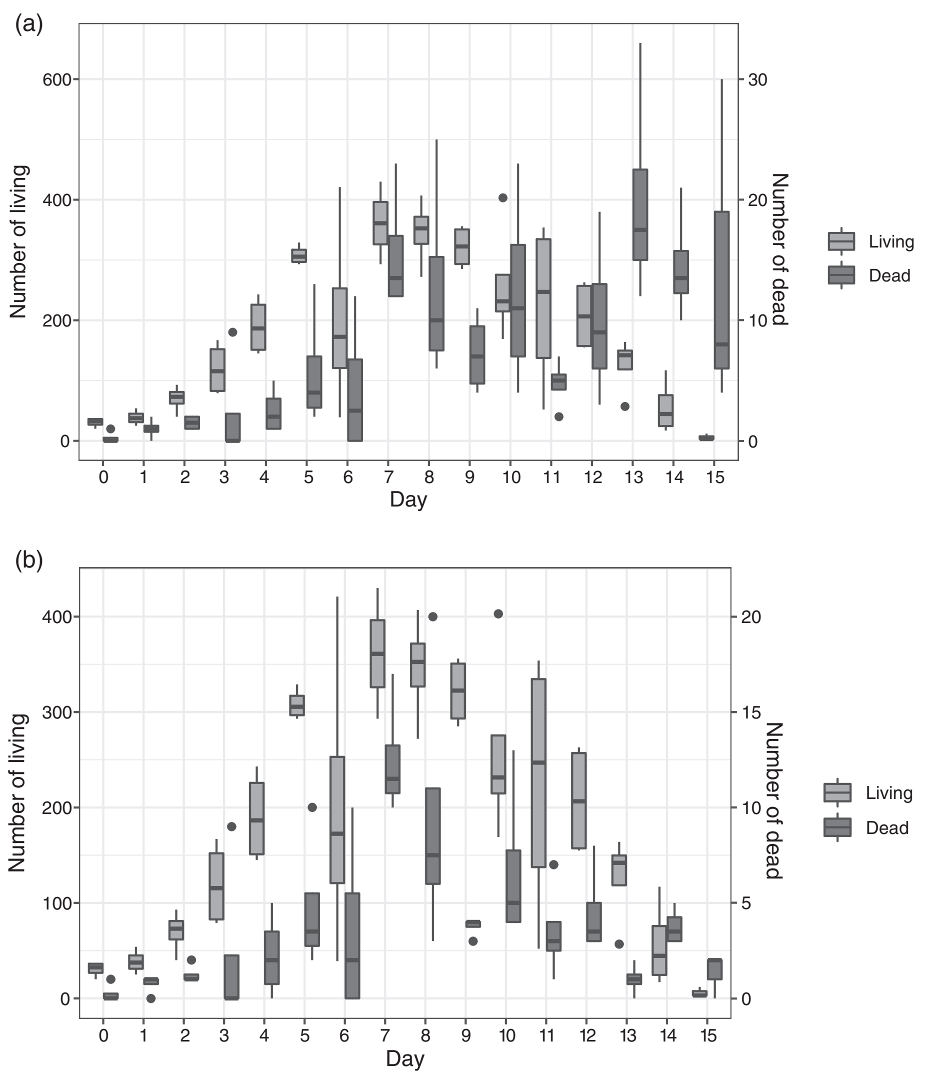

FIGURE 3 Number of dead bumblebees under linden trees (dark grey) and 1-min counts of living bumblebees in the same trees (light grey). All dead bumblebees are included in panel a, while those with injuries are excluded in panel b.

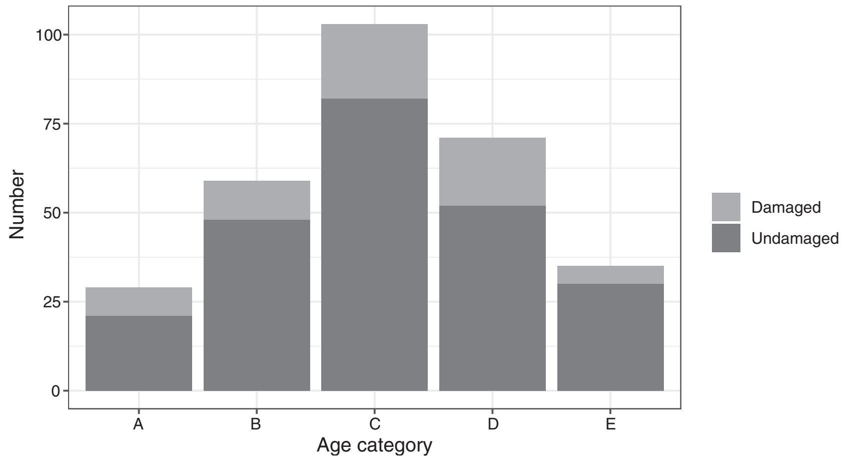

FIGURE 4 Age distribution of damaged and undamaged dead wild bumblebees ($n = 297$). Bumblebees in age category a are youngest, E are oldest.

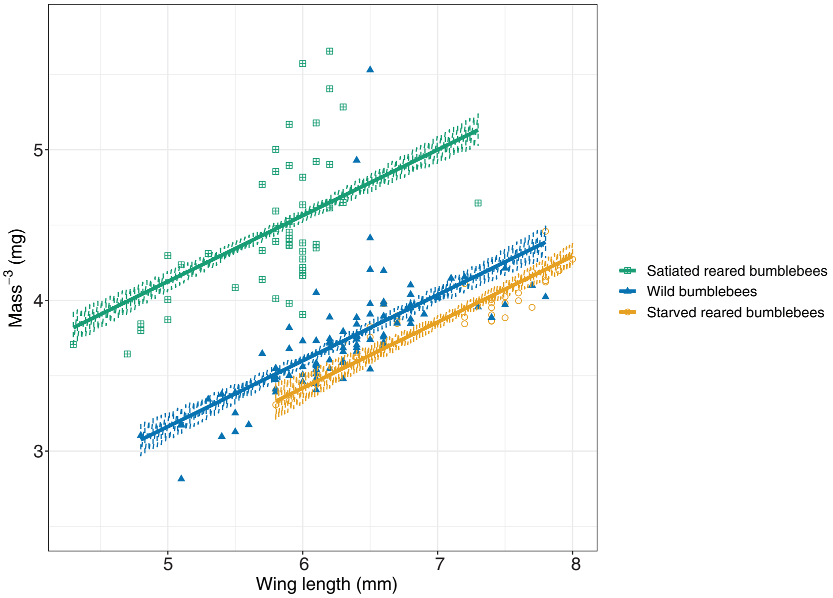

FIGURE 5 The relation between body mass (cube root transformed) and wing length. The lines were estimated by linear regression with a common gradient for wing length for all bumblebee categories. Shaded areas represent 95% confidence intervals.

(Figure 5; $t = 17.6$, $p < 0.001$), and only slightly larger than the body mass of reared bumblebees starved to death ($t = -2.72$, $p = 0.007$), after body size (wing length) had been accounted for.

The wild bumblebees with the highest mass$^{1/3}$/wing length ratio, i.e., those with the largest residuals from the fitted linear model, belongs to age category B ($n = 2$) and C ($n = 4$).

Feeding experiment

All bumblebees ($n = 10$) were in good condition 10.5 h after being fed nectar from linden flowers. They were foraging in the tent, showing behaviour as apparently healthy wild bumblebees do outside.

DISCUSSION

Predation

Injuries indicating that the bumblebees were eaten by birds were detected in about half of the dead wild bumblebees. However, it is not possible to determine from the data whether these animals died as a consequence of predation or if they were damaged although dying from other causes. Birds feeding on bumblebees on the ground were not observed during data collection. Birds can possibly hunt insects while hiding inside the dense linden tree crown, and then drop the remainder of the bumblebees bodies to the ground when finished eating.

The proportion having injuries indicating predation by birds was higher for the males than for the workers. Bumblebee males do not have a stinger to defend themselves, and generally have slower movements, making them more vulnerable to predation. The higher proportion of injuries observed for the males may therefore support the hypothesis that some bumblebees die through bird predation.

The proportion of damaged bumblebees increased throughout the season. One explanation could be that the general availability of nectar in the area decreased as the blooming of the linden trees declined. The insects could be easier targets for predators when they were already in a stressed situation, due to reduced access to food or increased competition (Goulson & Brown, 2009).

Predation cannot solely explain the findings of all dead bumblebees, as 49% of the insects did not have any visible predation injuries.

Physical degradation

Only a small proportion of the dead wild bumblebees were classified as old, in line with previous findings (Mühlen et al., 1994). The observed proportion of old bumblebees did not change throughout the season. The proportion of injured bumblebees increases throughout the season, and thereby the proportion of those not age categorized. However, the age distribution among the damaged that were age categorized was not age biased. A general ageing of the bumblebee population could therefore not be the explanation of the increase in abundance of dead animals with time.

Ideally, a similar age analysis should be done for a random sample of live bumblebees caught in the linden trees, to determine whether the dead bumblebees were relatively older than the general population.

Fossen et al. (2019) concluded that the cause of death for their sample of bumblebees was ageing, because all other hypotheses were rejected. However, our results show that ageing can be the cause of death for some bumblebees, but the majority of bumblebees in our study died from other causes.

Starvation

The mean weight of a dead wild bumblebee was found to be similar to the weight of a starved reared bumblebee of the same size. A small group of the dead wild bumblebees had much higher body weights than their starved comparisons. These cannot have died from lack of nutrition. Therefore, we find it reasonable to conclude that a large proportion of the bumblebees, but not all, that were found under linden trees died from starvation.

The dead wild bumblebees were slightly heavier than the starved ones (Figure 5). One possible explanation could be that the bumblebees from the study area might have died from overheating before starvation. This may happen when they land on hot asphalt weakened by starvation, or other factors.

Lande et al. (2019) found that the metabolites associated with energy production in crawling bumblebees under linden trees differed from those in healthy foraging bumblebees. They argued that in ambient temperatures below 30°C, bumblebees with an energy deficit would drop to the ground, crawling and ultimately dying, proposing that the low temperature will make the bumblebees unable to maintain a body temperature that is required for flight. This cannot be the situation in Norway where bumblebees are well adapted to ambient temperatures well below 30°C. However, linden trees with low nectar content may not provide enough energy for both thermoregulation and flight. Koch and Stevenson (2017) concluded that starvation can be a reasonable explanation for the observations of the dead bumblebees under the linden trees, but cannot in itself explain everything.

It was not possible to determine the starvation level of the predated bumblebees due to missing parts of the body. Thus, a relation between age and starvation level could not be found for the damaged bumblebees.

Poisonous nectar

The reared bumblebees that were fed linden nectar exclusively did not show any signs of being poisoned or weakened 10.5 h after feeding. This is in line with previous findings (Baal et al., 1994; Jacquemart et al., 2018; Surholt et al., 1992). Since poisons were expected to affect all bumblebees equally, and within a timeframe of 10.5 h, even a low sample size was sufficient to reject the toxic nectar hypothesis. The earliest explanation for bumblebee death under linden trees was that the nectar was toxic. Geissler and Steche (1962) and Madel (1977) proposed that the monosaccharide mannose was responsible, after Von Frisch (1928) and Staudenmayer (1939) found that mannose was toxic to honeybees and bumblebees. Chemical analyses have not found mannose in linden nectar (Baal et al., 1994; Fossen et al., 2019; Jacquemart et al., 2018; Krasenbrink et al., 1994; Lande et al., 2019).

Other potential mortality factors

Predation, ageing, and starvation may explain why many of the bumblebees died, but it is also clear that these three explanations together do not provide a complete understanding of why dead bumblebees are found under linden trees. A few animals were not damaged, not categorized as old, and did not have a weight that indicated starvation. It is unclear to what extent other hypotheses may help to explain the death cause of the bumblebees that did not die of any of the three causes.

Parasite infection among pollinators could be an alternative hypothesis explaining why a proportion of the bumblebees die. It is well known that bumblebees are hosts for different parasites, parasitoids, and pathogens, which include insects, fungi, bacteria, viruses, and protozoa (Goulson & Brown, 2009; Goulson et al., 2008; Goulson et al., 2015; Moret & Schmid-Hempel, 2000; Schmid-Hempel, 1998).

Dead bumblebees are observed under linden trees even in areas where the general nectar access is good, such as in botanical gardens

(Koch & Stevenson, 2017; Zucchi, 1996). It has therefore been speculated whether the linden trees can manipulate the pollinators to visit the trees even when they have little nectar (Koch & Stevenson, 2017). The alkaloid caffeine has, in experiments, been shown to do this (Couvillon et al., 2015). Naef et al. (2004) found caffeine and several other alkaloids in nectar from small-leaved lime (*Tilia cordata*), while Fossen et al. (2019) did not find caffeine or other alkaloids in nectar from common lime (*Tilia x europea*). Lande et al. (2019) found caffeine in linden nectar in 2016 but not in 2017. They suggested that production of alkaloids may vary among individuals, may be temporal, or an induced response to factors not yet determined. Further studies should attempt to identify, separate, and quantify these causal mechanisms.

CONCLUSIONS

The death of wild bumblebees under linden trees cannot be explained by one single factor, but rather by an interplay between several mechanisms. Starvation is a likely cause for a large proportion of the dead bumblebees found under linden trees. However, starvation cannot be the only mortality factor, as the weight of some of the dead bumblebees was much higher than the weight of starved reared bumblebees of the same size. Physical degradation, or age, serves as an additional explanation for the death of some of the bumblebees. About half of the collected dead bumblebees had injuries indicating that they had been eaten by birds. It is reasonable to believe that most of the damaged bumblebees were already weakened by starvation. Predation could serve as a secondary explanation for the observed mortality. This is plausible, as most of the undamaged bumblebees were starved. This study did not support the poisonous nectar hypotheses. To further understand why we find dead bumblebees under linden trees, it is necessary to explore the covariation between the suggested hypotheses, as well as other factors not examined in this study, more closely.

AUTHOR CONTRIBUTIONS

MKV, IMAH, and JOG conceived this research and designed and performed the experiments. MKV and OD performed the analysis. MKV, IMAH, JOG, OD, and FØ wrote the paper and participated in the revisions of it. All authors contributed critically to the drafts and approved the final manuscript.

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FUNDING INFORMATION

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CONFLICT OF INTEREST

All coauthors have consented to the submission to the journal.

ETHICS APPROVAL

No approval of research ethics committees was required to accomplish the goals of this study because experimental work was conducted on an unregulated invertebrate species.

DATA AVAILABILITY STATEMENT

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

CODE AVAILABILITY

All statistical analysis was carried out with standard packages and functions in R version 4.0.2 (R Core Team, 2020).

CONSENT FOR PUBLICATION

The participants have consented to submission to the journal.

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