

Agricultural land use yields reduced foraging efficiency and unviable offspring in the wild bee *Ceratina calcarata*

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Abstract. 1. Agricultural intensification generally leads to large-scale habitat changes marked by decreasing availability of nesting sites and flower resources for pollinators. However, little is known about how such changes impact wild bee maternal body size and foraging effort and, more importantly, whether there is a subsequent effect on their offspring.

2. Nests were collected from the common eastern North American stem nesting bee, *Ceratina calcarata*, across three land management types: (i) intensely managed conventional farms; (ii) moderately disturbed organic farmland; and (iii) least managed roadsides. The study assessed the effects of land use types on body size and wing wear (a proxy for foraging effort) of maternal bees, and on their offspring in terms of clutch size, survival, sex ratio and body size.

3. Findings revealed that more brood reached pupal stages from nests collected in conventional farmlands. This was due to the total lack of parasites, possibly because the host density is below the threshold that can support a brood parasite population in intensively farmed landscapes. A positive association between maternal bee size and clutch size was only found in least managed roadsides, while, in both farm types, body sizes for daughters and sons were smaller, barely reaching the predicted overwintering threshold.

4. The results suggest that the effects of intensified agricultural land use will be more pronounced in bee offspring, potentially leading to decreased fitness for subsequent generations. This implies far-reaching consequences for agricultural pollination services and declines in wild bee populations.

Key words. Agricultural intensification, body size, *Ceratina calcarata*, land use types, functional traits, offspring survival, reproduction, wild bees.

Introduction

Pollination is one of the most important ecosystem services in virtually all terrestrial ecosystems. In natural environments, native pollinators maintain biodiversity and ecosystem health by pollinating the vast majority of flowering plants (Kremen *et al.*, 2007; Ollerton *et al.*, 2011), whereas in agricultural landscapes, crop production is greatly enhanced by pollination services with an estimated value of billions of dollars annually (Klein *et al.*, 2007; Kleijn *et al.*, 2015). However, pollinators – especially wild bees – are under threat and their populations are rapidly declining, driven by a multitude of anthropogenically caused factors, ranging from agrochemicals,

pathogens, and habitat loss to large-scale landscape alteration and climate change (Winfree *et al.*, 2009; Goulson *et al.*, 2015). Land use modifications, foremost among them agricultural intensification (monocultures, frequent use of pesticides and regular disturbances), have emerged as the greatest potential threat to pollinators on a global scale (Brown *et al.*, 2016).

Bee declines are not uniform but rather species-specific and linked to a suite of ecologically relevant species traits (Williams *et al.*, 2010; Bartomeus *et al.*, 2013; Scheper *et al.*, 2014; Oliveira *et al.*, 2016). A global assessment of bee responses to agricultural land modification found that nesting type and sociality were important factors, but there were no consistent trends for bee body size (Williams *et al.*, 2010). Bee declines over the last century are associated with large body size and the loss of preferred host plant availability in the north-eastern U.S.A. (Bartomeus *et al.*, 2013; Burkle *et al.*, 2013) and in the Netherlands

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(Scheper *et al.*, 2014; Oliveira *et al.*, 2016). Increasing agricultural intensity has negatively affected large bodied pollinators in New Zealand (Rader *et al.*, 2014) and large bees in the north-eastern U.S.A. (Benjamin *et al.*, 2014).

This suggests that declining bees suffer from reduced fitness due to resource limitation, which is particularly pronounced for larger species, due to their greater nutritional requirements (Müller *et al.*, 2006). These results increase the urgency to assess the effects of agricultural land use types on wild bee fitness, not only from standing populations and biodiversity surveys but also from nest brood productivity and survivorship estimates.

Little is known about effects of land use types on maternal bee quality in terms of body size and, more importantly, whether there is a subsequent effect on their offspring. Most studies investigating impacts of agricultural land use forms collected bees with sweep nets and pan traps to characterise the residing bee fauna, in terms of abundance, species richness and floral associations (e.g. Klein *et al.*, 2002; Williams & Kremen, 2007; Kennedy *et al.*, 2013; Rader *et al.*, 2014; Tucker & Rehan, 2018). When nests of a focal bee species were assessed to investigate maternal investment, clutch size of the red mason bee (*Osmia rufa*) was negatively related to the area of oilseed rape fields in Germany (Jauker *et al.*, 2012). Clutch size and brood survival on conventional farms in California (U.S.A.) were reduced in the orchard mason bee, *Osmia lignaria* (Williams & Kremen, 2007), and in yellow-faced bumble bees, *Bombus vosnesenskii* (Williams *et al.*, 2012).

A better understanding of offspring viability and quality across different land use types can be gained by investigating body size, a fitness- and performance-related trait, which underlies continuous variations in response to natural selection and environmental modifications (Chown & Gaston, 2010). Studies in Europe have revealed variable responses of *Andrena* species to agricultural land use: *A. dorsata* and *A. nigroaenea* remaining stable; *A. flavipes* and *A. haemorrhoea* increasing; and *A. cineraria* decreasing in body size with increased habitat fragmentation (Warzecha *et al.*, 2016; Van Reeth *et al.*, 2018). In the United States, female congeners (*Andrena nasonii*) were also smaller in highly intensified agricultural landscapes (Renauld *et al.*, 2016). Thus, the effects of agricultural land use type on adult bee body size appear to be highly idiosyncratic and effects on the next generation are unclear.

In wild bees, reproduction success, sex allocation, and offspring size are closely related to female adult bee body size. Maternal bees can accurately determine the sex of the offspring – smaller females can allocate their investment towards sons, which are smaller in size and less costly to produce than daughters (Bosch & Vicens, 2005; Seidelmann *et al.*, 2009; Rehan & Richards, 2010a). Larger females produce more and larger-sized offspring in the leaf-cutter bee *Megachile apicalis* (Kim, 1999; Kim & Thorp, 2001), European orchard bee *Osmia cornuta* (Bosch & Vicens, 2005), red mason bee *Osmia rufa* (Seidelmann *et al.*, 2009), and in the small carpenter bee *Ceratina calcarata* (Rehan & Richards, 2010a). Size heritability between mother and daughter bees is weak (Tepedino *et al.*, 1984). Thus, larger offspring size is rather an effect of pollen quality and quantity (Roulston & Cane, 2002; Radmacher & Strohm, 2009; Helm *et al.*, 2017; Lawson *et al.*, 2017), supplied

by larger maternal bees that have higher provisioning rates if flower resources are available (Johnson, 1990; Kim & Thorp, 2001; Bosch & Vicens, 2005; Seidelmann *et al.*, 2009). These data highlight the need to investigate effects of human-modified landscapes on both, maternal body size, foraging efficiency and their investment, in terms of offspring numbers and body size.

The present study seeks to understand how three levels of land management intensity affect adult and offspring bee health by collecting nests for the stem nesting bee *C. calcarata*. The following aims were addressed: (i) assess the effects of land use types on maternal traits, including female body size and reproductive investment; and (ii) investigate associations of maternal traits with brood survivorship and offspring body size across landscapes. Based on previous research relating to bee declines over the last century and human-induced landscape modification (Williams *et al.*, 2010; Bartomeus *et al.*, 2013; Scheper *et al.*, 2014; Goulson *et al.*, 2015; Oliveira *et al.*, 2016), we hypothesise that more agriculturally intensified landscapes harbour smaller-sized adult bees (Renauld *et al.*, 2016) and that these produce fewer and smaller offspring.

Materials and methods

Study species

The small carpenter bee *Ceratina calcarata*, Robertson (Hymenoptera: Apidae: Xylocopinae), is a common native bee species throughout eastern North America, ranging from Georgia in the south to Ontario in the north (Rehan & Sheffield, 2011; Shell *et al.*, 2018). *Ceratina calcarata* is a stem nesting bee that is subsocial (Shell *et al.*, 2018) and polylectic, provisioning nests with pollen from a wide variety of plants (Lawson *et al.*, 2016). This common and widespread bee serves as an important crop pollinator (Kennedy *et al.*, 2013), occurring in high abundances, ranked within the top five most abundant genera, across a variety of agricultural systems, including vegetable, fruit crop and biofuel production (Tuell *et al.*, 2009; Gardiner *et al.*, 2010; Tucker & Rehan, 2018).

Study area

The present study was carried out in Strafford and Rockingham County, New Hampshire, U.S.A. (43.2383°N, 71.0236°W; 42.9931°N, 71.0498°W). We selected three land use types to represent different intensities of land management and agricultural farming practices (Tucker & Rehan, 2018). These were classified as 'conventional' and 'organic' farmland as well as 'roadsides'. Based on personal communication with farmers, conventional farms were characterised by the regular use of pesticides and frequent mowing (monthly). We classified this as the most intensely managed land use form. Organic farms had a similar mowing frequency, but no use of pesticides; we classified this as a less intensely managed farm type. All farms covered and area of c. 200 acres and were surrounded by forest landscape. Farm sites were at least 2.2 km apart. We selected roadsides with herbaceous vegetation at least 20 m wide and abundant stands of sumac, located within a 25-km radius of the farms. Roadsides

were infrequently mowed (twice annually) with no pesticide used; they were classified as the least managed land use type.

Nest collection

Nests from the stem-nesting bee, *C. calcarata*, were collected from the three land use types during summer (June and July) 2017. Twigs from stands of staghorn sumac (*Rhus typhina*, L., Anacardiaceae), which is *C. calcarata*'s preferred nesting plant (Rehan & Richards, 2010a), were clipped at the base of the shoot, early in the morning before 08.00 hours to ensure that maternal bees were inside, covered with masking tape and taken to the laboratory for further processing.

In the laboratory, nests were opened horizontally and subsequently classified into categories by assessing nest contents and the reproductive status of the adult female (Daly, 1966; Rehan *et al.*, 2009). As we were interested in relationships among land use types, maternal bee health and offspring, we only used nests classified as 'active' and 'full brood' nests. The former contains at least one pollen mass and/or immature bees and the latter contains brood cells with a larva or pupa in the youngest cell (Rehan *et al.*, 2009).

Maternal bees

The presence of an adult bee in the nest, which was assumed to be the mother, was noted. Two functional traits – wing wear and head width – were used to assess maternal bees. First, wing wear was scored from zero to five as an estimate of age and foraging effort (Cartar, 1992; Rehan & Richards, 2010b); undamaged forewings without nicks were scored as zero and damaged wings with a completely shredded apical margin were scored as five. Secondly, head width was used as a proxy for body size (Rust, 1991).

Offspring

For each collected nest, clutch size (i.e. the total number of brood cells) and the number of parasites was noted. To determine the number of live brood (i.e. the number of larvae reaching pupal stage) and sex of offspring, larvae were removed from the nest and reared in the laboratory. Each larva, including its pollen provisions, was placed individually into 200- μ l microcentrifuge tubes and incubated at 25 °C and 50% relative humidity until final eclosion (Lawson *et al.*, 2016). Offspring sex was determined by counting metasomal terga of adult offspring – females have six and males have seven terga (Rehan & Richards, 2010a). Sex ratio was used in subsequent analyses, which is the number of males divided by total number of live brood.

Morphometric measurements

To assess body size of maternal bees and their offspring, we used head width as a proxy (Rust, 1991). For each bee, measurements were carried out using a Nikon SMZ800 stereomicroscope (Melville, New York) with an ocular micrometer to

an accuracy of 0.01 mm. Head width measurements were taken in full frontal view, at the maximum width spanning the outer margin of both compound eyes (Rehan *et al.*, 2009). Head width of offspring, immature sons and daughters, was measured after the final moult was completed.

Data analyses

All statistical analyses were carried out using the statistical software R (R Development Core Team, 2017). We assessed the effects of land use types on bee body size and foraging effort, by comparing maternal head width and wing wear between land use types using simple ANOVA followed by Tukey *post hoc* comparisons for significant effects (Aim 1). We were also interested whether land use types had a follow-on effect on the next generation, reproduction and survival. Clutch size and offspring body size were compared between land use forms using simple ANOVA followed by Tukey *post hoc* comparisons. The effects of land use types on live brood and parasites were analysed using negative binomial generalised linear models (GLM.nb) in the package MASS (Venables & Ripley, 2002). The effects of land use types on sex ratio and maternal presence in the nest upon collection were analysed using a logistic regression.

Combined effects (Aim 2) of land use types and maternal quality (head width and wing wear) on the next generation, were analysed using a multiple regression approach. Potential multi-collinearity amongst explanatory variables was assessed by calculating the variance inflation values (O'Brien, 2007). Combined effects on clutch size and live brood were analysed using GLM.nb; effects on offspring size were analysed using a GLM and effects on sex ratio using a logistic GLM (Zuur *et al.*, 2009).

Results

A total of 321 nests were collected, of which 88 were from conventional farms, 153 from organic farms, and 80 from roadsides. Across all nests, 72% ($n = 231$) were occupied with maternal bees present at the time of collection. Of these, 63 (72% of the nests) were from conventional farms, 108 (71%) from organic farms, and 60 (75%) from roadsides. The presence of maternal bees in nests upon collection was not significantly different among roadsides and the two agricultural land use types (Wald $\chi^2 = 0.498$, $P = 0.618$).

Effects of land use types on native bee body size and foraging effort

Maternal head width, ranging from 1.65 to 2.43 mm, was slightly smaller at the least intensely managed roadsides (mean \pm SE, 2.03 ± 0.022) than on the two farms (2.05 ± 0.014). However, this difference was not significant ($F_{2,231} = 0.880$, $P = 0.416$). Maternal wing wear was highest on conventional farms (2.14 ± 0.160) and lowest at roadsides (1.90 ± 0.187), but did not differ significantly among land use types ($F_{2,227} = 0.570$, $P = 0.560$).

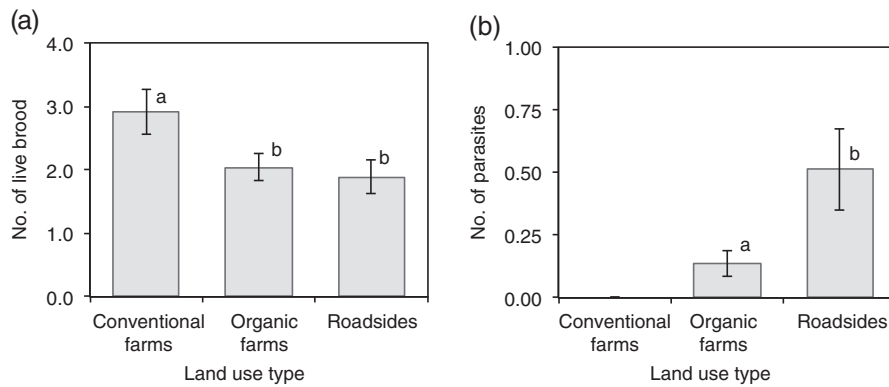


Fig. 1. (a, b) Average live brood (a) and number of parasites collected (b) from nests in three land use types. Data are average values per land use type (mean \pm SE); small letters indicate statistical significance.

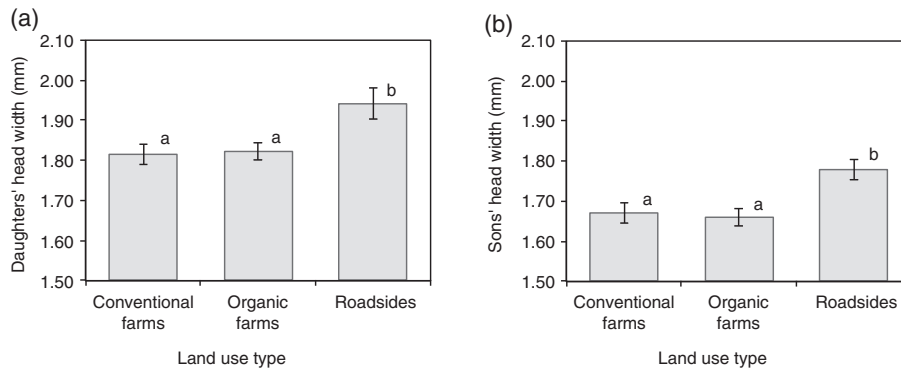


Fig. 2. Mean (\pm SE) head width of daughters and sons collected from nests in three land use types. Small letters indicate statistical significance.

Impacts of land use types on reproduction and survival

The average clutch size on conventional farms was slightly but not significantly higher (6.27 ± 0.426) than on organic farms (5.93 ± 0.28) and at roadsides (6.03 ± 0.395) ($F_{2,315} = 0.236$, $P = 0.790$). On the other hand, the average number of live brood was significantly higher on conventional farms (2.92 ± 0.358) and lower both on organic farms (2.04 ± 0.207) and at roadsides (1.89 ± 0.272) (Wald $\chi^2 = 2.333$, $P = 0.0197$; Fig. 1a). Further, we found absolutely no brood cells parasitised in nests from conventional farms. By contrast, parasites were present in 11 of 153 nests (7%) collected from organic farmland and in 12 of 80 nests (15%) at roadsides. Average numbers of parasites were significantly higher at roadsides (0.513 ± 0.162) as compared with organic farms (0.138 ± 0.052) (Wald $\chi^2 = 2.341$, $P = 0.019$; Fig. 1b).

Relationship between land use types and offspring size and sex

We found an effect of land use type on offspring body size. Daughters were consistently 8% larger than sons (Fig. 2). On average, daughter head width was significantly larger at roadsides (1.94 ± 0.039) ($F_{2,176} = 5.256$, $P = 0.006$) than on the organic (1.82 ± 0.022) and conventional (1.82 ± 0.026) farms. Sons showed a similar trend, being larger at roadsides

(1.78 ± 0.025) ($F_{2,176} = 5.990$, $P = 0.003$) than on organic (1.66 ± 0.023) and conventional (1.67 ± 0.026) farms. Offspring sex ratios were slightly female-biased on farms (0.41 ± 0.04) as compared with more equal ratios at roadsides (0.52 ± 0.054), but not significantly so (Wald $\chi^2 = 1.237$, $P = 0.216$).

Combined effects of land use types and maternal body size on offspring

We found combined effects of land use type and maternal quality on live brood and offspring size, but not for clutch size and sex ratio (Table 1). Clutch size was significantly associated with maternal body size but not with land use type or maternal wing wear (Wald $\chi^2 = 4.745$, $P < 0.0001$). Maternal bees had more live brood on conventional farms than in the other two land use types. This association was significant for maternal head width (Wald $\chi^2 = 3.208$, $P < 0.001$) and conventional farms (Wald $\chi^2 = 2.217$, $P = 0.02661$). Sex ratio was slightly but not significantly male-biased at roadsides (Wald $\chi^2 = 1.868$, $P = 0.0618$).

There was a significant positive association between maternal and daughter head width ($F_1 = 2.666$, $P = 0.0088$; Table 2). Roadside mothers produced significantly larger daughters and sons than those collected at any of the agricultural farm sites ($F_2 = 3.029$, $P = 0.003$; Table 2). Interestingly, mothers at

Table 1. Summary of generalised linear model (GLM.nb) for clutch size, live brood, and (GLM logistic) sex ratio and associated variables.

Variable	Parameter	Mean (\pm SE)	Estimate	SE	z-value	Pr(> z)
Clutch size	Conventional farms	6.27 (\pm 0.426)	0.0889	0.1035	0.860	0.3900
	Organic farms	5.93 (\pm 0.280)	-0.0889	0.1035	0.860	0.3900
	Roadsides	6.03 (\pm 0.395)	-0.1209	0.1186	-1.020	0.3079
	Maternal wing wear		-0.0181	0.0351	-0.514	0.6069
	Maternal head width		1.5110	0.3184	4.745	< 0.001
Live brood	Conventional farms	2.92 (\pm 0.358)	0.4505	0.2032	2.217	0.0266
	Organic farms	2.04 (\pm 0.207)	0.1875	0.2169	0.864	0.3875
	Roadsides	1.89 (\pm 0.272)	-0.1875	0.2169	-0.864	0.3875
	Maternal wing wear		0.0065	0.0700	0.092	0.9266
	Maternal head width		2.0571	0.6413	3.208	0.0013
Sex ratio	Conventional farms	0.40 (\pm 0.046)	0.2238	0.3880	0.577	0.5641
	Organic farms	0.42 (\pm 0.037)	-0.2238	0.3880	-0.577	0.5640
	Roadsides	0.52 (\pm 0.054)	0.8269	0.4427	1.868	0.0618
	Maternal wing wear		0.1256	0.1445	0.869	0.3847
	Maternal head width		-1.3293	1.2818	-1.037	0.3000

Shown are means (\pm SE) and the model coefficient (estimate), standard error (SE), z-value, and partial *P*, Pr(>|z|), of the Wald χ^2 statistic. Significant relationships are bold.

Table 2. Summary of generalised linear model (GLM) for daughters' and sons' head width and associated variables.

	Parameter	Mean (\pm SE)	Estimate	SE	t-value	Pr(> t)
Daughters' head width	Conventional farms	1.82 (\pm 0.026)	0.0206	0.0418	0.493	0.6227
	Organic farms	1.82 (\pm 0.022)	-0.0206	0.0418	-0.493	0.6227
	Roadsides	1.94 (\pm 0.039)	0.1619	0.0535	3.029	0.0036
	Maternal wing wear		0.0117	0.0166	0.701	0.4845
	Maternal head width		0.3652	0.1370	2.666	0.0088
Sons' head width	Conventional farms	1.67 (\pm 0.026)	0.0310	0.0367	0.837	0.4045
	Organic farms	1.66 (\pm 0.023)	-0.0310	0.0370	-0.837	0.4045
	Roadsides	1.78 (\pm 0.025)	0.0970	0.0418	2.324	0.0223
	Maternal wing wear		-0.0055	0.0132	-0.413	0.6806
	Maternal head width		0.4246	0.1203	3.529	0.0007

Shown are means (\pm SE) and the model coefficient (estimate), standard error (SE), t-value and partial *P*, Pr(>|t|), of the *F*-statistic. Significant relationships are bold.

agricultural sites produced daughters of much reduced body size (Table 2; Fig. 3a). A similar trend was observed for sons (Table 2; Fig. 3b).

Discussion

We assessed effects of land use types on adult female bee traits, including wing wear, body size and reproductive investment. Further, relationships of these maternal traits with brood survivorship and offspring body size across three land use types were investigated. Although there was no apparent effect of land use type on maternal bee foraging effort and body size, we found follow-on effects in the next generation: brood survival was highest on conventional farmland, where parasites were lacking. Offspring body size was smaller in both types of agricultural landscape – conventional and organic farms. Our results indicate a potential disconnection of *Ceratina* females' adjustment in offspring investment in agricultural landscapes. Mothers have increased wing wear, suggesting reduced foraging efficiency, and invest in many smaller (and

arguably unviable), rather than larger, maternally size-matched offspring.

Land use type effects on maternal bee body size or foraging effort

We found no effect of land use type on the body size of adult *C. calcarata*; adult bees on farms and at roadsides varied by < 1%. Our results are in line with previous findings from Germany, where body size of pan-trapped mining bees *Andrena dorsata* was not associated with agricultural land use intensity (Warzecha *et al.*, 2016), and a global analysis of bee responses to anthropogenic land use change, where agricultural intensification did not consistently affect adult bee body size (Williams *et al.*, 2010). However, our results differ from sweep net-collected adult female mining bees (*Andrena nasonii*) in the eastern U.S.A., which were smaller in intensified agricultural landscapes (Renauld *et al.*, 2016). Here, maternal bees from agricultural land use types had, on average, 10% more worn wings as compared with roadsides, suggesting higher

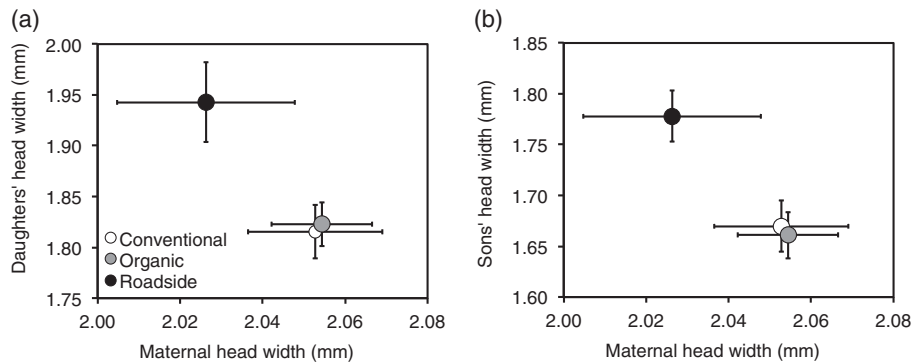


Fig. 3. Mean (\pm SE) head width of daughters (a) and sons (b) in relation to maternal head width from nests in three land use types. Conventional, conventional farms; organic, organic farms.

foraging effort. Moreover, wing wear in the present study was, on average, 30% higher than in active and full brood nests from a roadside study in Ontario (Rehan & Richards, 2010a). Wing wear in bees reflects age and foraging effort; it accumulates during the season (Mueller & Wolf-Mueller, 1993; Rehan & Richards, 2010b; O'Neill *et al.*, 2015), and can also be associated with foraging success and reproductive performance (Cartar, 1992; Foster & Cartar, 2011). Floral resources are sparser in intensely managed agricultural land use types (Williams & Kremen, 2007; Williams *et al.*, 2012).

Land use types affects brood survival

We found an effect of land use type on live brood and parasitism, whereas clutch size was comparable across the three tested land use types. Surprisingly, brood survival, i.e. larvae reaching pupal stage, was highest in nests collected from intensely managed conventional farmland. By contrast, offspring survival of the orchard mason bee *Osmia lignaria propinqua* in California was lower at conventional farms than at organic farms and semi-natural habitats (Williams & Kremen, 2007), which was attributed to reduced resource availability at conventional farms (Williams & Kremen, 2007; Williams *et al.*, 2012). However, brood survival is not solely dependent on the pollen mass provided, but also on the presence of natural enemies. Nest predators and parasites are associated with the mother's time spent outside the nest for foraging, making the nest vulnerable to intruders (e.g. Seidelmann, 2006). Despite the higher wing wear at conventional farmland, indicating that maternal bees spend more time foraging, we found no parasites in nests collected from conventional farmland. Although parasitism was present at organic farms and roadsides, it was quite low: only 7% of the nests were parasitised on organic farmland and twice as many at roadsides (15%). This suggests that regular management practices in agriculturally intensified landscapes – especially the regular application of pesticides such as neonicotinoids – not only has negative impacts on the health and fitness of the resident wild bee fauna (Gill *et al.*, 2012; Wood & Goulson, 2017), but also leads to a reduction of parasites, such as parasitoid wasps (Frewin *et al.*, 2014; Evans *et al.*, 2018). Lack or reduction of parasites (the topmost trophic layer) has been linked to poor

ecosystem health and decreased resilience to disturbances (Hudson *et al.*, 2006; Henson *et al.*, 2009).

Land use types affected offspring body size but not sex

Our study confirms previously described sex size dimorphism in *C. calcarata*. At all three land use types, male offspring was consistently about 8% smaller than female offspring, supporting previously observed differences between male and female offspring size of *c.* 10% in native habitats in the same area (Mikát *et al.*, 2017). Here, sex ratio at roadsides was slightly male-biased and comparable to that previously found in this species in native habitats (Rehan & Richards, 2010a; Mikát *et al.*, 2017). On farms, however, sex ratio was slightly female-biased (average 59% females), matching ratios for the same species found in social nests (Shell *et al.*, 2018).

We found an effect of land use type on offspring body size. Both sons and daughters were significantly smaller at conventional and organic farms as compared with roadsides. Offspring body size is directly related to the size of the pollen provided by the maternal bee (Johnson, 1990; Radmacher & Strohm, 2009; Rehan & Richards, 2010a; Lawson *et al.*, 2016). Here, pollen balls on farms, although not directly tested, were probably smaller, leading to the development of smaller progeny. In addition, maternal wing wear was highest at conventional farms. Thus, smaller offspring size and increased wing wear on farms point towards reduced flower resource availability in agricultural landscapes, which could be due to regular mowing and herbicide use. Our results indirectly support previous studies, where offspring body size or weight was related to the availability of resources and smaller pollen balls lead to the production of smaller offspring (Kim, 1999; Kim & Thorp, 2001; Lawson *et al.*, 2017; Radmacher & Strohm, 2009). The prevalence of smaller bees in agriculture-intensified landscapes (Renauld *et al.*, 2016) could also be due to the negative effect of pesticides on foraging efficiency (Gill *et al.*, 2012; Feltham *et al.*, 2014).

Offspring size in the landscape types investigated here were consistently smaller than previously described in meadow habitats in the same area (Mikát *et al.*, 2017); although roadside offspring were quite similar to this former study, this first examination of farmland offspring revealed considerably smaller sons

(7%) and daughters (9%). Furthermore, on farms, the body size of daughters barely overlapped with maternal bee body size, being, on average, 11% smaller than their mothers. Smaller bees are less likely to survive the winter and establish successful nests in the next season (Tepedino & Torchio, 1982; Bosch & Kemp, 2004). *Ceratina* overwinters as newly emerged adults in their natal nests; however, we know that not all offspring survive the winter and that there is a body size-related overwintering threshold: head width of female bees smaller than *c.* 1.9 mm will not survive the winter (Rehan & Richards, 2010b). This suggests that two-thirds of the daughters from farms would not survive the following winter, and therefore would not be able to propagate during the following season. These effects on offspring in agricultural landscapes – for both conventional and organic farmland – could potentially lead to population declines in the coming decades due to physiological restraints to surviving the winter, thus leading to a steady decline in bee population in agriculture-modified landscapes, unless bees can be recruited from nearby natural habitat. It is also conceivable that smaller offspring size might be one of the many contributing factors to the recent declines of pollinators in agricultural landscapes in the temperate zone.

Combined effects of land use type and maternal quality

Combined effects of land use types and maternal quality emerged for live brood and offspring body size, but not for clutch size and sex ratio. Clutch size was significantly correlated with maternal body size at roadsides, but not with size in agricultural land use types, thus supporting the previously documented strong predictor of maternal body size for clutch size only in natural habitats, where larger mothers produced more offspring (Rehan & Richards, 2010a). The lack of this relationship on farms indicates a mismatch in maternal quality and foraging efficiency in agricultural landscapes. Surprisingly, on conventional farms more brood survived for comparably larger adult females than at roadsides, a trend which is most likely driven by the lack of parasites in this land use type. Furthermore, at roadsides, comparably smaller maternal bees produced significantly larger daughters and sons than on farms, indicating that more resources were available or that bees foraged more efficiently at roadsides. *Ceratina* mothers and other solitary bee species typically adjust their offspring sex ratio, clutch size, and body size based on environmental conditions (Bosch & Vicens, 2005; Seidelmann *et al.*, 2009; Rehan & Richards, 2010a). Thus, our results indicate that in agricultural landscapes, maternal investment for *C. calcarata* is compromised, which leads to less viable offspring for the next season.

Conclusions

This study shows that land use types affect wild bees in a more nuanced way than previously detected, while effects on maternal bee quality in terms of body size and foraging effort might be negligible and easily overlooked when adult bees are collected by trapping and netting. The assessment of nests, however, revealed follow-on effects of agricultural

land use on maternal foraging efficiency and brood productivity for the next generation. Offspring body size for both daughters and sons were smaller on conventional and organic farms, on average below the overwintering threshold. Our results indicate that with increasing agricultural land use intensification in temperate zones, wild bees overwintering survival could be jeopardised, as populations could steadily decline over the coming decades, due to smaller offspring body size. Such an effect could be mitigated by smaller-sized farms and adjacent less-managed habitats as well as reduced pesticide use and mowing practices.

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