

Season length, body size, and social polymorphism: size clines but not saw tooth clines in sweat bees

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Abstract. 1. Annual insects are predicted to grow larger where the growing season is longer. However, transitions from one to two generations per year can occur when the season becomes sufficiently long, and are predicted to result in a sharp decrease in body size because available development time is halved. The potential for resulting saw-tooth clines has been investigated only in solitary taxa with free-living larvae.

2. Size clines were investigated in two socially polymorphic sweat bees (Halictidae): transitions between solitary and social nesting occur along gradients of increasing season length, characterised by the absence or presence of workers and offspring that are individually mass provisioned by adults. How the body size changes with season length was examined, and whether transitions in social phenotype generate saw-tooth size clines. We measured *Lasioglossum calceatum* and *Halictus rubicundus* nest foundresses originating from more than 1000 km of latitude, encompassing the transition between social and solitary nesting.

3. Using satellite-collected temperature data to estimate season length, it was shown that both species were largest where the season was longest. Body size increased linearly with season length in *L. calceatum* and non-linearly in *H. rubicundus* but the existence of saw-tooth clines was not supported.

4. The present results suggest that because the amount of food consumed by offspring during development is determined by adults, environmental and social influences on the provisioning strategies of adult bees may be more important factors than available feeding time in determining offspring body size in socially polymorphic sweat bees.

Key words. Body size, eusociality, size cline, social polymorphism, sweat bee.

Introduction

Intraspecific geographic variation in life history traits is common in many taxa (Roff, 1992; Stearns, 1992), and spatial variation in body size has received considerable research attention for more than 150 years (Blanckenhorn & Demont, 2004). In insects, body size can have a key influence on traits such as potential fecundity, resources allocated to offspring, thermoregulation, and overwintering success (May, 1979; Honěk, 1993; Fox & Czesak, 2000; Hunt & Simmons, 2000; Smith, 2002; O'Neill *et al.*, 2014). Within species, body size frequently varies either positively or negatively with latitude and altitude (Chown & Gaston, 2010; Shelomi, 2011). Positive relationships are known

as Bergmann clines (BCs) (Bergmann, 1847; Ray, 1960, but see Watt *et al.*, 2010), negative ones as converse-Bergmann clines (CBCs) (Park, 1949; Blanckenhorn & Demont, 2004).

In seasonal environments, insects can grow and reproduce only during the active season (Bradshaw & Holzapfel, 2007; Gullan & Cranston, 2010), which becomes progressively shorter with increasing latitude and altitude (Bradshaw & Holzapfel, 2007). Annual insects with long generation times can exhibit CBCs if a larger body size can be attained only by prolonging growth (Chown & Gaston, 1999; Blanckenhorn & Demont, 2004). Correspondingly, CBCs are observed in insects such as butterflies and crickets (e.g. Nylin & Svård, 1991; Mousseau, 1997), and are frequently found to have a genetic basis (Masaki, 1967; Blanckenhorn & Fairbairn, 1995; Telfer & Hassall, 1999). In contrast, species with many generations per year in which growth is not limited by season length can exhibit BCs, either because it is adaptive or as a consequence of temperature-mediated physiological processes (see Blanckenhorn & Demont, 2004 and references therein).

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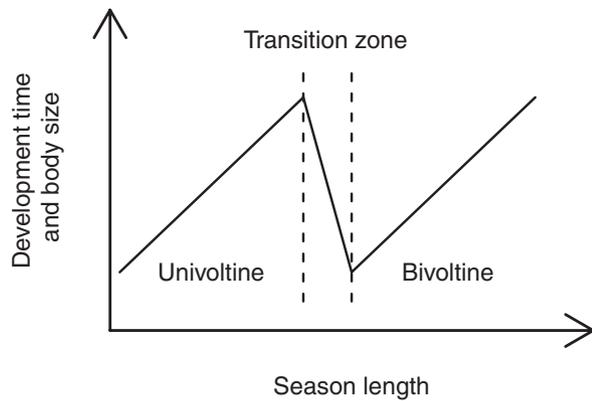


Fig. 1. A hypothetical saw-tooth cline, after Roff (1980) and Nygren *et al.* (2008). In socially polymorphic sweat bees, univoltine populations are solitary while bivoltine populations are social.

When the season becomes sufficiently long, fitness can be maximised by adopting a bivoltine life cycle (Masaki, 1972; Roff, 1980), because any benefits of reaching a larger size are offset by increased mortality risk during development (e.g. Johansson & Stoks, 2005). As the time available for each generation to develop is halved at the transition from univoltine to bivoltine life cycles, Roff (1980) predicted that there should be a concomitant sharp drop in body size (Fig. 1). As predicted, saw-tooth size clines are observed in a variety of groups where there are latitudinal changes from univoltine to bivoltine life cycles, including crickets (Masaki, 1972; Mousseau & Roff, 1989), butterflies (Nygren *et al.*, 2008), and moths (Välimäki *et al.*, 2013). However, saw-tooth size clines are not always found and the relationships between body size and season length may be complex (Kivelä *et al.*, 2011; Välimäki *et al.*, 2013). For example, counter gradient variation occurs where a higher growth rate evolves to counter the effect of a shorter available development time, which can over, under, or perfectly compensate for clinal variation in development time (Conover & Schultz, 1995; Blanckenhorn & Demont, 2004).

Socially polymorphic sweat bees (Hymenoptera: Halictidae) are a group in which the presence of saw-tooth clines might have more far-reaching implications. The same species can exhibit both solitary and social behaviour, characterised by either the absence or presence of a first brood of workers before the production of reproductives (Fig. 2; Schwarz *et al.*, 2007). Each spring, mated females (foundresses) emerge from hibernation and initiate subterranean nests. Foundresses then mass provision a series of separate brood cells with a ball of pollen and nectar, providing each offspring with all the food required for development. In solitary nests, all female offspring mate and enter directly into hibernation. In social nests, however, B1 females are typically smaller than the foundress (Packer & Knerer, 1985; Schwarz *et al.*, 2007), and at least some remain at the nest as workers to help rear a second brood (B2) of reproductive offspring.

Whether social or solitary behaviour is expressed correlates closely with season length, and is analogous to the univoltine and bivoltine populations of solitary taxa such as butterflies, moths, and crickets. Bees can nest socially only in southern or

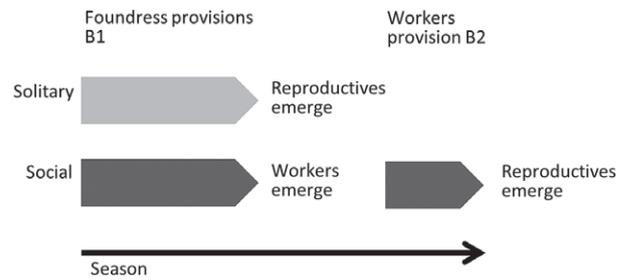


Fig. 2. Being social takes longer than nesting solitarily. Brood rearing in the solitary life cycle is completed when offspring provisioned by the foundress emerge, but in the social life cycle offspring must provision a second brood as workers. In both cases the life cycle must be completed before the end of the season.

lowland areas where the season is sufficiently long to rear two consecutive broods (Fig. 2; Soucy & Danforth, 2002; Davison & Field, 2016). Previous studies have generally found that sweat bees in more northern or upland areas are smaller and follow CBCs (Richards & Packer, 1996; Soucy, 2002; Field *et al.*, 2012; Davison & Field, 2016, but see Sakagami & Munakata, 1972), although measurements have been made only at widely scattered sites hundreds of kilometres apart. Field *et al.* (2012) predicted that socially polymorphic sweat bees could exhibit saw-tooth size clines, because double-brooded bees just to the south of the transition might be more time stressed than single-brooded bees just to the north (Fig. 1). Body size is strongly correlated with the amount and quality of food consumed during development (Plateaux-Quénu, 1983; Richards & Packer, 1994; Roulston & Cane, 2002). Thus, offspring size might also be influenced by environmental constraints on, and strategic investment decisions by, adult bees at the time of provisioning (Richards & Packer, 1996; Field *et al.*, 2012; Richards *et al.*, 2015).

In the present study, how transitions in social phenotype can impact on the body size of foundresses is examined. The presence is tested for of saw-tooth clines in two socially polymorphic sweat bees along a gradient of increasing season length, from the north of the United Kingdom (UK) southwards to western France. *Lasioglossum calceatum* Scopoli and *Halictus rubicundus* Christ are widely distributed throughout the Palaearctic and Holarctic, respectively, (Pesenko *et al.*, 2000; Pesenko, 2005), and each is socially polymorphic throughout its range (Sakagami & Munakata, 1972; Soucy & Danforth, 2002; Field *et al.*, 2010, 2012; Davison & Field, 2016). In the UK, both species nest socially in southern or lowland areas, but solitarily in northern and upland environments (Field, 1996; Soro *et al.*, 2010; Field *et al.*, 2012; Davison & Field, 2016). The present results generally support the existence of CBCs in both species, but not the existence of saw-tooth clines.

Materials and methods

Sampling range

Although *L. calceatum* is known to nest socially in western France (Plateaux-Quénu, 1992), no studies on the social behaviour of *H. rubicundus* from France have been published.

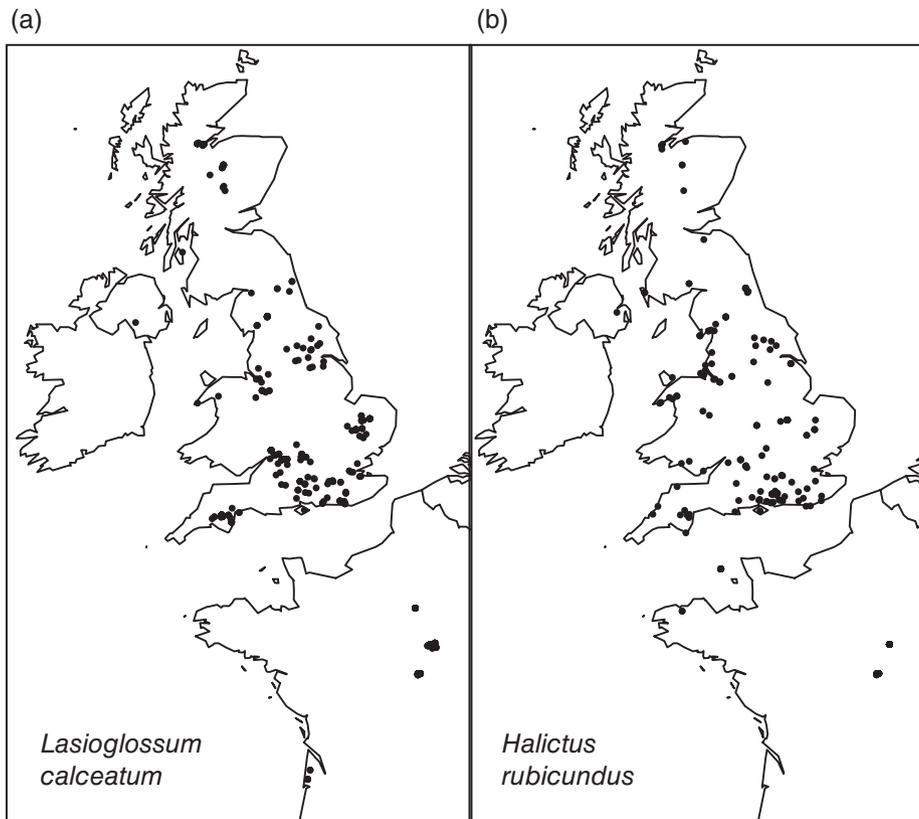


Fig. 3. Maps showing the locations from which specimens were collected within the United Kingdom and France for specimens of (a) *Lasioglossum calceatum* and (b) *Halictus rubicundus* that were measured and entered into the size cline analysis. Note that the number of specimens sampled from each location is not indicated.

However, it is highly likely that *H. rubicundus* nests socially in the regions of France sampled in this study. *Halictus rubicundus* nests socially in southern Britain (Soro *et al.*, 2010; Field *et al.*, 2012), and elsewhere in its range, the expression of social phenotype is closely linked to latitude and altitude (Soucy & Danforth, 2002). Therefore, although at present it is not known exactly where the transition from solitary to social occurs, the range of latitudes sampled for both species is expected to encompass the transition zone.

Specimens

Specimens were sourced from museum, private, and university collections spanning the years 1895–2014. In total, 487 *L. calceatum* and 356 *H. rubicundus* specimens from Britain and France were measured, covering 45–58 and 47–58 degrees of latitude, respectively (Fig. 3). Bee size was recorded as foundress head width (HW), measured at the widest point of the head in full-face view including the compound eyes. HW is a widely used proxy for body size in sweat bees (e.g. Soucy, 2002; Brand & Chapuisat, 2012), which correlates strongly with overall size and mass (Michener & Lange, 1958; Stubblefield & Seger, 1994; Potts, 1995; Roulston & Cane, 2000) and does not change after death (Daly, 1985). HW is advantageous because

the head capsule also does not degrade with age, whereas the wings of older bees can become frayed and difficult to measure.

In the present study, we focus on nest foundresses only. *Lasioglossum calceatum* and *H. rubicundus* workers are typically smaller than foundresses (Field *et al.*, 2012; Davison & Field, 2016; but see Field *et al.*, 2010), therefore to ensure workers did not confound the analysis we excluded bees caught after 15 June. This cut-off is justified because in southern UK (where season length is longest in the UK) *L. calceatum* B1 offspring have never been observed before July (Davison & Field, 2016), and the earliest *H. rubicundus* B1 offspring have been observed only in the second half of June (Field *et al.*, 2010, 2012). Further south in France, *L. calceatum* workers are typically observed earlier; however, all French specimens of both species were captured in either March or April, well before the period of worker emergence (Plateaux-Quénu *et al.*, 2000).

The location and date of capture were recorded for all specimens. Data on specimen labels varied considerably in detail from precise geographic coordinates and date of capture to vague or indecipherable place names without a date. Specimens without a verifiable location or date of capture were excluded. If the only location data were a verifiable place name (i.e. a town) this was considered sufficiently accurate, and coordinates for the town were used as the given location for the specimen. Coordinates were obtained from Google Maps©. Many specimen labels

provided an Ordnance Survey (OS) grid reference, the national coordinate system used in Great Britain. Locations given by OS coordinates were determined using the Grab a Grid Reference Tool provided by the Bedfordshire Natural History Society (available at <http://www.bnhs.co.uk/focuson/grabagridref/html/>). The tool shows a satellite image map and a square overlaying the area referred to by the given OS coordinate, which varied from two to three figures in accuracy. In each case, the centroid of the square was taken as the specimen location and its coordinates obtained from Google Maps©. Depending on the accuracy of the OS coordinates given, squares were either 100×100 m or 1×1 km.

HW measurements of most specimens were made at the University of Sussex using a Leica binocular stereomicroscope with an eyepiece graticule. Specimens kindly made available by the Oxford University Museum of Natural History were measured digitally on site. Twenty sweat bees to measure twice were selected, and obtained a measurement error of 0.8%.

Estimating season length

Season length at all sampling locations was estimated as a measure of the time available in the year for growth and reproduction. The number of days on which land surface temperature (LST) exceeds 16°C in an average year was used to estimate the likely length of the active bee season (Kocher *et al.*, 2014). To estimate season length, temporal Fourier processed LST data were used from the National Oceanographic and Atmospheric Administration's (NOAA) Advanced Very High-Resolution Radiometer (AVHRR) polar-orbiting satellites (Hay *et al.*, 2006). Temporal Fourier analysis is a noise reduction technique that describes variation in naturally occurring cycles such as temperature as a series of summed sine curves of different amplitude and phase (Rogers, 2000; Scharlemann *et al.*, 2008). Data are based on 14 daily images at a spatial resolution of 8×8 km, spanning a 20-year time series from August 1981 to September 2001. The annual, bi-annual, and tri-annual cycles, which together describe over 90% of variation from the original data (Hay *et al.*, 2006), were utilised to reconstruct average annual LST profiles for each sampling location.

Temporal Fourier processed data were imported into the software ArcGIS (Version 9.3), where the amplitude, phase, and mean LST for each 8×8 km grid cell containing sampling locations were extracted using the 'sample' function. Averaged annual LST profiles for each grid cell (td) were reconstructed by summing (eqn 1) the annual (eqn 2), bi-annual (eqn 3), and tri-annual (eqn 4) sine curves and adding the mean LST

$$td = \sum_i t_i + a_0 \quad (1)$$

where $i = 1-3$

$$t_1 = a_1^* \sin \left(\left((d + 365/4 - p_1) * 2 * \pi \right) / 365 \right) \quad (2)$$

$$t_2 = a_2^* \sin \left(\left((d + 182.5/4 - p_2) * 2 * \pi \right) / 182.5 \right) \quad (3)$$

$$t_3 = a_3^* \sin \left(\left((d + 121.66667/4 - p_3) * 2 * \pi \right) / 121.66667 \right) \quad (4)$$

where t_i is the given temperature profile, a_i is the amplitude and p_i the phase of the annual, bi-annual and tri-annual cycles respectively, d is days (1–365) in the year, and a_0 the mean LST. Kocher *et al.* (2014) was followed by calculating season length for each grid cell as the number of days from the averaged annual LST profile (td) on which the LST was greater than 16°C .

Statistical analysis

For the data to support the saw-tooth hypothesis, body size should follow the non-linear pattern shown in Fig. 1. As it is unknown precisely where transitions between social and solitary behaviour occur, Kivelä *et al.* was followed (2011) and used polynomial regression to test objectively whether latitudinal size variation in *L. calceatum* and *H. rubicundus* supports the saw-tooth hypothesis. Specimens collected in the same 8×8 km grid cell returned the same value for season length, and specimens were caught in different years. For each species, we, therefore, used a generalised linear mixed model (GLMM) to analyse clinal variation in head width and included 'grid cell' and 'year' as random effects. Explanatory variables included were season length, the square of season length, and the cube of season length (Kivelä *et al.*, 2011). Support for the saw-tooth hypothesis would be indicated if the model generated a significant positive cubic term for season length. Maximal models were checked for normality and heteroscedasticity of residuals before proceeding with stepwise model reduction, beginning with the highest order power terms (Crawley, 2013). In the analysis of *H. rubicundus*, residuals were highly non-normal. Head width was, therefore, transformed to the power of 5.45 before analysis, this being selected as the optimal transformation using the function `powerTransform` in the *R* package 'car' (Fox & Weisberg, 2011). Analyses were conducted in the *R* environment (R Core Team, 2013), using the `lme4` package (Bates *et al.*, 2015) for GLMMs. Supporting data are available in Table S1.

Results

The head width for 487 *L. calceatum* and 313 *H. rubicundus* foundresses (mean HW: *L. calceatum* = 2.38 ± 0.01 mm, *H. rubicundus* = 2.98 ± 0.01 mm) was measured. The head width increased significantly with increasing season length in both *L. calceatum* and *H. rubicundus*, supporting previous work suggesting that sweat bees follow CBC. Neither species showed evidence of following a saw-tooth cline (as in Fig. 1). However, the precise relationship between head width and season length differed between the two species (Table 1; Fig. 4a,b). In *L. calceatum*, the head width increased linearly with season length, following a classic CBC (Fig. 4a). In contrast, the head width in *H. rubicundus* generated a significant quadratic term for season length, indicating that the relationship was not linear (Fig. 4b). The head width in *H. rubicundus* appeared to show very little response to season length until it began to increase at the longest season lengths. Note that the regression lines shown in Fig. 4a,b are derived from the model estimates, and thus take account of 'year' and 'grid cell' (i.e. the 8×8 km squares of given season length) as random factors.

Table 1. Parameter estimates for linear mixed-effects models explaining variation in head width in relation to season length for *Lasioglossum calceatum* and *Halictus rubicundus*.

Species	Variable	Estimate	SE	<i>t</i>	<i>P</i>
<i>L. calceatum</i>	Intercept	2.115	0.095	22.468	
	Season length	0.001	0.001	2.287	0.024*
	Season length ²	-6.91×10^{-6}	9.46×10^{-6}	-0.730	0.464
	Season length ³	3.10×10^{-7}	3.53×10^{-7}	1.131	0.311
<i>H. rubicundus</i>	Intercept	39.716	9.542	4.162	
	Season length	-0.918	0.315	-2.913	<0.001***
	Season length ²	0.003	0.315	3.167	0.002**
	Season length ³	<0.001	<0.001	1.663	0.099

P-values were obtained by sequentially removing terms from the model. **P* < 0.05; ***P* < 0.01; ****P* < 0.001.

Discussion

Previous studies of saw-tooth clines in body size have focused exclusively on solitary taxa with free-living immature forms (e.g. Mousseau & Roff, 1989; Kivelä *et al.*, 2011). Socially polymorphic sweat bees are mass provisioners and transition from expressing solitary to social behaviour, characterised by the presence or absence of a worker generation before the production of reproductives (Soucy & Danforth, 2002). It was found that while both *L. calceatum* and *H. rubicundus* were largest where the season was longest, neither exhibited saw-tooth clines of the kind hypothesised by Field *et al.* (2012) and Davison and Field (2016).

Clinal variation in body size

Overall, the largest foundresses of both *L. calceatum* and *H. rubicundus* were from areas where the season was longest, supporting previous conclusions that sweat bees follow CBCs (Richards & Packer, 1996; Soucy, 2002; Field *et al.*, 2012; Davison & Field, 2016). The body size in taxa with free-living immature forms such as butterflies and crickets often follow CBCs, supposedly because as season length gradually shortens further north, immatures have less time to spend feeding and growing. In sweat bees, however, mothers supply each developing offspring with a single ball of pollen and nectar containing all the food it will consume before reaching adulthood. As offspring body size is highly correlated with the size and composition of the provision mass (Plateaux-Quénu, 1983; Richards & Packer, 1994; Roulston & Cane, 2002), the variation in body size of offspring is likely to primarily reflect the provisioning strategies of adult bees rather than the time available for offspring to feed per se.

Adult bees in more northern or upland populations may experience environments where resources are scarcer or available for less time, or where frequently inclement weather means there are fewer opportunities to provision and oviposit (Field, 1996; Richards, 2004; Field *et al.*, 2012; Richards *et al.*, 2015). These effects probably increase the costs of provisioning (e.g. Zurbuchen *et al.*, 2010) and may lead northern foundresses to allocate each offspring with less food relative to those further south (Field *et al.*, 2012, but see Kim & Thorpe, 2001). Indeed, studies have shown that smaller offspring are produced in years with poorer weather, and when fewer resources are available (Richards & Packer, 1996; Richards, 2004).

When the season becomes sufficiently long, populations of socially polymorphic sweat bees can be social, with the final (B2) brood provisioned by workers. Workers may be able to allocate more food to each offspring because as a group they bring resources back to the nest more rapidly than does a solitary foundress (Richards, 2004). Furthermore, as foraging increases adult mortality (Kukuk *et al.*, 1998; Cant & Field, 2001), and adult survival can significantly decrease brood mortality (Eickwort *et al.*, 1996; Soucy, 2002; Zobel & Paxton, 2007), selection is likely to favour foundress provisioning strategies that maximise both offspring size and foundress survival (e.g. Jørgensen *et al.*, 2011). In social nests, however, the death of a single worker has less effect on the survival of brood because other adults can still defend the nest (e.g. Smith *et al.*, 2003). Therefore, foundresses in solitary populations may provision less intensively than workers in social nests (Field, 1996; Richards, 2004; Neff, 2008). In addition, more southern social nests might contain more workers because foundresses emerge earlier (Plateaux-Quénu, 1992; but see Richards *et al.*, 2015), more B1 females choose to work rather than enter hibernation (e.g. Yanega, 1993) or there are additional worker broods (Yanega, 1993; Strohm & Bordon-Hauser, 2003). As sweat bee eggs are relatively large (Iwata & Sakagami, 1966), workers in larger nests might collect resources faster than foundresses can oviposit. If foundresses can nevertheless prevent workers from laying their own eggs, female reproductive offspring could be allocated with more resources (Frank & Crespi, 1989; Boomsma & Eickwort, 1993), providing a further boost to the body size of foundresses further south.

Countergradient variation in the growth rate could potentially mitigate seasonal constraints on development time if bees evolve faster growth rates where the season is shorter (Conover & Schultz, 1995; Kivelä *et al.*, 2011). However, field transplants of both *H. rubicundus* and *L. calceatum* have found no evidence for genetic differences in development time between northern and southern bees (Field *et al.*, 2012; P. J. Davison and J. Field, in prep.). Instead, growth rates in sweat bees appear to be plastic and most heavily influenced by temperature (Kamm, 1974; Weissel *et al.*, 2006; Field *et al.*, 2012).

Difference between the two study species

Head width increased linearly with season length in *L. calceatum* but non-linearly in *H. rubicundus*, which showed almost

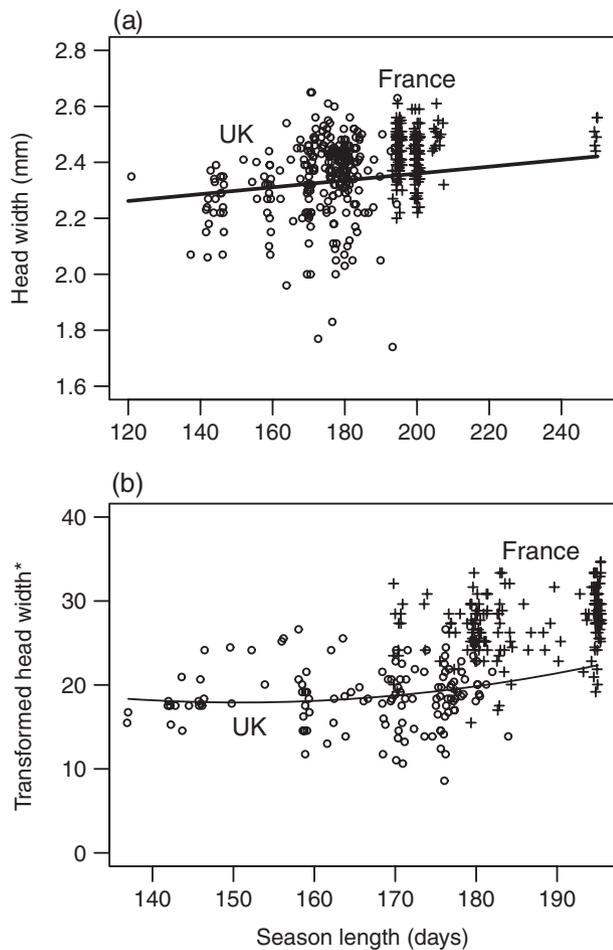


Fig. 4. Head width in relation to season length in (a) *Lasioglossum calceatum* and (b) *Halictus rubicundus*. Note the difference in the length of the x-axes. Lines shown are regression lines derived from the model estimates (see Table 1). Open circles represent specimens from the United Kingdom, crosses specimens from France. *Head width for *H. rubicundus* is transformed to the power of 5.45 using the *powerTransform* function in the R package ‘car’ (see Methods).

no change within the UK (Fig. 4). This contrasts with previous studies of *H. rubicundus* in which foundresses in cooler or more northern areas were smaller (Potts, 1995; Field *et al.*, 2012), suggesting that different results can be obtained when focusing on only a small number of sites. The near-absence of a size cline in UK *H. rubicundus* in the present study suggests that foundresses can maintain a consistent body size, perhaps by concentrating the same investment into fewer offspring as the season length shortens (e.g. Smith & Fretwell, 1974). This effect is likely to be seen most clearly where bees are solitary and offspring body size is determined by a lone foundress. As sweat bee foundresses are thought to provision only a single egg per day (Richards, 2004), differences in the effect of temperature on daily activity levels could explain this pattern (Weiner *et al.*, 2011). For example, *H. rubicundus* is a larger bee than *L. calceatum* (see Results), which might afford thermoregulatory advantages and enable foundresses to fly for longer on any

given day relative to *L. calceatum* (Stone, 1994; Bishop & Armbruster, 1999, but see Field *et al.*, 2012). However, there are no data regarding how brood sizes might vary with the change of season length in *L. calceatum* or *H. rubicundus*, and it would be particularly fruitful to determine brood sizes of both species across the range of latitudes within the UK studied in the present paper.

Why not saw-tooth clines?

In some solitary taxa such as butterflies and crickets, constraints on development may become apparent only in the directly developing first generation (Kivelä *et al.*, 2011). This is because directly developing offspring must complete their entire life cycle, whereas the diapausing generation need only reach the overwintering stage before completing development the following spring (Kivelä *et al.*, 2011). Consequently, saw-tooth clines can be more pronounced when only the directly developing first generation from bivoltine populations is considered (Masaki, 1972; Nygren *et al.*, 2008; Kivelä *et al.*, 2011). The present study focuses exclusively on the size of B2 offspring from social nests, and it is possible that a saw-tooth cline might be detected if we instead examined only B1 offspring from social nests. In sweat bees, B1 workers must emerge sufficiently early in the season to help rear a B2 (Hirata & Higashi, 2008; Field *et al.*, 2010). Moreover, smaller B1 offspring with a shorter period of growth might allow more time in the season to produce larger B2 offspring, which probably increases adult B2 female overwintering success (Sakagami *et al.*, 1984; Beekman *et al.*, 1998; Brand & Chapuisat, 2012, but see Weissel *et al.*, 2012).

As in most social insects, body size in socially polymorphic sweat bees size is intrinsically linked to social phenotype (Packer & Knerer, 1985; Schwarz *et al.*, 2007, but see Field *et al.*, 2010). Sweat bee workers are typically smaller than nest foundresses, and the production of smaller workers in sweat bees is typically viewed as a form of maternal manipulation (Richards & Packer, 1994; Brand & Chapuisat, 2012). Moreover, because foundresses in social populations can lay eggs in both broods, they have a potentially high residual reproductive value even after provisioning their B1 offspring (Kindsvater & Otto, 2014). By producing smaller B1 offspring, foundresses might conserve resources and increase their chance of remaining alive to lay B2 eggs (Field *et al.*, 2010, 2012).

Patterns analogous to caste-size dimorphism have also been detected in solitary bivoltine sweat bees, in which first generation offspring are smaller than second generation offspring despite the absence of castes (Plateaux-Quénu *et al.*, 1989, see also Kim & Thorpe, 2001). This suggests that disparity in the size of adults from spring and summer broods could occur independently of sociality (Lin & Michener, 1972; Michener, 1990). For example, resource availability may change during the year (e.g. Kim & Thorpe, 2001), and first-generation offspring may not need to be as large because they typically do not have to survive the winter. Investigating size clines in solitary bivoltine sweat bees could, therefore, help to separate the relative importance of sociality and voltinism as factors influencing how body size responds to changes in season length.

Implications for sociality

Environmental constraints on foundress body size might also generate clinal variation in caste-size dimorphism (Field *et al.*, 2012). This could have important implications for reproductive conflict within nests, because foundresses may dominate workers more easily when caste-size dimorphism is greater (Kukuk & May, 1991; Richards & Packer, 1996, but see Field *et al.*, 2010). Field *et al.* (2012) proposed that foundresses at higher latitudes might produce the smallest workers, to maximise the time available for production of B2 offspring that are sufficiently large to endure hibernation in a harsher climate. However, empirical data for *L. calceatum* and *H. rubicundus* imply that caste-size dimorphism is actually greatest in warmer areas (Sakagami & Munakata, 1972; Yanega, 1989; Plateaux-Quénu, 1992; Soucy, 2002; Davison & Field, 2016), a pattern mirrored in other social sweat bees (Packer *et al.*, 1989). It is not clear how these patterns are generated. In ants, workers tend to be largest in cooler environments, possibly as an adaptation against starvation (Heinze *et al.*, 2003; Purcell *et al.*, 2016). In sweat bees, however, workers often live for only a few days or weeks (P. J. Davison, pers. obs.). If there is little advantage in maximising worker size (Strohm & Liebig, 2008), workers may not follow a size cline at all, and larger southern foundresses might simply produce a larger number of workers given more time and resources (e.g. Robin, 1988). This would lead to a north–south cline of increasing caste-size dimorphism due entirely to changes in foundress size (Frank & Crespi, 1989). Further work simultaneously examining clines in workers and queens could prove particularly fruitful, as well as detailed studies of wild social nests to determine whether nests situated further south contain a greater number of workers.

Acknowledgements

We wish to thank the following institutions and people for the loan of specimens included in the size cline analysis: Professor Simon Potts and Rebecca Evans at the University of Reading; the Natural History Museum of London, the World Museum in Liverpool, Samantha Bailey, Mike Edwards, and Thomas Wood. David Benz, University of Oxford provided access to the AVHRR data, and Jörn Scharlemann kindly advised on analysis. This work formed part of a studentship (1119965) awarded to P.J.D. funded by the Natural Environment Research Council and the University of Sussex, supervised by J.F.. We have no conflict of interest to declare.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/een.12448

Table S1. Head width, specimen capture location, and season length data used in the study.

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Accepted 7 June 2017

Associate Editor: Hans Van Dyck