

# The role of nest composition and sunlight for thermoregulation in the nests of *Formica exsecta* (Hymenoptera: Formicidae); implications for conservation

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## Abstract

Mound building ants are dominant, ecologically important species in temperate ecosystems. In Britain, the distribution of the endangered narrow-headed ant, *Formica exsecta*, has contracted and is now restricted to several remnant populations. Ecological knowledge of this species is still in its infancy, and further insight is becoming increasingly important with the rising use of assisted colonisation. To date, research suggests that temperature and sunlight conditions largely underpin the survival of this species. In an isolated population at Chudleigh Knighton Heath, the temperature variability of populated nests was separately compared with both undisturbed soil and abandoned nests in conjunction with analyses of above-nest hemispherical photographs. Various temperature measures were quantified, followed by pairwise comparison for both monitoring periods. Light parameters were quantified through Gap Light Analyser, followed by pairwise comparison with nest size. Populated nests exhibited clear differentiation in temperature to undisturbed soil ( $t_{3552} = 59.74$ ,  $P < 0.0001$ ), but comparatively little with abandoned nests ( $t_{938} = -1.88$ ,  $P = 0.06$ ). Nests were generally situated in open areas, but no correlates were found between nest size and light parameters. The daily temperature regime of *F. exsecta* nests is likely to be predominately controlled by nest composition. In addition to the selection for nest sites in open areas, this suggests that *F. exsecta* thermoregulates nests according to sunlight induced thermal gradients. This could explain the differences in nest phenotype exhibited by this species relative to other mound building species, and could facilitate more effective conservation at this site.

**Keywords** Endangered, Formicidae, Thermoregulation, Nesting strategies

**Journal style:** Journal of Insect Conservation

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## Introduction

Ants play important ecological roles in many habitats (Del Toro et al. 2012), often as the dominant species either through sheer abundance or overall biomass, and key determinants in ecosystem structure and function (Jouquet et al. 2006; Del-Claro and Torezan-Silingardi 2009). The general consensus is that they influence ecosystems through acting as ecosystem engineers and major generalist consumers (Wills and Landis 2018). As ecosystem engineers they can affect seed dispersal (Schütz et al. 2008), nutrient cycling (Lane and BassiriRad 2005), soil structure and therefore the water infiltration and retention capacities therein. On the other hand, as consumers they can have multitrophic effects, through directly or indirectly affecting the population dynamics of other species (Del-Claro 2005; Sanders and Platner 2007). Direct effects take the form of predation and competition with other species, most of which are other arthropods (Sanders et al. 2011; Wills and Landis 2018). Indirect effects are generally induced by the presence of the ant species itself, altering prey responses (Cembrowski et al. 2013), and the distributions and survival rates of plant species (Dostál 2009).

The importance of ants is not only prevalent in ecosystems themselves; ants mediate many ecosystem services that are invaluable to humans (Del Toro et al. 2012). Moreover, ants can be used as bioindicators for many environments (Tibcherani et al. 2018). They make up a substantial proportion of the animal biomass in most ecosystems, as well as forming key myrmecophilous relationships with many species (Crist 2009). This can mean ant populations can register ecosystem changes, and can inform conservation decisions seeking to tackle these issues (Underwood and Fisher 2006).

Despite the wide range of literature addressing the importance of ants, they are severely understudied. As of 2012, out of the 12,500 species formally described (Del Toro et al. 2012), only a small proportion of species had been extensively researched beyond taxonomy. Ecological knowledge of terrestrial organisms has a clear bias towards larger vertebrate species; smaller invertebrate species, such as arthropods are often poorly understood (Jenkins et al. 2013).

In Europe, mound building ants are key, dominant organisms in grassland and forest ecosystems (Laine and Niemelä 1980); comprising up to 24% of the species in some European ant communities (Jurgensen et al. 2008). Their presence can elicit effects on soil bulk density (Jurgensen et al. 2008), mineral and nutrient composition (Lenoir et al. 2001), aphid - tree dynamics (Styrsky and Eubanks 2007) and soil fauna responsible for decomposition (Lenoir 2003). In Britain, mound building ants are continually threatened by increasing land use and fragmentation of suitable habitat (Stockan et al. 2010). Of the species that are included in the IUCN red list, the majority are listed as threatened or near threatened (Vié et al. 2008). In particular, the narrow-headed ant, *Formica exsecta*, is endangered and now only found in two remnant sites: in Devon and the Scottish Highlands (Guénard et al. 2017). Its distribution at these sites is contracting, with the loss of several former sites in Scotland (Hughes 2006). In Devon it only occurs at a single site, a reserve in Chudleigh Knighton (Littlewood and Young 2008), where it is potentially at risk from clay mining activities (Carroll 2009). The current state of *F. exsecta* is further worsened by the specific ecological conditions it requires for survival (Katzerke et al. 2010; Stockan et al. 2010). Like many mound building ants, *F. exsecta* is long-lived and is generally immobile (Katzerke et al. 2010); once established, it is slow to adapt to changing habitat conditions by relocating to more suitable areas (Bestelmeyer and Wiens 2010). Suitable nest site conditions are therefore essential for successful colony establishment and persistence (Maggini et al. 2002). Sunlight availability has generally been found to be the most important factor dictating nest survival (Maggini et al. 2002; Kilpeläinen et al. 2008; Stockan et al. 2010). This is due to the fact that *F. exsecta* cannot sufficiently thermoregulate its nests through metabolic processes, and instead relies on solar radiation to meet thermal requirements (Seifert 2000). Maintaining relatively high nest temperatures is key to brood development and production (Liebig and Poethke 2004), especially that of gyne production in this species (Kümmerli and Keller 2008). In sites that are suboptimal, *F. exsecta* queens will offset the lack of sunlight by allocating more resources to worker production, increasing the foraging capacity and retrieval of resources from nearby vegetation (Brown and Keller 2006; Kümmerli and Keller 2007). Thus the majority of nests are situated in open to marginally shaded areas, such as heathland and grassland or forest edge ecoclines respectively (Maggini et al. 2002; Schütz et al. 2008; Stockan et al. 2010). Nest construction and foraging in this species commences relatively early in spring, potentially to coincide with the development of alates (Goryunov 2016). Nest founding typically begins mid-summer, accompanied by continual growth of primary nests and

activity generally ceases in late-autumn (Goryunov 2016; Walters 2018). This relatively long nesting phenology constricts the time period over which direct conservation measures, such as translocations can take place.

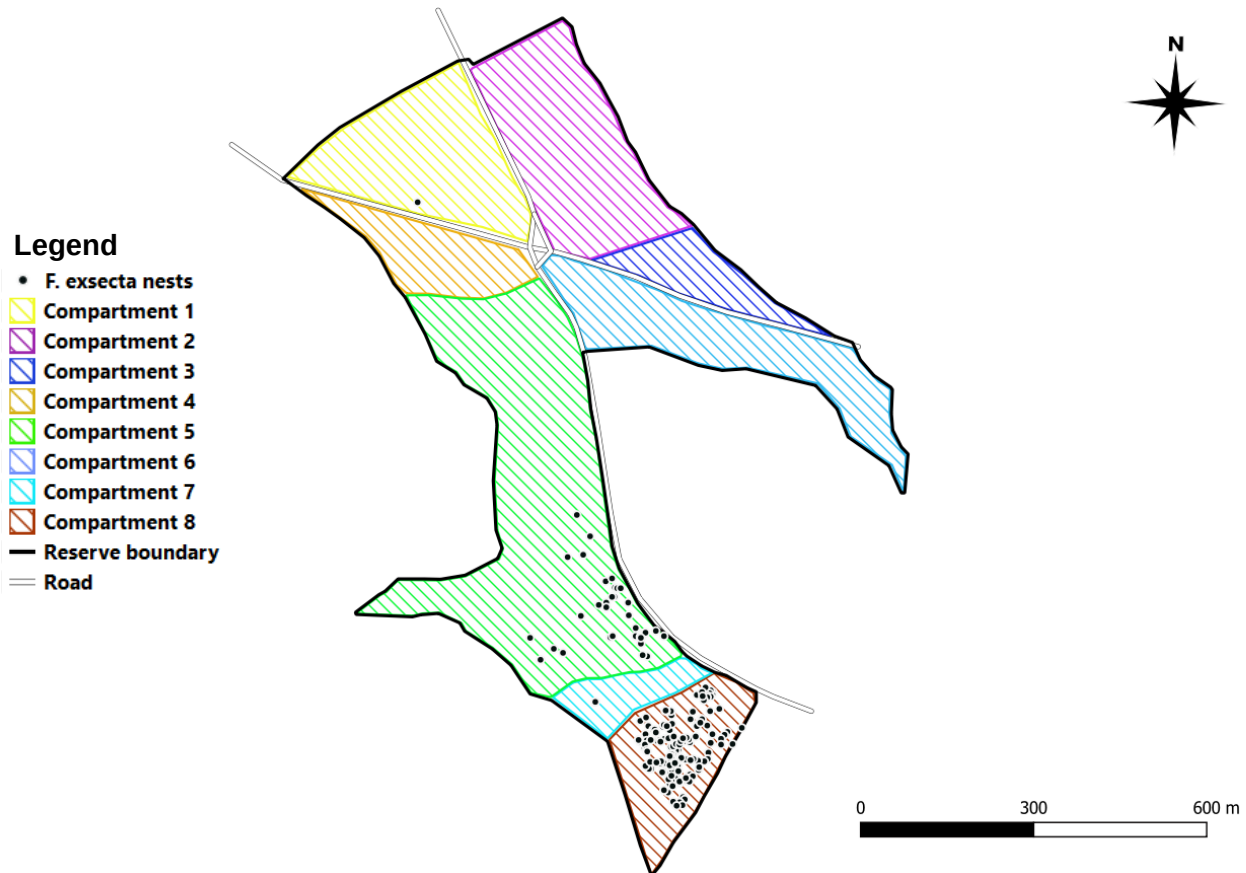
Despite recent advancements in ecological research in *F. exsecta* (Bliss et al. 2006; Stockan et al. 2010), knowledge therein is still in its infancy. This is becoming increasingly concerning given the wealth of literature recording inbreeding in this species (Sundström et al. 2003; Vitikainen and Sundström 2011; Vitikainen et al. 2015), especially in Britain, where translocation is becoming imperative in isolated populations (Carroll 2009). Previous research has outlined that both light and temperature conditions are fundamental to the survival of this species (Seifert 2000; Bliss et al. 2006; Kilpeläinen et al. 2008; Stockan et al. 2010; Goryunov 2016). Therefore, further research into the preferred light conditions and strategy of thermoregulation of this species will allow substantiation of previous hypotheses, as well as expanding current knowledge. The following questions form the basis of this study; do *F. exsecta* nests exhibit a different daily temperature regime to undisturbed soil? Does the presence of *F. exsecta* elicit an effect on nest temperatures? What are the light conditions over individual *F. exsecta* nests? To address these questions, separate comparison of monitored temperatures was conducted between a) populated, active *F. exsecta* nests and undisturbed soil, and b) populated, active *F. exsecta* nests and abandoned, inactive *F. exsecta* nests. Analyses of hemispherical photographs was also conducted to investigate the above-nest light conditions of this species.

## Materials and Methods

### *Study area*

Fieldwork was carried out between June and August - November 2018 at two compartments within the Devon Wildlife Trust reserve, Chudleigh Knighton Heath (50° 35' 5.64" N, -3° 38' 31.56" W). This site houses the only *F. exsecta* population in England (Stradling and Hoy 1993), with the only comparable sites in Strathspey, Scotland (Stockan et al. 2010). Compartment 8 and 5 contain the largest proportion of the reserves' population, with compartment 8 housing the majority (see Fig. 1). Both compartments are managed through a combination of rotational cattle grazing and controlled burning regimes, with annual mowing

of select paths. This creates a mosaic of habitat types, with patches dominated by Bracken (*Pteridium aquilinum*), mature Western Gorse (*Ulex gallii*), and recently burnt areas undergoing secondary succession. Both compartments are fragmented through mown paths and contain a small percentage of mature trees.



**Fig. 1** Location of *F. exsecta* nests and corresponding reserve compartments at Chudleigh Knighton Heath SSSI (GPS coordinate data obtained from Walters (2018)).

### *Temperature monitoring*

Data collection for this aspect of the study was carried out in two observation periods; the first for 74 days from June 21<sup>st</sup> to 2<sup>nd</sup> September 2018, the second for 18 days from the 28<sup>th</sup> September to 17<sup>th</sup> October 2018. A total of nine nests were used for the first observation period, and 8 for the second observation period. In the first observation period, the temperature difference between nests and undisturbed soil was quantified. This entailed the deposition of data loggers within nests and a randomly selected point in the surrounding habitat (1 m away from the edge of the given nest), at a nest thatch and soil depth of 3-5 cm

respectively. The largest nine nests of the population were selected for this period, on the basis that the largest nests are the least vulnerable and most resilient (Middleton and Latty 2016) and as such are the least affected by physical perturbation of nest material when inserting data loggers. Soil temperatures were considered as a control, against which nest temperatures would be compared. In the second observation period, the temperature difference between populated and abandoned nests was quantified. This second observation period involved the insertion of data loggers within both populated and abandoned nests. Eight nests were selected for this observation period, comprising four populated and four abandoned nests. Nests were deemed to be populated and active if they only contained *F. exsecta* individuals and no other ant species. Selected populated nests were either the most proximate nest to the abandoned nest, or previously identified as the colony responsible for the production of the abandoned nest due to relocation. Nests identified as abandoned were nests which had no ant species within the mound and were previously identified as populated nests earlier in the season. All data loggers were attached to garden wire for ease of retrieval. In contrast to the first observation period, individual pairs were not assigned in the second observation period as none were selected. All data loggers were inserted at a depth of 3-5 cm for both observation periods.

DS1922L-F5# Thermochron iButton 8K (Temperature range: -40 to 80 °C) data loggers were used for all temperature monitoring, as they provided long term monitoring and could be deposited within nests with relatively little disturbance to the colony itself. iButton data loggers were programmed using OneWireViewer version 1.5 to measure temperature at 30-minute intervals, from the midnight of the first day of deposition until the day of retrieval. All data loggers were set to the standard Greenwich Mean Time (GMT).

### *Hemispherical photography*

A representative sub-sample of nests (n=56) was selected from both compartments to quantify light conditions. A total of 56 nests was used for this aspect of the study, the majority of which were situated in compartment 8 simply due to the larger quantity of nests located there (see Fig. 1). All photography was carried out using a Nikon E990 camera, Fisheye lens FC-E8, JB01505-BWW GorillaPod 325 Tripod and a spirit level. The hemispherical photography was conducted in accordance with the protocol outlined in Frazer et al. (1999).

In addition, the location of the camera in relation to the nest was centred as the mid-point of a predetermined cross-section, and the GorillaPod made flush with the nest thatch.

All photographs were post-processed in ImageJ, using the colour threshold tool to avoid inclusion of above-canopy sky area. Analysis of images was conducted in Gap Light Analyser (GLA) version 2.0 (Frazer et al. 1999), obtaining data on gap fractions, solar irradiation, leaf area index (LAI), sun-path plots and sunfleck distribution. As recommended by Sasaki et al. (2008), leaf area index data was only obtained from ring 5 (0-75°) due to the fact that this measurement takes more of the canopy area into account. Configuration with regards to the geographical location of the site was only produced for the site, rather than individual configurations for each nest location.

### *Data analysis*

All data analyses were conducted using R (Development Core Team 2018) through RStudio version 3.5.1 (Rstudio Team 2016); using packages ggplot2 (Wickham et al. 2018), ggpmisc (Aphalo 2018), lubridate (Spinu et al. 2018), dplyr (Wickham et al. 2019), gridExtra (Auguie 2017) and tidyverse (Wickham 2017). Data outputs from GLA were processed and analysed using packages tidyverse and dplyr. Transformation of date and time data from OneWireViewer was carried out using package lubridate to ensure compatibility with analyses. R base functions were used for shapiro-wilk tests, paired t tests, Pearson's product-moment correlation test and calculation of temperature measures. Heating and cooling rates were obtained from the mean diurnal temperature trends of each logger. Heating rates were quantified as the hourly rate of increase in temperature between the mean minimum temperature and the corresponding mean maximum temperature. Cooling rates were calculated as the hourly rate of decrease in temperature between the mean maximum temperature and the corresponding mean minimum temperature. Finally, packages ggplot2, ggpmisc and gridExtra were used for the visualisation of key findings.

## Results

As predicted, temperatures within populated *F. exsecta* nests were dissimilar to temperatures in undisturbed soil (Table 1). Generally, populated nest temperatures were significantly higher than soil temperatures ( $t_{3552} = 59.74$ ,  $P < 0.0001$ , see Table 4 in appendix for pairwise comparison). Moreover, populated nests had far better thermal conductance than the surrounding soil (Table 1), producing clearly steeper diurnal temperature trends (Fig. 2a). Specifically, populated nests had substantially higher heating rates (Table 1), resulting in higher maximum temperatures ( $38.2 \pm 5.54$  vs  $35.29 \pm 14.89$ ), and significantly lower cooling rates ( $t_8 = 3.67$ ,  $P < 0.01$ ), resulting in lower minimum temperatures ( $6 \pm 1.53$  vs  $6.5 \pm 4.97$ ).

**Table 1.** Comparison of temperature measures between populated *F. exsecta* nests (n=9) and their respective soil controls (n=9) obtained from iButton data loggers in Chudleigh Knighton Heath.

Measure	Nest	Control	t	d.f.	P-values
$T_{\text{mean}}$	$20.84 \pm 6.32$	$18.19 \pm 4.14$	59.74	3552	$P < 0.0001$
$T_{\text{max}}$	$38.2 \pm 5.54$	$35.29 \pm 14.89$	0.6	8	$P = 0.57$
$T_{\text{min}}$	$6 \pm 1.53$	$6.5 \pm 4.97$	-0.29	8	$P = 0.78$
Heating rate ( $^{\circ}\text{C hr}^{-1}$ )	$1.68 \pm 0.45$	$1.14 \pm 0.54$	2.23	8	$P = 0.056$
Cooling rate ( $^{\circ}\text{C hr}^{-1}$ )	$-1.11 \pm 0.21$	$-0.7 \pm 0.27$	3.67	8	$P < 0.01$

Shown are mean  $\pm$  1 standard deviation, t statistic, degrees of freedom and significance level from paired t-tests. T denotes temperature ( $^{\circ}\text{C}$ ) of the corresponding measure, i.e.  $T_{\text{mean}}$  is the mean temperature,  $T_{\text{max}}$  is the mean maximum temperature and  $T_{\text{min}}$  is the mean minimum temperature.

**Table 2.** Comparison of temperature measures between populated (n=4) and abandoned (n=4) *F. exsecta* nest structures obtained from iButton data loggers in Chudleigh Knighton Heath.

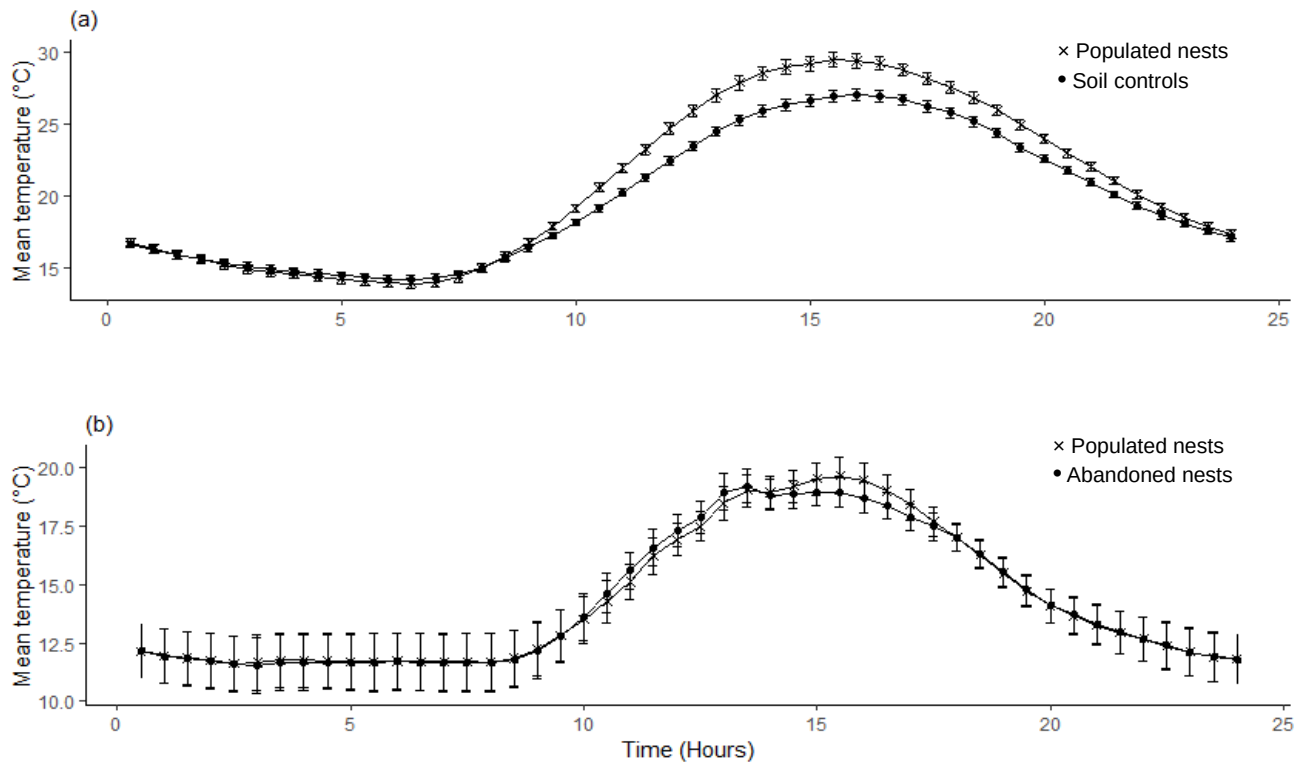
Measure	Populated	Abandoned	t	d.f.	P-values
$T_{\text{mean}}$	$14.26 \pm 5.07$	$14.23 \pm 5.05$	-1.88	938	$P = 0.06$
$T_{\text{max}}$	$30.3 \pm 2.42$	$28.6 \pm 2.80$	0.92	3	$P = 0.43$
$T_{\text{min}}$	$1.1 \pm 2.59$	$0.96 \pm 2.3$	0.15	3	$P = 0.9$
Heating rate ( $^{\circ}\text{C hr}^{-1}$ )	$0.8 \pm 0.38$	$0.77 \pm 0.18$	0.28	3	$P = 0.8$
Cooling rate ( $^{\circ}\text{C hr}^{-1}$ )	$-0.59 \pm 0.23$	$-0.61 \pm 0.2$	0.25	3	$P = 0.83$

Shown are mean  $\pm$  1 standard deviation, t statistic, degrees of freedom and significance level from paired t-tests. T denotes temperature ( $^{\circ}\text{C}$ ) of the corresponding measure, i.e.  $T_{\text{mean}}$  is the mean temperature,  $T_{\text{max}}$  is the mean maximum temperature and  $T_{\text{min}}$  is the mean minimum temperature.

Contrary to predictions, populated nests were not substantially different in temperature to abandoned nests ( $t_{938} = -1.88$ ,  $P = 0.06$ ). Further, temperature measures were relatively similar between the nest types (Table 2). This is best exemplified in Fig. 2b, wherein the mean daily temperature regime was relatively similar, only showing slight differentiation in the afternoon hours where populated nests reached a somewhat higher mean temperature. Specifically, populated nests had slightly higher heating rates than abandoned nests ( $0.8 \pm$



0.38 vs  $0.77 \pm 0.18$ ), consequently reaching relatively higher maximum temperatures ( $30.3 \pm 2.42$  vs  $28.6 \pm 2.80$ ). Conversely, populated nest cooling rates were relatively similar to abandoned nests ( $-0.59 \pm 0.23$  vs  $-0.61 \pm 0.2$ ), resulting in very little difference in minimum temperatures between the two nest types ( $1.1 \pm 2.59$  vs  $0.96 \pm 2.3$ ).



**Fig. 2** Mean daily temperature curves including standard error bars comparing (a) populated nest temperature and corresponding soil control temperature, and (b) populated nest temperature and corresponding abandoned nest temperature.

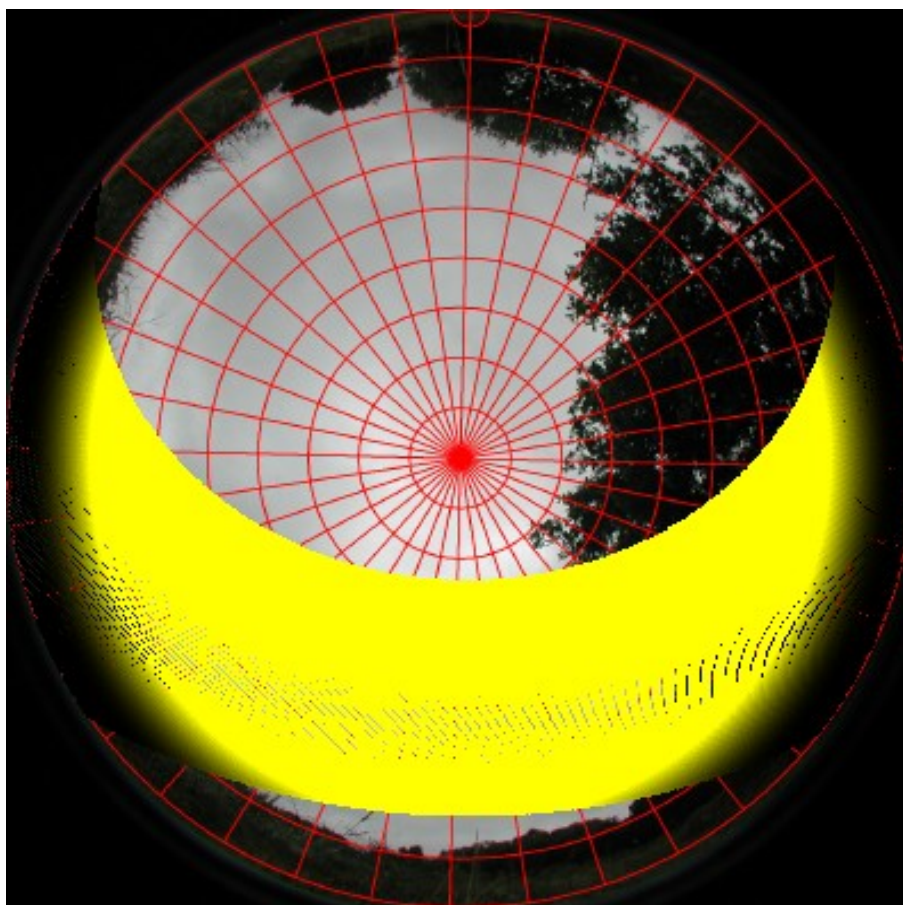
Nests of *Formica exsecta* were predominately situated in relatively open, bright areas with a high incidence of sunlight (Table 3). Sun-paths were found to be closer to the zenith relative to the nest position (Fig. 3). If canopy cover was present, the majority was proximate to the edge of the fisheye photographs, i.e. near the horizon relative to the nest position (Fig. 4). Interestingly, nest diameter had no significant relationships with any of the light parameters (Table 3).

**Table 3.** Light parameters obtained from GLA describing the canopy structure above *F. exsecta* nests (n=56) in Chudleigh Knighton Heath, with corresponding correlation results with diameter of nests (cm).

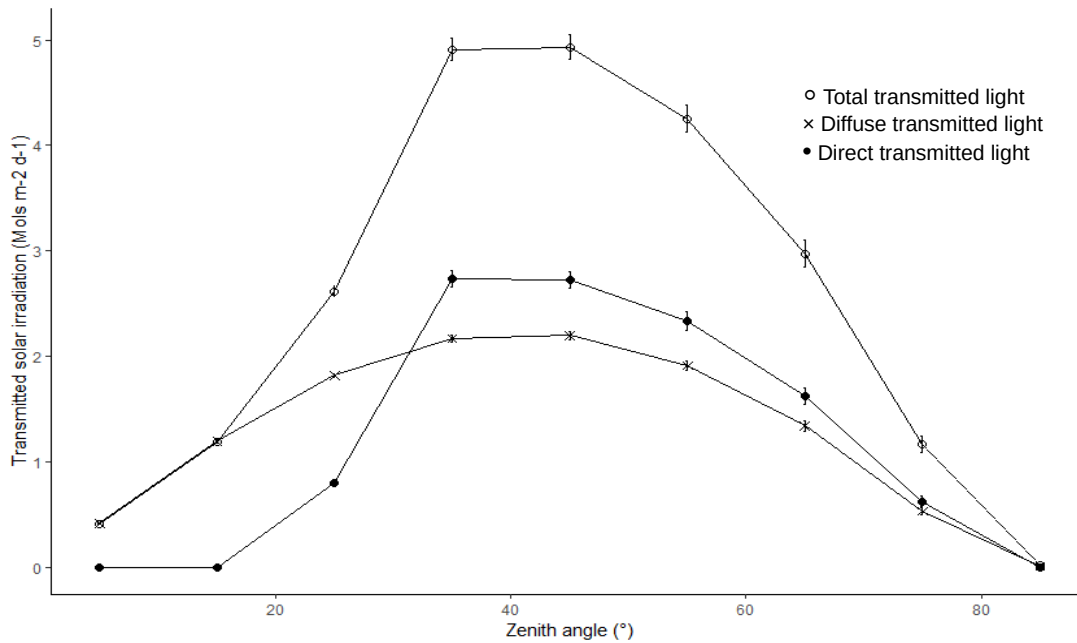
Parameter	Mean	r	t	d.f.	P-values
Canopy openness (%)	7.18 ± 4.36	-0.029	-0.19	43	0.8486
Total transmitted light (Mols m <sup>-2</sup> d <sup>-1</sup> )	2.5 ± 1.91	-0.023	-0.14882	43	0.8824
Direct transmitted light (Mols m <sup>-2</sup> d <sup>-1</sup> )	1.21 ± 1.19	0.0039	0.026	43	0.9797
Diffuse transmitted light (Mols m <sup>-2</sup> d <sup>-1</sup> )	1.21 ± 1.19	-0.074	-0.49	43	0.6285
Gap fraction *	0.76 ± 0.33	-0.06	-0.4	43	0.6931
Leaf area index	0.23 ± 0.18	-0.018	-0.12	43	0.907
Total sunfleck frequency	3383.18 ± 2270.68	0.039	0.26	43	0.7976
Daily sunfleck duration (Minutes)	393.21 ± 97.08	0.2	1.32	43	0.1962

Shown are mean ± 1 standard deviation, r value, t statistic, degrees of freedom and significance level from Pearson's product moment correlation test.

\* Gap fraction is expressed as the ratio of sky pixels to total pixels per sky region segment (see Frazer et al. 1999).

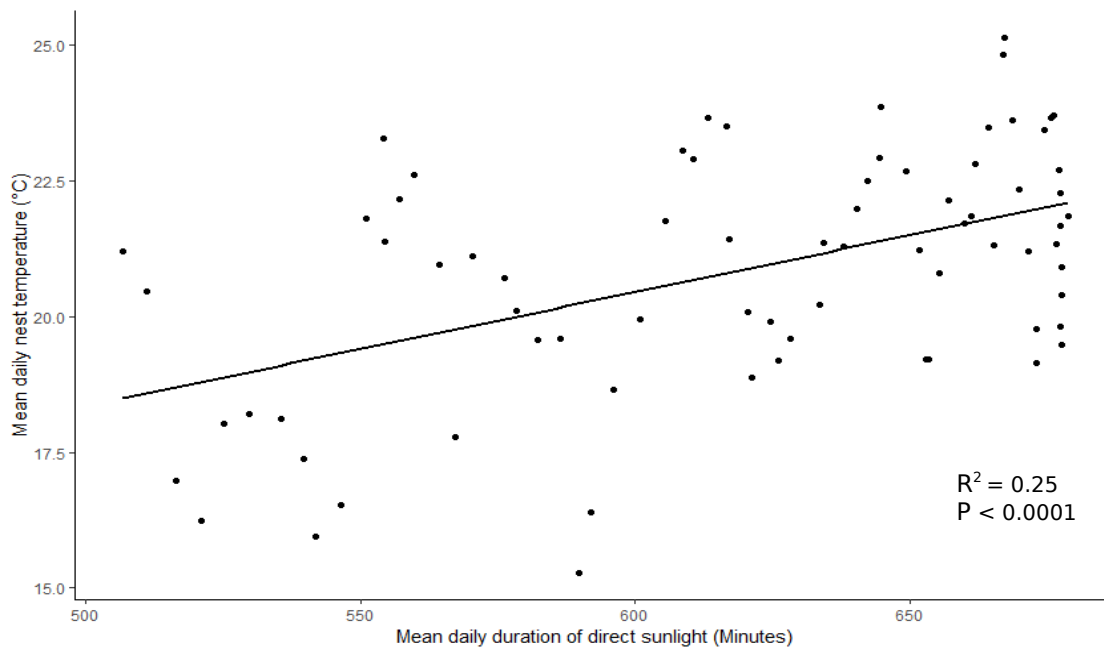


**Fig. 3** Example projection of sun-paths on a hemispherical photograph of the above-nest canopy at Chudleigh Knighton Heath, obtained from GLA.



**Fig. 4** Mean transmitted solar irradiation (Total, direct and diffuse light) including standard error bars, over corresponding Zenith angles.

Canopy cover was found to share a significant association with nest temperatures ( $t_{72} = 4.91$ ,  $P < 0.0001$ ), wherein increasing daily duration of sunlight corresponded to an increase in mean nest temperatures (Fig. 5).



**Fig. 5** Scatter plot with corresponding regression line for the relationship between mean daily duration of direct sunlight and mean daily nest temperature. Included are  $R^2$  and P-value from the corresponding Pearson's product-moment correlation test.

## Discussion

Nest temperatures were found to be generally higher than undisturbed soil temperatures, as well as having higher heating and cooling rates (Table 1). Moreover, populated nests exhibited little differences in nest temperature in comparison to abandoned nests (Table 2). Considering both findings, *F. exsecta* nests appear to have higher thermal conductance than the surrounding soil, which may be driven by the unique composition of the thatch layer considering the lack of temperature differentiation found between populated and abandoned nests (Table 2, Fig. 2b). Some degree of nest heating may be induced by the ants themselves, considering the higher heating rates found in populated nests (Table 2, Fig. 2b). Investigation into thermoregulation and nesting temperatures has been widely conducted in *Formica* ants (Rosengren et al. 1987; Kadochová and Frouz 2014) but is relatively understudied in *Formica exsecta*. In studies of similar *Formica* species, daily temperature regimes similar to those observed in this study were found to be caused by three main factors; the unique composition of the nest material, the biological activity of the ants themselves or that of microbial species (Frouz 2000; Kadochová and Frouz 2014). Research where nest composition was observed to elicit significant effects on nest temperature, found that the thatch layer had surprisingly lower thermal diffusivity than undisturbed soil (e.g. *Formica obscuripes*, McIver et al. (1997)). This is in opposition to the findings in our study, but it is important to bear in mind the differences in thatch construction between the species; *F. obscuripes* constructs a much larger and denser thatch than *F. exsecta* (McCahon and Lockwood 1990; Seifert 2000) and so insulation properties would be expected to be higher in the former. Nonetheless, further study into the degree of heat transfer between the thatch layer and soil core of *F. exsecta* could provide invaluable insights. Heating induced by microbial activity is unlikely in nests of *F. exsecta*, as most remain dry nests due to minimal canopy cover (Seifert 2000; Stockan et al. 2010). Nests of *Formica* species where microbial activity does have a substantial influence are situated in shaded, wet conditions where humidity is higher, and temperatures are more stable (Frouz 2000). Moreover, nest temperatures would be expected to be higher during the night when microbial activity causes a noticeable heating effect (minimum nest temperatures were in fact lower than corresponding soil controls, Table 2) (Frouz 2000; Jílková and Frouz 2014). Given the variation in canopy cover measurements (Table 3), thermoregulation by microbial activity may be apparent in some more shaded nests but is likely to be negligible relative to the population

as a whole. Heating induced by the ants themselves has been substantiated in other studies, which found that differentiations in nest temperature relative to undisturbed soil corresponded with changes in worker ant activity (Rosengren et al. 1987; Frouz 2000; Horstmann and Schmid 2013; Kadochová and Frouz 2014). The highest temperatures in both observation periods were during afternoon hours (Fig. 2), with nests containing *F. exsecta* having additionally higher temperatures; this corresponds with other studies where the return of foragers stimulated heating of nest material (Frouz 2000; Kadochová and Frouz 2014). However, the species where this phenomenon was reported had large nests with distinct foraging groups (namely *F. polyctena*, Frouz (2000); Horstmann and Schmid (2013)), which would be largely absent from the relatively small nests of *F. exsecta* at Chudleigh Knighton Heath. Further investigation would be required to confirm if foraging behaviour did in fact affect the daily temperature regime of *F. exsecta* nests.

Thermoregulatory strategies found in mound building ants generally fall into the following two categories: either moving brood according to thermal gradients or maintaining stable temperatures within their nests (Kadochová and Frouz 2014). Considering the results obtained in this study, it can be speculated that *Formica exsecta* moves their brood according to thermal gradients. In light of the fact that little temperature differentiation was found between populated and abandoned nests (Table 2, Fig. 2b) and that duration of direct sunlight shares a positive association with nest temperature (Fig. 5), thermal gradients within individual nests are likely to be natural (i.e. caused by sunlight) rather than induced by the biological activity of the ants themselves. This is further supported by field studies at this site, wherein workers translocated brood when nest temperatures were artificially increased in the nest thatch (Walters 2018). Moving brood to warmer conditions could accelerate brood development and egg production (Liautard et al. 2003; Kümmerli and Keller 2008; Alfimov et al. 2011), but at the cost of worker longevity. Favouring reproduction over growth in this way could explain why *F. exsecta* nests never reach the size of larger *Formica* species (Kilpeläinen et al. 2008; Kadochová and Frouz 2014). Employing this strategy would be of great benefit to the colonisation of early successional habitats which *F. exsecta* inhabits (Seifert 2000). Higher worker production rates would allow for rapid construction of nests, either for relocation or creation of satellite nests; both of which are often required in stressed environments (Stockan et al. 2010). Considering that nest relocation and budding (production of satellite nests) is frequent at Chudleigh Knighton Heath (Walters 2018), habitat conditions

may be sub-optimal and potentially stressed. Of further support is the fact that nest diameter, a measure of colony success (Stockan et al. 2010), appears lower relative to populations elsewhere (e.g. Mark et al. 2012).

Initial analyses of light parameters indicated that in general, *F. exsecta* nests were located in characteristically open areas (Table 3). This result further supports previous findings in the literature, where *F. exsecta* was found to select nest sites with a high degree of sunlight (Stockan et al. 2010). This is due to the unique thermal requirements of this species (Seifert 2000), whereby individual nests are not large enough both in size and worker count to be capable of sufficient nest thermoregulation (Chen and Robinson (2014)). As such, nests require a higher degree of solar radiation to achieve adequate nest heating for key developmental processes (Kümmerli and Keller 2008). This has been widely reported and could be suggested as the primary reason why this species is outcompeted by more populous species in forest stands (Vepsäläinen and Pisarski 1989; Cerdá et al. 2013; Adams 2016).

Much of the above-nest canopy cover was found to be proximate to the horizon relative to the nest position in this study (Fig. 4). Considering that the majority of sun-paths are closer to the zenith (Fig. 3), the proportion of direct sunlight would be higher closer to the zenith. Direct sunlight has a higher intensity than diffuse sunlight (Press 1976), and as such would elicit higher heating rates of nest material. Nest sites situated in areas where there is less obstruction of direct sunlight would therefore have greater heating of nest material during daytime hours. This is supported by the significant positive correlation found between the duration of direct sunlight and nest temperature (Fig. 5). In line with the previous finding, this additional criteria for selecting nest sites is likely explained by the fact that sufficient nest heating is essential for key developmental processes in *F. exsecta* (Liautard et al. 2003; Kümmerli and Keller 2008). Increased nest heating capabilities by means of increased direct sunlight would be expected to benefit this, explaining the selection of nesting areas found in this study.

Nest size was not associated with any of the light parameters reported in this study (Table 3), indicating that there are other ecological factors to account for to understand what determines nest size in *F. exsecta*. There are many ecological determinants of nest size for mound building ants, the majority are temperature related factors and resource availability

determinants (Sudd et al. 1977; Rosengren et al. 1987; Sorvari and Hakkarainen 2005; McGlynn et al. 2009; Pearce-Duvet and Feener 2010; Chen and Robinson 2014). Nest size may therefore not be associated with canopy cover, as it is only one potential determinant among many contributing factors, even if it is hitherto referred to as the most important for *F. exsecta* (Bliss et al. 2006; Schütz et al. 2008; Stockan et al. 2010). Other ecological factors, such as proximity to key foraging resources, will need to be investigated to explain the variance in nest sizes within the population. Moreover, the only measure of nest size used in this study was diameter, as it was assumed that colony size increases with nest diameter. Other studies investigating the effects of canopy cover on nest size quantified the total worker count of individual nests (e.g. Chen and Robinson (2014)). Direct measurement in this way will provide a more accurate representation of any potential relationships than the proxy used here, and could form the basis of future investigation where time constraints would not restrict the use of this methodology.

Assisted colonisation through translocation is becoming vital to the practical conservation of *F. exsecta* at this site. Current efforts focus on habitat management of already occupied areas, with annual translocations attempting to broaden the range of this species. Translocation attempts thus far have been met with some difficulties, particularly with ensuring establishment and persistence of translocated nests (Carroll 2009; Walters 2018). Similar issues have been found in other populations, and were suggested as symptoms of sub-optimal habitat (Stockan et al. 2010). Ecosystem pressures that could cause this are intraspecific and interspecific competition, disturbances and resource limitation (Vepsäläinen and Pisarski 1989; Seifert 2000; Kümmerli and Keller 2008; Schütz et al. 2008; Stockan et al. 2010; Adams 2016). Intraspecific competition is known to be high between monogynous nests (Seifert 2000), and polygynous, polydomous colonies are often referred to as a safer strategy in stressed environments (Maggini et al. (2002); but see Mark et al. (2012)). Considering that not all nests are polygynous, polydomous at Chudleigh Knighton Heath (Goropashnaya et al. 2007; Carroll 2009) and that nest density is particularly high in some areas (Walters 2018), interference and exploitative competition between conspecifics could therefore be high. Moreover, *F. exsecta* also exhibits obligate dominance (Vepsäläinen and Pisarski 1989; Putyatina et al. 2017); unlike polydomous nests, intra-territorial boundaries exist between monogynous nests (Erős et al. 2009). Maintenance of territory coupled with high intraspecific competition, could lead to especially difficult nest establishment in novel territory. Interspecific

competition is also likely to be present at Chudleigh Knighton Heath, considering both *Lasius niger s.l.* and *Formica rufa* have been found to occur in close proximity to *F. exsecta* nests (Walters 2018). Both species are known to competitively exclude *F. exsecta* (Carroll 2009; Adams 2016; Walters 2018) and could explain the large amount of suitable but unoccupied nest sites. The presence of grazing ungulates, whether cattle or red deer, are also likely to put pressure on *F. exsecta* either through exploitative competition or the trampling of nests; both pressures have been observed impacting other populations (Schütz et al. 2008). It could be speculated that each one of these pressures could explain the particular thermoregulatory and nest site selection strategies exhibited by *F. exsecta* at this site, and potentially in other populations. Both strategies could be employed as a means to increase reproductive output as outlined above; mediating territorial dominance between conspecifics and other species. The establishment and persistence of translocated nests may therefore depend on selecting nest sites where such pressures are lessened in severity or can be moderated.

In conclusion, the nest thatch of *F. exsecta* has been shown to have higher thermal conductance relative to undisturbed soil, most likely due to its unique composition. Individual nests were also found in relatively open, bright areas with little canopy cover, which may be selected as nest sites to complement the specific thermal requirements of this species. Considering both findings suggests that *F. exsecta* thermoregulate according to sunlight induced thermal gradients, possibly to thermoregulate their brood. Of further support is the positive correlation found between direct sunlight duration and temperature. The particular thermoregulatory and nest site selection strategies observed in this study are likely employed to complement the developmental processes of this species. These strategies could also be employed as a response to ecosystem pressures, indicating that habitat at Chudleigh Knighton Heath may be sub-optimal. Finally, further investigation into the interactions between *F. exsecta* and their biotic environment could provide invaluable insights and facilitate more effective conservation management.



## Acknowledgements

The author would like to thank Dr. Miguel Franco for his advice throughout this study and invaluable comments on a previous version of this manuscript. The author would also like to thank Stephen Carroll, John Walters, Jane Akerman, Alex Fraser, and Daria Wisniewska for their assistance with fieldwork. Funding for this study was provided by the University of Plymouth. The author declares that this article content has no conflicts of interest.

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## Appendix

**Table 4.** Pairwise comparison of temperature measures between populated *F. exsecta* nests (n=9) and their respective soil controls (n=9) obtained from iButton data loggers in Chudleigh Knighton Heath.

Measure	Nest	Control	t	d.f.	P-values
Pair 1	21.93 ± 8.14	17.72 ± 4.29	57.34	3552	P < 0.0001
Pair 2	18.3 ± 4.25	18.33 ± 3.92	-1.4	3552	P = 0.163
Pair 3	21.28 ± 7.19	19.15 ± 7.05	32.31	3552	P < 0.0001
Pair 4	21.69 ± 8.22	19.23 ± 3.96	30.01	3552	P < 0.0001
Pair 5	19.98 ± 6.15	16.84 ± 2.13	42.69	3552	P < 0.0001
Pair 6	21.23 ± 5.98	18.23 ± 8.41	29.27	3552	P < 0.0001
Pair 7	19.95 ± 4.74	18.62 ± 5.01	40.35	3552	P < 0.0001
Pair 8	20.54 ± 6.54	16.69 ± 2.05	48.9	3552	P < 0.0001
Pair 9	22.63 ± 6.84	18.91 ± 3.51	63.63	3552	P < 0.0001

Shown are mean ± 1 standard deviation, t statistic, degrees of freedom and significance level from paired t-tests.