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**Geographic variation in air temperature
leads to intraspecific variability in the
behavior and productivity of a eusocial insect**

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**Running head: Intraspecific differences in behavior and colony
productivity**

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Abstract

30 In primitively eusocial insects, air temperature is the environmental factor that
primarily affects colony cycle. Several studies demonstrated interspecific differences in
the adaptation of eusocial insects to local air temperature. Nevertheless, studies on
intraspecific adaptations are rare. In this study, we investigate the influence of air
temperature on local adaptations in behavior and colony productivity of *Polistes biglumis*
35 foundresses living in warm and cold temperate zones. We hypothesized that foundresses
from warm temperate zones would show a higher activity level compared to those from
cold temperate zones before brood emergence, based on differences in air temperature
between the two zones. After brood emergence, we expected a reduced foundress
activity level in the warm climate zone, due to workers' help. In contrast, foundresses
40 living in the cold-climate zone, which do not produce workers, were expected to remain
active throughout the nesting season. We also hypothesized that colony productivity was
higher in warm-climate colonies. As expected, warm-climate foundresses reduced their
activity level after brood emergence and, with their relatively large number of workers,
continued egg production throughout the nesting season. Further studies are necessary
45 to assess if these intraspecific differences are attributable to phenotypic plasticity or
genetic divergence.

**KEY WORDS: SOCIAL INSECTS; *POLISTES BIGLUMIS*; SOCIAL
TRAITS; PRODUCTIVITY; INTRASPECIFIC VARIABILITY**

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Introduction

Climate is a physical force that can shape numerous life history traits of an organism and thus delineate distinct characteristics that define a species. Nevertheless, sometimes different climate regimes also generate
55 trait differences among individuals or populations belonging to the same species (e.g., Husby et al. 2010; Oliveira et al. 2013). Understanding the effects that climate has on the ecology and phenology of a species, as well as determining the ability of a species to adapt to different climate regimes, is essential because it gives us the ability to foreseen how
60 ecosystems will react to climate changes in the long-term (Somero 2010).

In eusocial insects, air temperature can impact the activity level of colony members, their social roles, the colony cycle, and the colony productivity. Differences in local air temperatures cause, for example, marked interspecific differences in social structure and behavior in the
65 genus *Polistes* (Hymenoptera, Vespidae; Yamane 1996). *Polistes* paper wasps are independent-founding eusocial insects. Species living in temperate zones share common features in their colony cycle: mated females hibernate in winter, then found a nest solitarily or in association, and incur very expensive processes, like provisioning of a first brood of
70 workers. After first-brood emergence, namely during the post-emergence phase (Reeve 1991), these workers take over foraging and provision a second brood that consists typically of reproductives (males and gynes). However, species living at different climatic conditions present differences in their colony cycle and social structure. Lorenzi and Turillazzi (1986)
75 documented that *P. biglumis* foundresses living in cool temperate zones in

the Alps were the most active females in their colonies, foraging and feeding larvae both before and after brood emergence. Foundress active behavior was most likely due to the harsh climate conditions they experienced. Low annual mean air temperature (3.7 °C) limited the length of the colony activity to 3.5-4 months and the number of brood produced annually to less than 30 individuals. In contrast, *Polistes* spp. from warm temperate zones, living at relatively lower altitudes and higher temperatures, have a longer nesting season (approximately 6 months; Reeve 1991) and foundresses produce relatively larger broods (e.g., about 250 adults produced annually in *P. chinensis* colony; Miyano 1980). Up until now, most studies have focused on interspecific variation in *Polistes* colony productivity in response to climatic conditions, while studies on intraspecific variation have been rare (e.g., Yamane 1972; Yamane and Kawamichi 1975; Miyano 1980; Inagawa et al. 2001).

In the present study, we investigated the influence of climate on activity level and productivity of *P. biglumis* foundresses living in warm and cold temperate zones. We expected that foundresses living in warm temperate zones would exhibit higher activity level than foundresses living in cold climate during the pre-emergence phase, and that they would reduce their activity in the post-emergence phase. We also expected that warm-climate foundresses would produce higher numbers of brood compared to their cold-climate conspecifics.

Materials and methods

100 Study sites and populations

During the summers of 2006 and 2007, we studied in the field foundress behavior and colony productivity of three *Polistes biglumis* populations living in the Alps and one living in the Apennines. For details on the species distribution and colony cycle, see Lorenzi and Turillazzi
105 (1986) and Fucini et al. (2009).

Alpine populations – Alpine populations were located near Montgenèvre (Hautes Alpes, France, 1850 m a.s.l.), Ferrere (Valle Stura di Demonte, Cuneo, Italy, 1900 m a.s.l), and Carì (Val Leventina, Cantone Ticino, Switzerland, 1650 m a.s.l). The mean monthly air temperature in
110 the nesting season ranged between 8 and 13 °C. Wasps were active for about 6 hours/day (Fucini et al. 2009).

Apennine population - The Apennine population was located near Monte Mare (Abruzzo National Park, Lazio and Molise, Isernia, Italy, 1740 m a.s.l). The climate was relatively milder than the Alpine climate, with
115 mean monthly air temperatures 6-7 °C higher. The length of the wasp daily activity period was about 9 hours (Fucini et al. 2009).

A total of 478 colonies was found in 2006 (Ferrere: n = 129, Montgenèvre: n = 139, Carì: n = 71 and Monte Mare: n = 139) and a total of 349 in 2007 (Ferrere: n = 104, Montgenèvre: n = 96, Carì: n = 72 and
120 Monte Mare: n = 77). We individually marked each nest with a number and each foundress with a unique color combination using enamel paint.

Foundress activity

We conducted behavioral observations in the field on a total of 79
125 colonies in 2006 and 106 in 2007. We collected behavioral data for
one/two continuous hours per nest (depending on weather conditions)
between 0830 and 1700 hours local time in the Apennines and between
1000 and 1600 hours local time in the Alps, for a total of about 320 hours
of observation time (149 hours in 2006 and 171 in 2007), during both the
130 pre- and post-emergence phase (see Table 1 for details).

We measured time spent off nest (i.e., foraging) by noting departure
and arrival time of the foundresses. We also measured the time spent
resting on the nest. Other activities performed by the foundresses during
the observation time were noted but not included in the analyses.

135 Behavioral data were analyzed as percentage of the observation time
spent foraging or resting on the nest.

Colony productivity

We measured nest size and colony productivity by counting the total
140 number of cells and immature brood in each nest approximately once a
week throughout the nesting season. During pre-emergence, we classified
large larvae and pupae as first brood, while eggs and small larvae were
defined as second brood. Cells that were not occupied by immature brood
(usually peripheral cells) were classified as empty.

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Statistical analyses

We tested data from different years (2006 and 2007; two-sample Kolmogorov-Smirnov test) and populations in the Alps (Montgenèvre, Ferrere, and Cari; Kruskal-Wallis test) for homogeneity, before pooling
150 them (all $P > 0.05$). Where needed, we checked whether the data accommodated the assumptions of normality and homogeneity of variance.

Foundress activity - We used Generalized linear models (GZLMs) for binomial distributions (logit link) to compare foundress activity (i.e.
155 foraging/[foraging + resting]) between brood-emergence phases (pre- and post-emergence) and zones (Apennines vs Alps). In the GZLMs foraging was the dependent variable, zone and phase were categorical factors, and the number of larvae in the nest and the mean monthly temperature were covariates.

160 *Colony productivity* - We used MANOVA to compare colony productivity in the Apennines and in the Alps at the end of the pre-emergence phase, since most of the foundress reproductive success results from eggs laid during this phase and nest size usually does not increase significantly during the post-emergence phase (Lorenzi and
165 Turillazzi 1986). Number of cells, number of empty cells, and first and second brood were the dependent variables and zone was the categorical factor.

Sample sizes were not consistent throughout the study period, because we discovered some nests later in the season, nest predation
170 occurred at different stages during colony cycle, and a few nests were

missed on some surveys. Statistical tests were performed using SPSS 14.0 statistical package for Windows (SPSS Inc, Chicago, IL).

Results

175 Foundress activity

The proportion of time that foundresses spent foraging vs resting changed in different ways between zones relatively to brood-emergence phases (GZLM on foraging: factor zone: Wald $\chi^2 = 1840.271$, $df = 1$, $P < 0.0001$; factor phase: Wald $\chi^2 = 29088.193$; covariate number of larvae: 180 Wald $\chi^2 = 1242.234$, $df = 1$, $P < 0.0001$; covariate temperature: Wald $\chi^2 = 2713.181$, $df = 1$, $P < 0.0001$). Indeed, during the pre-emergence phase Apennine foundresses foraged significantly longer and rested significantly less than Alpine foundresses. These differences were significantly associated to the zone (and expectedly they were associated to 185 temperature and number of larvae in the nests) (GZLM on foraging: factor zone: Wald $\chi^2 = 736.023$, $df = 1$, $P < 0.0001$; covariate number of larvae: Wald $\chi^2 = 2232.533$, $df = 1$, $P < 0.0001$; covariate temperature: Wald $\chi^2 = 157.889$, $df = 1$, $P < 0.0001$). During the post-emergence phase, the difference between zones in the time foundresses spent foraging vs 190 resting reverted: Apennine foundresses spent significantly less time foraging (and rested longer) than Alpine foundresses (GZLM on foraging: factor zone: Wald $\chi^2 = 6894.287$, $df = 1$, $P < 0.0001$; covariate number of larvae: Wald $\chi^2 = 576.529$, $df = 1$, $P < 0.0001$; covariate temperature: Wald $\chi^2 = 5511.595$, $df = 1$, $P < 0.0001$).

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Pre-emergence colony productivity in the Apennines and in the Alps

In late pre-emergence, the number of cells built by the foundresses in the Apennine zone and Alpine zones did not vary significantly (MANOVA: 200 $F_{1,128} = 3.107$, $P = 0.08$). However, fewer cells were left empty in Apennine nests than in Alpine nests ($F_{1,128} = 26.081$, $P < 0.0005$). Apennine foundresses produced significantly more first brood and second brood than Alpine foundresses (first brood: $F_{1,128} = 12.429$, $P = 0.001$; second brood: $F_{1,128} = 20.862$, $P < 0.0005$; see Table 2 for mean values \pm 205 standard deviation).

Discussion

Our results provide evidence that cold-temperate (Alpine) and warm-temperate (Apennine) populations of *P. biglumis* differ in terms of
210 foundress behavior and colony productivity. Apennine foundresses were more active outside their nests, and produced a higher number of both first and second brood than those from the Alpine populations. We attribute these differences mainly to the different climate conditions of the two zones and to how foundresses allocate resources to brood production and
215 energetically costly tasks. Fucini et al. (2009) demonstrated that in the Apennine population the first female offspring emerges as workers, i.e., as females that are active both on and outside the nests. These workers take care of energetically costly tasks, such as nest construction, foraging and provisioning of larvae. Apennine foundresses take advantage of the
220 elevated number of workers emerged during the post-emergence phase, and save energy that they allot to egg production. Indeed, after the emergence of the first brood, Apennine foundresses rested longer on their nests and foraged less (Fig. 1). Foraging is an energetically costly task that reduces the opportunity of direct reproduction in social insects in
225 general (Schmid-Hempel and Wolf 1988), and in *Polistes* wasps in particular (Markiewicz and O'Donnell 2001). Thus, *P. biglumis* foundresses living in the Apennines had brood production patterns similar to those of other *Polistes* species, which live at lower altitude in warm climate conditions (e.g., Pardi 1942, 1946; Miyano 1986).

230 In the Alpine populations, the situation was strikingly different. Cold climatic conditions reduced the foundress activity during the pre-

emergence phase, and thus limited the production of first and second brood with respect to the Apennine foundresses. Alpine foundresses were relatively active during the post-emergence phase, compared to the
235 Apennine foundresses. The difference was not only due to the small numbers of first brood produced in the Alps, but also to the fact that this brood emerged as future gynes (Fucini et al. 2009). A behavioral comparison between the pre- and post-emergence phase reveals that Alpine foundresses spent about 30% of the time out of their nests both
240 before and after brood emergence (Fig. 1). Resource-consuming activities, such as foraging, may reduce the resources for egg production (Markiewicz and O'Donnell 2001). The cold weather contributes to reducing fertility as well (Karsai 1997). The strategy of Alpine *P. biglumis* foundresses consists in forgoing worker production and continuing to be
245 active over the whole nesting season. By doing so, they ensure the production of reproductive brood in an extremely short daily and seasonal activity period (Fucini et al. 2009).

The nests in the Apennines had less peripheral empty cells than those in the Alps. Peripheral empty cells may serve for thermoregulation, i.e. to
250 protect immature brood from cold weather (Yamane 1969, 1972; Yamane and Kawamichi 1975; Lorenzi and Turillazzi 1986; Hozumi et al. 2008). Our results support this hypothesis.

In conclusion, we observed that *P. biglumis* foundresses can adapt to local conditions, exhibiting high flexibility in their social traits. Air
255 temperature seems to play a key role in influencing the activity level of *P. biglumis* foundresses (indeed it was a significant covariate in our models). Future studies are needed to assess if the observed variability in *P.*

biglumis populations is determined either by phenotypic plasticity or by genetic differentiation.

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Table 1. Total number of colonies observed, divided by study site, and total observation hours.

	Pre-emergence		Post-emergence	
	2006	2007	2006	2007
Ferrere	17	9	2	6
Montgenèvre	12	9	1	1
Cari	10	15	3	4
Monte Mare	27	40	7	22
Total colonies	66	73	13	33
Total observation hours	125	121	24	50

355 Table 2. Colony productivity in Apennine and Alpine colonies in the late pre-emergence phase. Values are means \pm standard deviations.

	Pre-emergence	
	Apennine	Alpine
Total cells	48.45 \pm 7.63	44.75 \pm 11.20
Empty cells	9.15 \pm 6.45	17.66 \pm 8.79
First brood	14.42 \pm 2.97	10.80 \pm 5.63
Second brood	24.91 \pm 6.91	16.29 \pm 10.05

Fig 1. Proportion of time that Apennine and Alpine foundresses spent foraging (grey) and resting (black) during the pre- and post-emergence phase. Column heights represent mean percentage values. Vertical bars represent \pm standard deviation.

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