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Foundress association in the paper wasp *Polistes simillimus* (Hymenoptera: Vespidae)

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Abstract

In many animal species, females are faced with at least 2 reproductive options: independent or cooperative breeding. Some individuals in cooperative groups choose to help in rearing the broods of conspecific females. Through observations of how females of *Polistes simillimus* Zikán, 1951 (Hymenoptera: Vespidae) started new nests in the field, we investigated whether ecological constraints and the geographic variations explain group formation in this species. The founding of nests was studied between 1996 and 2000 in various localities of 2 states of southeastern Brazil. Weekly observations were carried out on 109 pre-worker nests. We kept track of 40 colonies in Minas Gerais State and 69 in São Paulo State, each started either by a single female or by an association of females. There was a chance that worker production would become numerically similar in both solitary and associative colonies in both states. An increased number of foundresses did not improve the chance of colony success in Minas Gerais State, but it improved this chance in São Paulo State, so that colonies each with 3 or more foundressess were always successful. In colonies in both states, nest cell productivity was higher with a greater number of associated females per nest. Females were able to start building nests alone, being the only reproductive, or 2 or more females could cooperate to found a nest, thus increasing worker production. However, the type of environment chosen to establish the nest (anthropogenic or natural) seemed to influence strongly the choice of the founding strategy.

Key Words: ecological constraints; foundress number; group augmentation; helping; Polistinae

Resumen

En muchos animales, las hembras se enfrentan con por lo menos 2 opciones de reproducción: la reproducción independiente o cooperativa, asi como, el cuidado de los progenies. A pesar de ser potencialmente capaz de reproducción directa, algunos individuos en grupos cooperativos optan por ayudar en criar los progenie de hembras conspecificas. ¿Por qué se asuma el papel de ayudar? Esta pregunta es de interés general, como se observa cría cooperativa en muchas especies de aves, mamíferos e insectos. Basado en las observaciones de campo de la forma en que las hembras de la avispa papel *Polistes simillimus* Zikán, 1951 (Hymenoptera: Vespidae) fundaron nuevos nidos durante 4 años consecutivos, se discuten algunas hipótesis que pueden explicar la cría cooperativa en esta especie. Una hembra de *P. simillimus* puede empezar un nido por sí misma y ser la única reproductiva. Por otra parte, varias hembras pueden cooperar para fundar un nido, y de ese modo mejorar la probabilidad de que la cría llegue a la etapa de la producción de los trabajadores. A pesar de informes anteriores que mostraron asimetrías inmediatos o un sesgo reproductivo entre las hembras que cooperan, los ayudantes pueden mejorar su aptitud indirectamente al criar los que no son descendientes de ellas, o incluso mejor su aptitud directamente por esperar de una oportunidad para aparearse.

Palabras Clave: restricciones ecológicas; aumento del grupo; Polistinae; seguro de sobrevivencia

Females of *Polistes* Latreille, 1802 (Hymenoptera: Vespidae) paper wasps have the options of independent or cooperative breeding, and usurpation in a few species in temperate climates (Reeve 1991). In the latter, individuals potentially capable of direct reproduction choose to assist in the rearing of broods of conspecific females. Why they accept a helping role is a question central to sociobiology. The choice of cooperative breeding is thought to be affected by several factors. For example, ecological constraints on solitary reproduction can be important, as single-foundress nests (i) are less likely to be rebuilt after a predation event (Strassmann et al. 1988), (ii) tend to be usurped more often (Gamboa 1978; Klahn 1988), (iii) have less survival chances (Metcalf & Whitt 1977; Gibo 1978; Pfenning & Klahn 1985; Queller & Strassmann; 1988), and (iv) are less productive than multiple-foundress nests (West-Eberhard 1969; Tibbetts & Reeve 2003). Additionally, indirect fitness benefits of cooperative breeding also can be involved, as helpers can rear non-descendant kin (Hamilton 1964; Foster et al. 2006).

According to Tibbetts & Reeve (2003), numerous models have been developed to predict the circumstances that favor association (Reeve 1991; Reeve & Ratnieks 1993; Reeve & Emlen 2000). In general, these studies used correlational data to show that multiple-foundress *Polistes* colonies were more successful than single-foundress colonies, because

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they were usurped less often (Gamboa 1978; Klahn 1988), survived better (Metcalf & Whitt 1977; Gibo 1978), and were more productive than single-foundress colonies (West-Eberhard 1969; Gamboa 1980).

Reeve (1991) presented a model in which the ecological constraints explain the optimal nesting strategy. In agreement with the model, the joining of females occurs more frequently in species with lower solitary-foundress success probabilities. Makino (1985), for example, showed that solitary-foundress success rates of Japanese species indicated relatively weak ecological constraints on solitary nesting. Multiple-foundress associations were rare in those species, with solitary founding and usurpation occurring as the principal founding strategies.

Despite all previous studies (see Tibbetts & Reeve 2003), the possible role of geographic variation in a species has not been addressed. The study of this subject will help to improve the understanding of the relationship between the founding strategy and the influence of geographical variation of the species.

In the Neotropical eusocial paper wasp *Polistes simillimus* Zikán, 1951, both solitary and cooperative breeding are common reproductive tactics exhibited by females (Prezoto 2001). When females cooperate to found a nest, a reproductive division of work established by aggressive interactions occurs. The dominant female spends the most time in the colony laying eggs and is the predominant participant in direct reproduction, whereas subordinate females assume the role of workers, foraging for food (Grazinoli et al. 2010). By studying the nest founding period in *P. simillimus* over a 4 yr period, we investigated whether ecological constraints and the geographic variation explain group formation in this species.

Materials and Methods

The founding of *P. simillimus* nests was studied between 1996 and 2000 in various localities of Minas Gerais and São Paulo States of Brazil (Table 1). To verify how females begin new nests, weekly observations were carried out on 109 pre-worker nests, immediately after dark (between 6 and 8 PM). In each observation, the number of associated females in each nest was registered. Solitary nest founding occurred when a single female was registered during all observations in a given nest, and associative nest founding occurred when a particular nest was inhabited simultaneously by more than 1 female. We located most nests at a very early pre-emergent phase (number of nest cells when a colony was registered for the first time averaged 6 ± 6 (range: 1–24); however, we located some colonies late in the pre-emergent phase. As a result, the process of observing foundress association was not always the same for each colony. Nests were observed until they reached the worker production phase, characterized by the presence of cells with vestiges of cocoons and the presence of newly-emerged adults. Additionally, the number of cells in each nest was registered at the end of the pre-worker period.

Statistical analysis was performed with GraphPad InStat 3.0®. The significance level was fixed at 5%.

Results

We kept track of 40 colonies of *P. simillimus* in Minas Gerais State. In this state, nests were started either by a single female (50%) or by an association of 2 to 15 females (50%). The chances of reaching the worker production phase were similar (2-sided Fisher's exact test: P = 0.6262) in both solitary (40%) and associative (40%) colonies. Further, an increase in the number of foundressess did not improve the chance of colony success (Spearman's correlation test: r = 0.6513, P = 0.1612). An increase of the number of associated females per nest resulted in higher nest cell productivity at the end of the pre-worker phase (r = 0.8295, P = 0.0411).

In São Paulo State, 69 colonies of *P. simillimus* were studied. In this state, nests were started by a single female (61%) or by associations of 2 to 6 females (39%). The chances of nests reaching the worker production phase were similar (2-sided Fisher's exact test: P = 0.0975) in both associative (36%) and solitary females (42%). An increase in the number of foundressess improved the chance of nest success (Spearman's correlation test: r = 0.8450, P = 0.0342), so that colonies with 3 or more foundressess were always successful. Finally, an increase in the number of associated females per nest resulted in a higher nest cell productivity at the end of the pre-worker phase (r = 0.9976, P < 0.0001).

Discussion

Associative nest founding was a more successful reproductive strategy than the solitary nest founding. However, increased colony benefits in multiple-foundress associations were not necessarily benefits to all individuals that had been selected for cooperation. If individual *P. simillimus* females, like many other *Polistes* species, can successfully found colonies by themselves and each female can be the only reproductive in the colony, why do they form groups in which an aggressive female performs all or most of the direct reproduction, whereas the less aggressive females play a subordinate role as a helper with a low fraction of direct reproduction (Grazinoli et al. 2010)? In colonies with up to 4 females, the greater the number of associated foundresses, the greater the probability of colony success. This suggests that survival insurance benefits may be important in small group formation. Thus, in a solitary nest, the single female must perform all colony tasks, but in a foundress-associative colony, subordinate females perform the riskier

Table 1. Location, number of *Polistes simillimus* nests studied, and type of environment sampled in the states of São Paulo and Minas Gerais, southeastern Brazil.

State	City	Coordinates	Colonies studied (n)	Environment
São Paulo	Ferraz	22°23′28.59″S, 47°34′07.31″W altitude 627 m	18	Anthropogenic
	Piracicaba	22°44′02.50″S, 47°38′52.94″W altitude 534 m	33	Anthropogenic
	Rio Claro	22°24′49.28″S, 47°33′52.35″W altitude 619 m	18	Natural
Minas Gerais	Ibitipoca	21°42′13.37″S, 43°53′08.02″W altitude 1453 m	25	Natural
	Juiz de Fora	21°45′44.35″S, 43°20′36.24″W altitude 678 m	2	Anthropogenic
	Lima Duarte	21°50′22.50″S, 43°47′31.24″W altitude 742 m	13	Anthropogenic

tasks such as foraging, whereas the dominant female focuses on direct reproduction (Grazinoli et al. 2010). As a result, the dominant female in foundress associations would have increased survival probability compared with solitary females. Because *P. simillimus* foundresses are closely related (Simikomaki & Del Lama 2000), subordinate females would still gain in indirect fitness.

In *Polistes dominula* (Christ, 1791), foundresses in cooperative nests may benefit from increased survivorship in relation to single foundresses, but unlike what we observed for *P. simillimus*, these benefits are not directly correlated with the number of foundresses in the group (Zanette & Field 2011). This suggests that the relevance of survival insurance may be higher for *P. simillimus* than for *P. dominula*. However, because groups of 4 or more *P. simillimus* females have the same probability of success, survival insurance alone does not explain large group formation, and therefore other factors may be involved.

Alternatively, it is possible that long-term survival and reproduction benefit from helpers being present, as has been observed in many cooperatively-breeding vertebrates (Hatchwell et al. 2004; Hodge 2005; Russel et al. 2007; Sparkman et al. 2011; Brouwer et al. 2012). Therefore the long-term survival and reproduction benefits from helpers may play an important role in promoting large group formation in *P. simillimus*. In this sense, such direct benefits may play a role in group formation (Field et al. 2006; Field & Cant 2007; Sumner et al. 2010). Shreeves & Field (2002) showed a strong positive correlation between group size and breeder productivity in the hover wasp *Liostenogaster flavolineata* Cameron. In a similar way, in *P. simillimus* as in many other paper wasps (West-Eberhard 1969; Tibbetts & Reeve 2003; Tindo et al. 2008), a correlation between nest cell productivity and group size was observed. Thus, if a female helped to rear the current breeder's offspring, she acquired more helpers for herself if later she inherited the breeding position. Thus, the importance of group augmentation benefits must depend on the chance that the helper later inherits the breeder position. Inheritance may be an important component of helpers' fitness in both hover wasps and *P. simillimus* because the brood rearing period extends year round (Prezoto 2001; Shreeves & Field 2002), so the time available to queue for breeding positions is not strongly constrained by the arrival of winter. Finally, *P. simillimus* colonies are among the largest formed by *Polistes* spp. Prezoto (2001) reported some *P. simillimus* nests with more than 1,000 cells (1,065–1,325), with productivity ranging between 759 to 1,355 individuals. Large colonies of this species are probably polygynous (Gobbi et al. 1993), illustrating another way by which helpers could achieve direct reproduction.

Regarding geographic variation, there was no significant difference between the data for nests started by a single female or by an association of females in the states of São Paulo and Minas Gerais. Therefore in this study, geographic variation did not have significant influence on the founding strategy of *P. smillimus*. Nevertheless, for São Paulo State, increases in the number of foundressess improved the chances of nest success. This may be explained by the fact that a higher number of foundings registered in this locality were by single females, usually in anthropogenic environments. This data suggests that, in this type of environment, ecological constraints to solitary founding are much reduced. This allows the species to invest in the founding of more nests (through more isolated foundings) rather than joining associations of females.

According to Prezoto et al. (2007), anthropogenic environments, such as urban areas, present various characteristics that favor the establishment and success of wasp nests. Among these characteristics, we can mention: (i) a great offering of nesting places, (ii) protection against harsh weather conditions, (iii) reduced predation pressure, and (iv) reduced competition for resources. Our results agree with the theory proposed by Reeve (1991), in which variation in ecological constraints either may or may not favor the occurrence of isolated foundings or of associative foundings. In the particular case of *P. simillimus* in our study, the results attained for São Paulo State show the founding behavior to be closer to *P. biglumis* in Japan (Makino 1985), whose predominant founding strategy is by individual females, because ecological constraints in the São Paulo environment are small.

In conclusion, each individual *P. simillimus* female can start the nest by herself and be the only reproductive individual in the nest. Alternatively, *P. simillimus* females can cooperate to found a nest, and thereby improve the chance of reaching the worker production phase. Despite the immediate asymmetries concerning the reproductive skew of cooperative females (Grazinoli et al. 2010), helpers may gain indirect fitness by rearing non-descendent kin or even direct fitness by waiting for a breeding opportunity. However, the type of environment (anthropogenic or natural) chosen to establish a nest seems to exert a strong influence on the choice of the founding strategy.

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