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Abstract.—Two occurrences are described in which a *Polistes* paper wasp of one species took up residence on a nest built by and containing the brood of a different *Polistes* species. These observations are placed in the context of previous reports of shared nesting, intraspecific and interspecific nest usurpation, and intraspecific and interspecific adoption of orphaned nests. These observations suggest a scenario for the possible origin of social parasitism in *Polistes*.

Roy Snelling's first publication (Snelling 1952) reports observations that apparently were made in the nesting season of 1950 and in non-nesting seasons that could have been even earlier. His short note is given here in its entirety.

NOTES ON NESTING AND HIBERNATION OF POLISTES

(Hymenoptera: Vespidae)
Robert [sic] Snelling
Turlock, California

Students have known for some time that occasionally two females (queens) of *Polistes* will found a nest together. Those recorded were noted to be of the same species. However, on one occasion I have taken a female each of *Polistes fuscatus aurifer* Saussure[1] and *P. apachus* Saussure contributing toward a future colony together. As they were watched for some time there is very little chance of an error. In a letter of January 30, 1951, J. C. Bequaert comments that, ''Whether queens of different species could be successful in this is not known.'' Unfortunately, I collected the wasps and nest at once. At the time, there were thirteen cells with larvae and eggs.

In hibernation, the social Vespidae are rather gregarious. At various times I have taken *P. f. aurifer*, *P. apachus*, *P. hunteri californicus* Bohart, *Vespula pennsylvanica* Saussure, and *Mischocyttarus flavitarsis* Saussure hibernating together. In fact, I have taken three of *aurifer*, seven of *P. h. californicus*, two of *M. flavitarsis* and a few inches away, several of *V. pennsylvanica*.

Multi-species wintering aggregations of *Polistes* had been previously reported (e.g. Rau and Rau 1918, p. 285), but Snelling's observation of shared nesting between two *Polistes* species may have been the first of its kind. Two publications subsequent to Snelling (1952) report similar observations. Hunt and Gamboa (1978) reported shared nesting between *Polistes metricus* Say and *P. fuscatus* (Fabricius). In one case, in Missouri, a single *P. metricus* shared a nest with two *P. fuscatus*. Numerous *P. fuscatus* but no *P. metricus* were reared from the nest. In another case, in Kansas, two *P. metricus* were apparently dominant to a *P. fuscatus* on a nest that was subsequently lost to parasitoids. O'Donnell and Jeanne (1991) reported a case from Costa Rica in which a single *P. canadensis* (L.) was behaviorally dominant over three *P. instabilis* Saussure that had apparently initiated the nest. In time, the *P. instabilis* females

[1]The wasps were identified by Dr. R. M. Bohart. I am indebted to him and to Dr. J. C. Bequaert for help.

disappeared from the nest, and other *P. canadensis* females joined the colony. Only *P. canadensis* brood was identified in the nest.

In the Missouri case, the nest had been initiated by a single foundress of a third species, either *Polistes carolina* (L.) or *Polistes perplexus* Cresson. These two species are distinctive by virtue of their red color and are easily recognized among the Missouri paper wasp fauna, yet they can be distinguished from one another only by close examination. Both have been recorded at the study site. I had moved the nest from its initial location to a window observation box, and the foundress was present 1 and 3 days following the transfer, but she abandoned the nest thereafter. The two other species were together on the nest when it was checked 10 days later. Thus the shared nesting was also a case of interspecific adoption of an orphan nest. Here I report two additional observations of interspecific nest adoption in *Polistes*.

RESULTS

Daily monitoring of a population of *Polistes metricus* in nest boxes at Washington University's Tyson Research Station near St. Louis, Missouri, revealed a colony in which the single foundress was last seen on 3 June, 2005. Five pupae plus nine larvae of various instars remained in the untended 14-cell nest until 15 June, 2005. On that date a single female *Polistes carolina* or *Polistes perplexus* was found to be present on the nest. The *P. metricus* brood was intact and had not been cannibalized. The red *Polistes* was standing on the face of the nest in a posture characteristic of foundresses. The *P. metricus* pupal brood was due for experimental collection on that date (Hunt et al. 2007), and the red *Polistes* escaped collection. The nest, with larvae still present, could have been replaced, but it was not, thus it cannot be known if this incipient interspecific adoption of an orphan nest might have been successful.

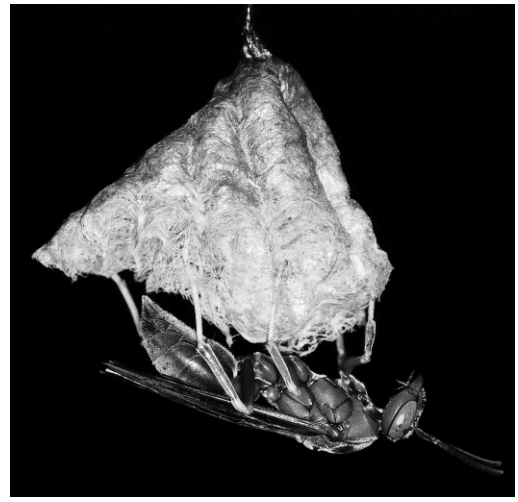

Fig. 1. A female *Polistes metricus* on a nest constructed by *Polistes exclamans*. Photo taken on 26 June 2008 by Freddie-Jeanne Richard.

On 21 May 2008, a nest of *Polistes exclamans* Viereck in a nest box at North Carolina State University's Lake Wheeler Honey Bee Research Facility near Raleigh, NC, was recorded to have a single foundress with eighteen larvae and three eggs in its 21-cell nest. The nest was not checked again until 6 June, at which time a single female *Polistes metricus* was present on the top of the nest. On 7 June it was determined that only three fifth-instar larvae and two eggs were present; the female *P. metricus* was still on top of the nest. On 8 June the female *P. metricus* had moved to the face of the nest (Fig. 1), where she was seen during eight of eighteen nest inspections until she was last seen on 28 June. Two of the larvae pupated on 12 June, and the third did so on 14 June. The adult wasp apparently cannibalized one of the eggs on 10 June, and she laid an egg (in a different nest cell) on 10 June and another on 17 June. One of the pupae was destroyed by a parasitoid on 29 June. Another pupa apparently yielded an adult on 30 June, but that adult was not seen. The third pupal cocoon remained intact, and the cell was subsequently found to contain evi-

dence of parasitoids. The eggs laid by the *P. metricus* eclosed into small larvae, but they failed to develop. The adult wasp was not seen to forage or to feed the larvae.

DISCUSSION

Much has been learned about *Polistes* subsequent to Snelling's (1952) observations. Of relevance to the observations reported here, it has been learned that pre-emergence nests may be usurped (forcefully taken over) by conspecific wasps that then become the colony queen. Perhaps the earliest report of aggressive intraspecific nest takeover was the graphic description by Yoshikawa (1955). Later it was learned that intraspecific usurpation can occur commonly in some populations (Klahn 1988; Makino and Sayama 1991), and still later it was suggested that conspecific nest usurpation may, in fact, reflect ''sit and wait'' behavior as a primary reproductive tactic (Starks 1998). (It can be noted that intraspecific usurpation is commonplace in yellowjackets [Greene 1991]). A similar behavior that is less well known but that may also be common in at least some *Polistes* populations is the takeover by a conspecific of an ''orphan'' nest. Death of a haplometrotic foundress due to predation or calamity seems the most likely cause of orphan nests. Perhaps the earliest report of such adoptions was by Kasuya (1982). Nonacs and Reeve (1993) present a thorough analysis of adoption of naturally-orphaned and transplanted (*i.e.*, artificially orphaned) nests in a population of *Polistes dominulus* (Christ), and they suggest that adoption could be a primary reproductive strategy. In all these cases, workers would provide care for unrelated brood being reared from eggs laid by the dominant co-nester or by the usurping/adopting queen.

Southern Europe is home to three species of socially parasitic (inquilinous) *Polistes* that forcefully evict or behaviorally dominate a foundress of another species (Weyrauch 1937; Cervo and Dani 1996). Intraspecific usurpation or adoption, as described above, seems a likely scenario for the evolution of such social parasitism, which would result in social parasite and host species being closely related (so-called ''Emery's rule''). However, it has been demonstrated that the three species of obligate social parasite *Polistes* are monophyletic, and they are not more closely related to their hosts than they are to one another (Choudhary et al. 1994). Thus, social parasitism in *Polistes* has not evolved via speciation of social parasites from their hosts. What, then, might be a likely scenario for the origin of social parasitism in *Polistes*? The interspecific usurpations and adoptions reviewed and reported here suggest a possible framework. Elements of a plausible scenario include co-nesting of two species via any of the modes described above, commingling of chemical recognition profiles, further such commingling of recognition odors in mixed species overwintering groups as described by Snelling (1952), and delayed nesting as a primary reproductive tactic by one of the co-nesting species. A few successive successful generations could conceivably establish a trajectory.

In an amusing yet thought-provoking short note, Tordoff (1967) reports an unusual death of a caged bird. While scratching its head, the bird inadvertently caught a claw in the nictitating membrane of an eye, fell in its water dish, and drowned. Tordoff noted that the conditions could have been replicated in nature, and he further noted that the bird was scratching its head in a manner atypical for the species. He then queried whether this was an insignificant observation, or was it the very stuff of evolution? The same question can be asked about the observations reported here.

ACKNOWLEDGEMENTS

In the summer of 1971, after several increasingly assertive invitations, I went to the Los Angeles County Museum to meet Roy Snelling. ''I hear you're going to work on ants,'' he said. ''Yes,'' I replied. ''Sit down,'' he said. I did. Whatever he was doing was set aside,

and for the next day and a half I was taken through a fast-paced, intensive short course in myrmecology. We discussed collecting and preservation. He taught me to point ants and kept me at it until my specimens at least came close to his high standards. He taught me to identify the common ants of California chaparral, with unknowns being put before me until I was batting over 500. At last satisfied (or seemingly satisfied) that I was started in the right direction, Roy wished me well in my research and said that he would help. One product that benefited from that collaboration was my dissertation. The most lasting outcome was ''The ants of Chile'' (Snelling and Hunt 1975). That work is 95% Roy's, of course, yet I am as proud of it as of anything I have done. Roy Snelling was a deeply respected mentor and colleague without whom my early successes would have been fewer and lesser. I have always been grateful.

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