

Nest usurpation and sequential nest occupation in the digger wasp *Crabro monticola* (Hymenoptera: Sphecidae)

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Females of *Crabro monticola* regularly abandoned the nests which they had been provisioning, sometimes for no apparent reason, sometimes because the nest had been entered in their absence by a conspecific usurper. After giving up her nest, a female had the option of digging a new nest or entering an already constructed burrow and usurping it from its owner, if it were occupied. Both options were exercised by members of the population. The result was that individual nests were held by as many as six different females over the course of 26 days. Each female occupied 2.2 nests on the average during the study. The adaptive advantages of nest usurpation and burrow switching are unclear. Nest usurpation attempts never resulted in joint occupation of a burrow in this species. Therefore, whatever its benefits, the entering strategy can evolve even if it does not lead to joint defense of a nest by its "communal" occupants.

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Il arrive souvent que des femelles de *Crabro monticola* abandonnent les nids qu'elles sont en train d'approvisionner; quelquefois il n'y a pas de raison apparente, d'autres fois, le nid a été violé par un usurpateur de la même espèce. Après avoir abandonné son nid, la femelle a le choix de creuser un nouveau nid ou d'entrer dans un terrier déjà creusé et de l'envahir s'il est occupé. Ces deux options sont utilisées dans la population. Il en résulte que certains nids ont été utilisés par plusieurs femelles différentes (jusqu'à six) pendant une période de 26 jours. Chaque femelle a occupé une moyenne de 2,2 nids pendant la durée de l'étude. Les avantages évolutifs de cette usurpation des nids et des changements de nids ne sont pas évidents. Dans aucun cas, chez cette espèce, les tentatives d'usurpation ne résultent en une occupation conjointe. En conséquence, quels qu'en soient les bénéfices, la stratégie d'investissement peut se développer même si elle ne mène pas à une défense commune du nid par ses occupants "communaux".

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Introduction

The natural history of a number of North American species of *Crabro* has been reviewed by Kurczewski and Acciavatti (1968) and Evans et al. (1980). These reviews have shown that females of this genus share many behavioral characters in common such as a tendency to build their nests in association with other individuals, to construct fairly long and elaborate multicelled burrows (up to 40–60 cm in length in some species), and to provision the nest with various flies. There has been no detailed report, however, on the occurrence of nest usurpation and changes in nest ownership for any species of *Crabro*, probably because most studies have not been long term nor have the females under observation usually been individually marked. I present data in this paper showing that females in a Minnesotan population of *C. monticola* Packard may either abandon their nests or be evicted by a usurper of the same species; the females may then either build an entirely new nest or attempt to steal the already constructed nest of another female in the area. Nest usurpation has been described for a fairly large number of sphecid wasps (see review in Brockmann and

Dawkins 1979) and there has been brief mention of its occurrence in *C. rufibasis* (Miller and Kurczewski 1973) and *C. cribrellifer* (Barrows et al. 1978). It is a phenomenon of some theoretical significance because it provides the setting for interactions within one burrow between two usually solitary-nesting females (Brockmann and Dawkins 1979). As such it has been suggested that joint occupation of a burrow resulting from failed attempts to usurp a nest may set the stage for the primitive origins of insect sociality (Lin and Michener 1972). This paper concludes with a discussion of the relevance of nest switching in *C. monticola* for this hypothesis.

Methods

In June of 1980 a nesting aggregation of *C. monticola* was found on the campus of the University of Minnesota's Forestry and Biological Station, Lake Itasca, MN. The nests were located in an open sandy area with a sparse cover of low-lying weeds and grasses on either side of a dirt service road. The sandy patch was at the edge of a clearing surrounded by woodland.

Several females were marked in June 1980 with enamel or acrylic paints or liquid eraser and the population was moni-

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TABLE 1. A comparison of the behavioral characteristics of females of *C. monticola* found in Minnesota and Massachusetts

	Geographic location of population	
	Lake Itasca, MN (this study)	Bedford, MA (Evans et al. 1980)
Time of first departure of foraging female	0630–1000 CDT*	0630–0900 EDT†
Time spent outside the nest by a foraging female per morning	$\bar{X} = 132$ min (SD = 39.1, $N = 49$)	
Prey species	Primarily Tabanidae; a few syrphids and tachinids	Primarily Therevidae; a few tabanids, syrphids, and calliphorids
No. of prey taken per female per morning	Range 1–11 $\bar{X} = 2.3$ (SD 1.2, $N = 91$)	Range 1–8, usually 3–5
Prey per cell	Range 1–6 $\bar{X} = 3.3$ ($N = 10$)	Range 2–7, usually 3–5
Cells per nest	Maximum 8	Maximum 13

*CDT, Central Daylight Time.

†EDT, Eastern Daylight Time.

tored for a period of 9 days. This resulted in the discovery that some females did not remain in the nest which they occupied when marked and that the same burrow might be held by a succession of different females. As a result, a much more extensive study was undertaken in the period from 15 June to 10 July 1981 of another aggregation of females (the descendants of the population observed in 1980?) that were nesting in precisely the same location used by females the previous year.

All nests were flagged and given a number as they were discovered. As of 15 June there were already 21 active burrows at the site and over the course of the study an additional 22 nests were constructed. The large mound of sand at the entrance of a freshly built nest facilitated the location of new burrows. During the study a total of 23 females were captured and given a distinctive color combination using the materials listed above. The marks were reasonably durable and in those few cases in which fading or chipping occurred, the female was recaptured and additional paint or liquid eraser added. A record was kept of the history of each nest, its occupants and the number of prey brought to the nest during each day's observation time (which ranged from 1 to 4 h on almost all sunny mornings). On some days the nests were also checked for from 1 to 3 h in the evening, a second period of provisioning activity that follows a long midday bout of inactivity when the wasps remain within their burrows. From 1–16 observers (the field ethology class of the University of Minnesota and its instructor) watched the area simultaneously in an attempt to record every foraging event during the period of observation. The total man-hours of observation was roughly 150.

In addition to monitoring aboveground activity, four nests were excavated over the 2 years in order to secure information on nest design and brood cell contents.

Results

Nesting behavior

Females in the Minnesota population of *C. monticola* behave in much the same manner as females in New York and Massachusetts studied by Evans and his associates (Evans 1960, 1974; Evans et al. 1980). The similarities include the time of nest construction (the evening), the presence of a prominent tumulus, the internal closure of the nest when the female entered after a period of provisioning, and a bimodal pattern of provisioning with early morning and evening foraging sessions separated by a midday period of no activity outside the nest. Some additional comparisons for which there are quantitative data are presented in Table 1.

Changes in nest ownership

The female wasps frequently changed the burrows in which they lived. Seventeen of the 24 marked females occupied from two to four nests during the 26-day study (the mean for the entire marked population during this time was 2.17, SD = 1.01). The time spent in any one nest ranged from 1 day to a maximum of 16 days for four females. Because the study began when the aggregation was at its peak, the maximum longevity of females may

TABLE 2. The history of burrows that were left by a female and the nest selection of a female after she had left her old burrow

	No. of occurrences	Fate of nest
Female leaves burrow; burrow is occupied the next morning by a conspecific female		
Yes	14*	Nest abandoned
No	15	Nest abandoned for no apparent reason (8) Nest abandoned because of ants (2) Nest receives final closure (5)
Female that left burrow		
Builds a new nest	11	
Occupies an abandoned, already-constructed nest	4	
Takes a nest that was held by another female	14	

*The presumption was that in most cases the new occupant had usurped the nest from its previous resident causing her to abandon her burrow.

substantially exceed 3 weeks and the total number of nests occupied during a female's entire life may have been greater than four in some cases.

The marked population of females provided a total of 29 records of nest changes within the 8 × 9 m study plot. The mean distance moved by a female was 2.1 m, SD = 2.2. The events that preceded a move from one burrow to another were varied (Table 2). For about half the records the loss of a nest to a conspecific usurper was the likely or the known cause of a change in residence by a female. In these cases, the burrow from which a female moved was held by a new owner the morning after the move took place. Several times we observed a female return to her nest after a strange female had entered and plugged the burrow from within. Sometimes the original owner burrowed through the plug and evicted the intruder. On other occasions, however, the owner made a brief series of attempts to enter but failed, and then abandoned the nest. Once an owner burrowed through the plugged entrance but was chased from the nest by the newcomer who appeared at the entrance immediately after the original owner had backed hastily out of the burrow.

For the other half of the records, the female left her nest after making a final closure or she abandoned the nest leaving the entrance open. In making a final closure the owner spent several hours filling the nest by scraping sand into it from the tumulus (or what remained of the mound in the area about the entrance). This activity blocked most of the main burrow but left a large hole several centimetres deep at the original entrance. Final closures were not often performed and instead many nests were simply abandoned, occasionally because of interference from ants but usually for no obvious reason.

Once having left her most recent burrow, a female had

several options. She could build an entirely new nest and this occurred regularly. But in a substantial majority of cases, the nest-switching female appropriated an already constructed burrow, sometimes one that had been abandoned by another owner or one that had been left empty when the resident female died. More often, however, the female took a burrow that was currently occupied and being provisioned by a fellow wasp. Nest searchers were most often seen in the early morning or late evening provisioning periods when the entrances to nests whose females were out hunting were conspicuously open (because foraging females do not close their nests while hunting). The behavior of the nest searcher was highly characteristic. She flew close to the ground at low speed, hovering about the entrances to ant colonies and at the burrow openings of conspecifics, frequently entering another female's burrow only to exit after an inspection of a few seconds or minutes. Thus, for example, one female entered four burrows in a 15-min period on the morning of 30 June. Eventually the nest searcher would either settle on a new location in which to construct a nest or slip into an established burrow and push sand up, blocking the entrance. As indicated above, this was sometimes sufficient to deter the owner from attempting to reclaim her burrow upon her return to the nest from a foraging trip.

The relatively high frequency of nest usurpation and abandonment of nests sometimes created a "musical nests" phenomenon in which the thievery of one nest apparently set in motion a series of additional usurpations and nest moves. Thus, for example, on 27 June, nest No. 26 which had been held by "white-green" was occupied by an unmarked female; "white-green" apparently then took nest No. 28 from its owner "white-orange" which moved to a new location and constructed

another nest (No. 33) overnight. On 1 July the nest (No. 28) of "white-green" was taken by a different unmarked female and "white-green" had once again apparently usurped the nest of "white-orange" which was now the owner of a new burrow (No. 39) which it had built in one evening.

As a consequence of burrow usurpation and the reuse of abandoned nests, 14 of 42 burrows were occupied by from two to six females and 10 of these burrows were known to be provisioned by more than one female. Although some nests were occupied for as little as a single day, the multiowner nests were in continuous use for as long as 24 days.

Discussion

This study has documented that females of one population of *C. monticola* often occupied more than one burrow during their lives, sometimes "voluntarily" leaving the nest for another and at other times leaving because their burrow had been taken over by another female. In turn, females that left a burrow, for whatever reason, commonly usurped the nest of another female in the aggregation, although they also had the option of digging a new burrow.

These results raise several questions. First, why do some females leave a nest for no apparent reason to move to a new location? One would think that, in species whose females build burrows with a large and indefinite number of brood cells, individuals should provision one nest for the duration of their lives. A female that abandons her nest has to find or build a new one, a task that requires time and energy and perhaps some risk in the form of increased exposure to predators and the risk of injury, if the female attempts to take over a well-defended burrow. These costs do not appear excessive in *C. monticola* because a new nest can be completely constructed in some portion of one night and because already constructed burrows can be easily located and fairly easily usurped. Nevertheless, nest changing does cost a female something.

The major benefit that might outweigh the costs of moving could perhaps be a wider distribution of one's offspring, thus reducing the probability that a highly localized disaster would destroy all one's progeny. But the distances moved were not great; frequently only a metre or two separated the nests occupied in sequence by the same female. As an additional minor benefit, nest usurpers may sometimes acquire a cache of one or a few prey in a stolen burrow which they could use to provision their own brood cells. In *C. monticola* females probably cannot easily locate the brood cells of another female to steal prey or destroy a rival's offspring because they are placed some distance from the end of the burrow and the tunnels to the cells are completely filled with sand after each cell is stocked and the egg laid.

In the last analysis it is difficult to see why a female would voluntarily leave a burrow she had built, especially since abandoned burrows were often reoccupied promptly and provisioned successfully by another female. Brockmann and Dawkins (1979) were also unable to determine the reason for burrow abandonment in the very large majority of cases in *Sphex ichneumoneus*.

A second puzzle is the failure of females to resist takeovers more vigorously. Perhaps if there are some modest benefits to changing the location of one's nest this could help explain the weak defense of burrows. In other words, if selection favors females with a low threshold for voluntary burrow abandonment, then females may not gain much by attempting to repel an intruder from an old burrow. This would be especially true if the female that is within the nest, whether owner or usurper, has a strategic advantage in a contest within the burrow for its control. Most takeovers probably occurred when the resident was foraging outside her nest. When she returned to a burrow plugged by an invader, the original owner had the option of attempting to maneuver *around* the intruder and then forcing her out of the nest or finding a new nest of her own. Both options require an expenditure of time and energy and involve risk (the females have powerful mandibles that are extensively used in nest building and which appeared capable of damaging an opponent). As the costs of the two options may be closely balanced the slight benefits of moving to a new location (whatever these might be) may tend to favor exercise of that option in response to a takeover attempt.

A third question has to do with the relevance of the behavior to an understanding of the evolution of sociality in the insects. Several authors, including Lin and Michener (1972), Miller and Kurczewski (1973), and Alcock (1975) have suggested that nest usurpation attempts may lead to joint occupancy of a burrow (when one individual fails to evict the other at once) and that both burrow dwellers might then enjoy certain mutual benefits of living together. Primary among these gains could be the reduced risk of parasitism and nest usurpation by still other conspecifics because of the increased likelihood that at least one female will be in the nest at any time to repel these unwanted intruders. This in turn could select for the frequency-dependent strategy of "joining" occupied nests because of these advantages.

Brockmann and Dawkins (1979) have tested a quantitative model based on the hypothesis that females of *S. ichneumoneus* possess these alternative strategies: joining another female in her nest versus digging one's own nest. They have shown for one population that this hypothesis is most unlikely and that a better fit of the data is possible if one assumes that the females exercise instead the two strategies of (1) digging one's own nest and (2) entering and using an already constructed nest.

They believe that what looks like "joining behavior" is in reality simply "entering" without respect to whether the nest is occupied or not. Joint occupation of burrows occurs, they argue, as the *incidental* result of wasps sometimes entering a currently occupied, rather than an abandoned, burrow. The female wasps apparently are unable to discriminate between the two classes of burrows.

The two nesting options of females of *C. monticola* appear to be the same as those proposed by Brockmann and Dawkins (1979) for *S. ichneumoneus*. In both species some females abandon nests that are perfectly capable of accommodating more cells and then are faced with a "decision" whether to build a nest from scratch or to enter and occupy an already constructed nest. A female may do both in the course of her lifetime. Unlike *S. ichneumoneus*, joint occupation of a nest does not occur at all because no female tolerated another within the nest for more than a very brief period and because the wasps were so quick to abandon their old nests if they found them occupied. Indeed the frequency of nest switching would have been difficult to document had not the females been marked because turnovers occurred so rapidly. In any event, females of *C. monticola* clearly do not have a "joining" strategy or option in which they enter a nest to remain with its resident, jointly provisioning and defending the burrow against nest enemies. They enter nests to take them over completely. If they cannot succeed in this endeavor, they leave at once. Although "entering" may in some species set the stage for the evolution of social cooperation among two usually solitary individuals, it need not as the entering strategy can evidently be adaptive in its own right.

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