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Protandry in western cicada killer wasps, (*Sphecius grandis*, Hymenoptera: Sphecidae): an empirical study of emergence time and mating opportunity

Jon Hastings
Northern Kentucky University, Highland Heights, Kentucky 41076, USA

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Summary. *Sphecius grandis* is a univoltine, colonial wasp. Females mate once and are sexually receptive when they emerge in July and early August. Males generally emerge earlier in the summer than females. The opportunity for each male to acquire mates is a function of the number of females emerging during his lifetime and the number of competitiors that are active when the females emerge. I determined a mating opportunity index (MOI) for each male in an aggregation of wasps for three separate summers, and correlated the MOI of individual males with their emergence date. The MOI of a male estimates the potential contribution that timing of emergence makes to his reproductive success. In 1984 males emerging near the mean of the male emergence distribution had the highest MOI. These males emerged between one and two weeks prior to the mean female emergence date. However, in 1981 late emerging males had the highest MOI. In 1983 there was no significant difference in MOI among males. As a result of between-year variation in female emergence schedules and in the duration of male lifetime, the selection pressures influencing male emergence time vary between years.

Introduction

Naturalists have long realized that it is common for males of insect species to emerge earlier in the year than females. Darwin (1871) hypothesized that this pattern of emergence had evolved by natural selection operating at the level of the individual, and that males emerging before females are likely to have an advantage in competition for mates. In recent years the term "protandry" has been used to describe this pattern of emergence (Wiklund and Fagerstrom 1977; Thornhill and Alcock 1983). Protandry is a common emergence pattern among butterflies (Wiklund and Fagerstrom 1977) and solitary Hymenoptera (Evans and West-Eberhard 1970; Gwynne 1980) as well as some other groups of insects (Richards 1927; Nielsen and Nielsen 1953). In many of these species females mate only once and are sexually receptive upon emergence or soon after (Wiklund and Fagerstrom 1977; Thornhill and Alcock 1983). In such species, individual males that emerge before females and remain alive until females emerge, will have the highest mating success.

The timing of female *S. grandis* emergence has apparently evolved to correspond with the emergence of the cicadas (*Tibicen duryi* and *Tibicen parallela*) that they hunt for nest provisions (Hastings 1986). Females mate only once, and are sexually receptive upon emergence (Alcock 1976; Hastings in press). They apparently exercise no mate choice, but simply copulate with the first male attempting to mate. Males generally emerge earlier in the summer than females, but overlap exists between the male and female emergence periods. Males compete for mating territories that encompass areas from which receptive females will emerge. Successful territory defense enhances the mating success of individual males (Hastings in press).

As females are receptive when they emerge, an individual male has little chance of mating with a given female unless he emerges before she does. The ideal male emergence strategy would be to emerge just prior to the emergence of the first females and remain alive throughout the entire period of female emergence. However, as the female emergence period is long relative to a typical male lifetime, this ideal male strategy cannot be employed. The next best strategy for a male might be to emerge just prior to the peak in female emergences. However, the mating opportunity of an individual male is determined not just be how many female emerge during his lifetime, but also by how many other males are competing with him (Thornhill and Alcock 1983). If many males are active during peak female emergence, the opportunity for any individual male to acquire mates will be lowered as a result. Conversely, an individual male emerging when few other males are active may have a relatively high mating opportunity even if few females emerge during his lifetime. In this paper I examine how the seasonal timing of emergence by individual male western cicada killer wasps influences their opportunity to acquire mates. I also compare the observed relationship between emergence date and mating opportunity with the predictions of two contrasting models for the evolution of protandry.

Thornhill and Alcock (1983) suggest that the emergence time of individual male insects may vary with differences in their ability to compete with other males for mates. Males that are better able to compete for mates could profit most by emerging just prior to the peak female availability, regardless of how many competitors are active at that time. However, males that lack competitive ability may profit more from emerging at times when few other males are active, even though the absolute number of females is relatively low at these times. Competitive ability of male *S. grandis* is determined primarily by their size; large males usually win disputes over mating territories, and consequently have relatively high mating success (Hastings in press). If variation in individual male emergence time is at all influenced by their ability to compete with other males, large males should emerge just prior to the peak in female emergence, even if many males are active at this time of the summer. Smaller males should emerge when the competition for mates is low. This may correspond to very early and very late parts of the female emergence season. Here I investigate the possibility that the competitive ability (i.e., body size) of individual male *S. grandis* is correlated with the timing of their emergence.

Methods

I studied an aggregation of *S. grandis* in Cave Creek Canyon of the Chiricahua mountains in southeast Arizona, during July and August 1981–1984. I thoroughly searched the area for other aggregations, but found none. I assumed that this was an isolated aggregation. Wasps were captured as they emerged from their underground nest cells or when they first appeared in the nest area. The right forewing of each wasp was measured to 1 mm with dial calipers. Winglength is highly correlated with dry body weight within each sex (Hastings 1986). Each wasp was uniquely marked on the dorsal thorax with one or two dots of Testor's luminescent acrylic paint. Dambach and Good (1943) state that eastern cicada killers do not reappear in the nest area for a week or two following their emergence. However, I captured and marked many individuals as they emerged, and generally saw them again in the nest area the same day or the day following their emergence. I was usually able to capture individual wasps the first day they appeared in the nest area. I use the date of capture and marking of an individual as an estimate of its date of emergence.

I took half-hourly censuses of males on territories each day of the study. I also periodically checked nearby trees for the presence of individual males that were not territory residents. This information provided estimates of the lifetime of each male in the aggregation, and of the number of males that were active in the area each day. When males permanently disappeared from the nest area, I considered them to be dead.

I calculated a mating opportunity index (MOI) for each male that was captured and marked. The MOI for a male is the daily operational sex ratio (Emlen and Oring 1977) summed over his entire lifetime. The daily operational sex ratio is simply the number of females emerging on a given day divided by the number of males that were known to be alive that day. The MOI for a male would be the sum of these daily values for all days that he was known to be alive. The MOI estimates a male's opportunity for acquiring mates, and how the timing of this emergence potentially contributed to his mating success. I correlated the MOI of individual males with their emergence date. Many males were seen only one day. I assumed these individuals dispersed from the area, and I excluded them from the calculation of mean lifetime, and from the correlation of MOI with emergence date.

Results

Emergence schedules, survivorship, and MOI for 1984

The schedules of male and female emergence for 1984 are shown in Fig. 1. Males generally emerged earlier in the year than females. The cummulative frequency distributions of emergence were significantly different (Kolmogorov-Smirnov, $D=0.48$, $P \ll 0.001$). Female emergence spanned a period of 30 days. In 1984 the mean lifetime for males was 13.6 days, with a standard error of 6.5; the median was 12 days. The number of males active in the nest area varied considerably during the female emergence period (Fig. 1). In general the peak in male activity preceeds the bulk of the female emergences. The largest number of males in the nest area was observed one day prior to the median day of the female emergence period. Early and late female emergences occurred at times when relatively few males were active.

The mating opportunity index (MOI) was calculated for every male that was captured and marked in 1984. Fig. 2 shows the MOI of each

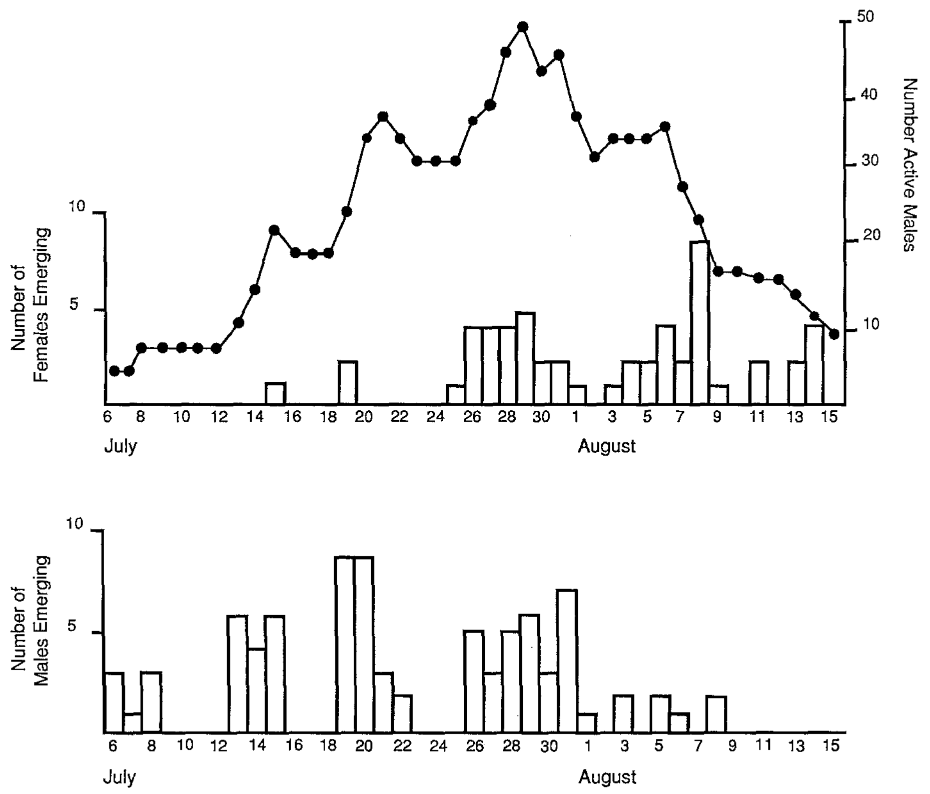

Fig. 1. Frequency distribution of dates of male and female *S. grandis* emergences for 1984. Also shown on the female frequency distribution is the number of males active on each day (line graph)

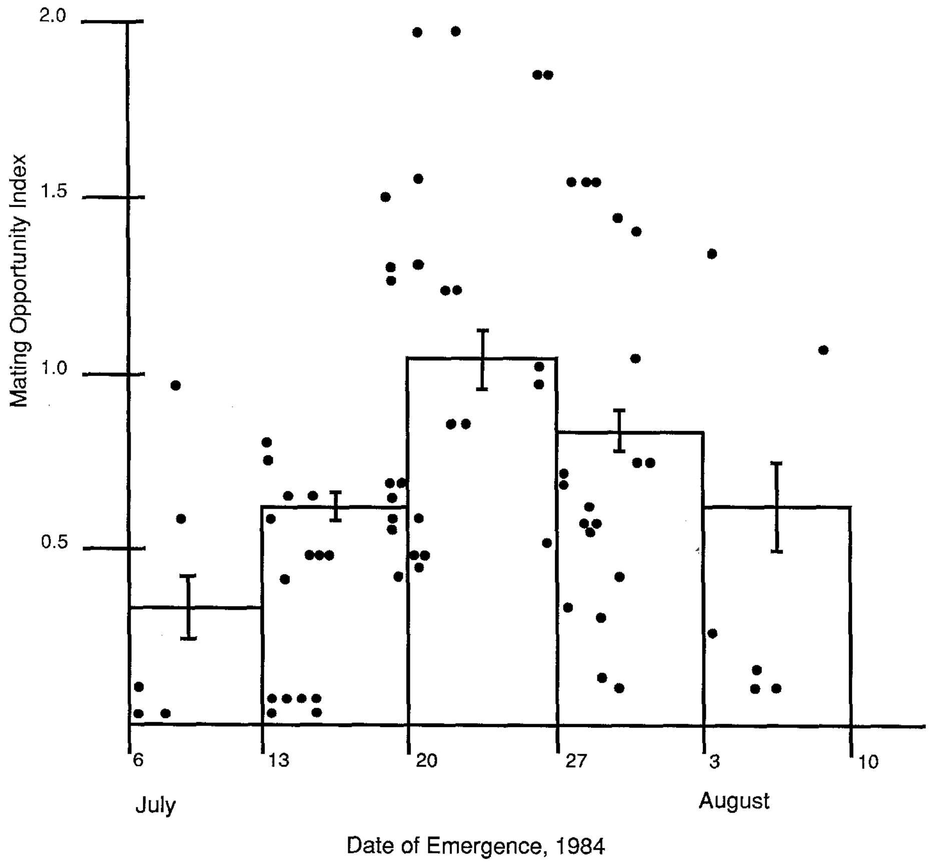

Fig. 2. Mating opportunity index (MOI) of individual male *S. grandis* as a function of emergence date, in 1984. Also shown are the mean MOI values (+ or − SE) for males emerging during each quintile of the emergence period (bar graph)

male as a function of his emergence date. In general males with the highest MOI emerged near the middle of the male emergence period. I divided the entire emergence season into five one week periods and calculated the mean MOI of males emerging during each quintile. The mean MOI for each quintile is shown in Fig. 2. The differences between these mean MOI's are highly significant (ANOVA, $F=4.67$, $P<0.0025$, $N=71$). The highest mean MOI was found for males that emerged from 20 through 26 July, the week just prior to the bulk of the female emergences in that year.

Emergence schedules, survivorship, and MOI for 1981 and 1983

Similar results were not obtained for the other two years of the study. The male and female emergence schedules for 1981 and 1983 are shown in Fig. 3. As in 1984, males generally emerged earlier in these years than did females (Kolmogorov-Smirnov, 1981: $D=0.69$, $P\ll 0.001$, 1983: $D=0.66$, $P\ll 0.001$). The mean male lifetime in 1981 was 10.6 days (SE = 5.7), which was significantly shorter than it was in 1984 or in 1983 (ANOVA, $F=3.54$, $P<0.05$). In 1981 there was a significant positive correlation of MOI with emergence date ($r=0.3212$, $P<0.05$, $N=44$); in general late emerging males had the highest MOI. In that year both male and female *S. grandis* began emerging in early July, and the female emergence continued for 49 days into mid-August. Few males remained alive past early August, and those still alive late in the season had few competitors for mates, and as a consequence, had a relatively high MOI.

In 1983 female emergence was compressed into a period of 23 days. The variance in male emergence date was also low; all but one of the only 27 males that emerged did so before the median female emergence date. The average male lifetime that year was 14.5 days (SE = 9.9). There was no significant correlation between MOI and male emergence date that year. Average weekly differences in mean MOI were not significant (ANOVA, $F=1.67$, $P>0.10$). Table 1. summarizes all of the differences between years that are mentioned above.

Body size and date of emergence

There was no correlation between date of male emergence in 1984 and winglength. The 1984 male emergence period was divided into five time periods as described above, and the mean winglength of males emerging during each of these quintiles

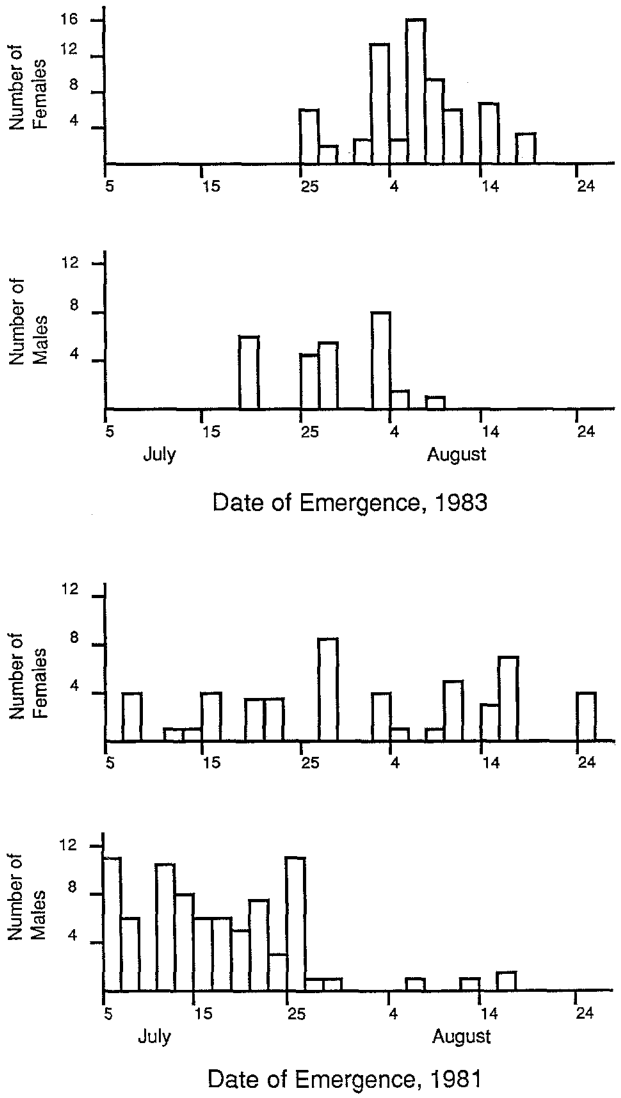

Fig. 3. Frequency distribution of dates of male and female *S. grandis* emergences for 1981 (two lower graphs), and for 1983 (two upper graphs)

Table 1. Comparison of duration of female emergence period, mean male lifetime, and relationship between MOI and male emergence date for 1981, 1983, and 1984

Year	Duration of female emergence period	Mean male lifetime	Correlation between MOI and male emergence date
1981	49 days	10.6 days (SE = 5.7)	Late emerging males had the highest MOI
1983	23 days	14.5 days (SE = 9.9)	No correlation
1984	30 days	13.6 (SE = 6.5)	Males emerging one to two weeks prior to mean female emergence date had the highest MOI

was calculated. A comparison of the means indicated they were not significantly different (ANOVA, $F=1.25$, $P>0.25$).

Discussion

The evolution of protandry

Wiklund and Fagerstrom (1977) present a model for the evolution of protandry. The life history and mating system of western cicada killer wasps meet the key assumptions of their model including:

1. Females mate once.
2. Females mate on the day of their emergence.
3. Males are capable of multiple mating.

The Wiklund and Fagerstrom model also assumes that male and female populations emerge according to given time schedules that are under genetic control. However, I have no way of assessing the degree to which variation in emergence time of *S. grandis* males and females is genetically based. The model assumes that for a given distribution of female emergences, there is an optimum date for males to emerge. It predicts that this optimum date preceeds the mean female emergence date by a period of time directly related to the average male lifetime duration. Males emerging before or after this optimum date will have lowered fitness as a result of their "mistimed" emergence. Sexual selection acts only on the mean of the male emergence schedule, and not on the variance or the shape of the distribution. Variance in male emergence date is presumably maintained by environmental unpredictability.

An alternative model for the evolution of protandry, presented by Iwasa, et al. (1983) assumes that males can predict exactly when to emerge. The emergence takes into account variance in female emergence and competition with other males over mates. What evolves is a male emergence schedule in which all males have the same opportunity to acquire mates, and therefore have the same fitness. In this ideal free distribution model, sexual selection acts not only on the mean of the male emergence distribution, but on the variance and the shape of the distribution was well.

The correlation of male *S. grandis* MOI with date of emergence in the 1984 season provides support for the Wiklund and Fagerstrom model. In that year males emerging near the mean male emergence date, and one to two weeks before the mean female emergence date, had the highest mating opportunity. These males were favored by sexual selection because they had the highest potential mating success. Males emerging earlier or later had lower MOI's, and as a result had lower potential fitness. Variance in emergence date may reflect underlying genetic variation or uncontrollable environmental influences.

In 1983 only 27 males emerged and all but one of them emerged before the median female emergence date. As a result of the comparatively low variance in male emergence and the small sample size, it is difficult to properly evaluate the relationship between male emergence date and MOI for this year. However, no correlation between emergence date and MOI was found. This equivalence of MOI for all males may be viewed as support for the apostatic model presented by Iwasa, et al. (1983).

In 1981 sexual selection did not favor protandry; late emerging males had the highest MOI. In that year the female emergence period was spread over 49 days, and mean male lifetime was comparatively short. As a result of these two factors, few males remained alive near the end of the female emergence period. Due to the lack of competition, many late-emerging males had a high MOI and therefore, high potential fitness. However, this late emergence strategy in males could not be evolutionarily stable. The only reason it was a successful strategy in 1981 was that few males employed it. Had many males emerged late, the MOI for late emergers would have been lower than was observed.

Given the western cicada killer mating system and life history, it would always be to the benefit of an individual male to emerge before most females emerge if his life expectancy is long relative to the female emergence period. Possibly in most years, individual males that emerge just prior to the onset of the major female emergence period have the highest mating opportunity, and are therefore favored by sexual selection. This selection has lead to the evolution of the protandry that was observed in all years of the study. However, because the life expectancy of males, and the duration of the female emergence period may vary between years, the selection pressures that influence male emergence times may vary from year to year. The results of this study point out the shortcomings of using a single field season to evaluate models for the evolution of emergence patterns.

Body size and timing of emergence

Because large males have an advantage over smaller males in acquiring mates, the emergence of males is predicted to be influenced by their body size. Large males are likely to acquire mates regardless of the number of competitors present, providing they are active when females emerge. Therefore their mating success could be maximized by emerging just prior to peak female emergence. On the other hand small males are not likely to acquire mates if many competitors are present. Their emergence should be timed so as to avoid competition with larger males. However, I observed no correlation between male size and emergence date. Apparently selection has not lead to an ability of individual males to assess their competitive ability prior to emergence, and time their emergence accordingly.

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