THE EFFECT OF AGE AND SOCIAL ENVIRONMENT ON DEALATION IN *SOLENOPSIS INVICTA* (HYMENOPTERA:FORMICIDAE) FEMALE ALATES

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ABSTRACT

The fire ant (*Solenopsis invicta* Buren) queen produces a primer pheromone that prevents dealation (wing removal) of cohabiting female alates presumably by suppressing endogenous titers of juvenile hormone (JH). Alates are released from the effects of this primer pheromone when they are separated from the queen by physical disturbance, queen death, or mating flights. We investigated whether maturity influences the time at which female alates shed their wings. Results indicated that dealation rates were not different for newly-eclosed (sexually immature) or sexually mature alates. The dealation inhibitory pheromone did not suppress the casting of wings in newly-eclosed female alates that were relieved of their antennae. Dealation normally occurs within 1 h of a mating flight, whereas uninseminated alates isolated from colony members shed their wings significantly later. Therefore, dealation in the context of the colony and after mating flights appears to occur via separate mechanisms.

Key Words: fire ant, primer pheromone, mating flight

RESUMEN

La reina de la hormiga de fuego (*Solenopsis invicta* Buren) produce una feromona que previene la remoción (o eliminación) de alas de hembras aladas que cohabitan con ella, presumiblemente por la represión en el titer (volumen) de la hormona juvenil (HJ) endogena. Las aladas son libres de los efectos de esta feromona primaria cuando se separan de la reina por una alteración física, la muerte de la reina, o por el vuelo de apareamiento. Nosotros investigamos si la madurez influye en el tiempo de cuando las hembras aladas desprenden sus alas. Los resultados indican que la tasa de eliminación de alas no fue diferente para las hembras recientemente eclosionadas (sexualmente inmaduras) o las hembras aladas sexualmente maduras. La feromona que inhibe la eliminación de alas no suprimio la remoción de las mismas en hembras recientemente eclosionadas que tenían sus antenas cortadas. La eliminación de alas normalmente ocurre dentro de 1 hora del vuelo de apareamiento, mientras que las hembras aladas no inseminadas, aisladas de los miembros de la colonia, desprendan sus alas significativamente mas tarde. Por eso, la perdida de las alas en el contexto de la colonia y después del vuelo de apareamiento parece que ocurre por medio de mecanismos distintos.

The fire ant, *Solenopsis invicta* Buren, was accidentally imported into the United States in the mid-1930s from South America (Lofgren et al. 1975). This species quickly dominated the native ant fauna in the southeast and southwest (Porter et al. 1988). The reasons for this domination were many: (a) they entered the United States without their natural enemies from South America (Porter et al. 1992); (b) each colony can contain up to 250,000 highly aggressive workers that have a potent sting (Tschinkel 1990, 1993; Blum 1992), (c) population densities can reach 150 mounds per hectare (monogyne, Porter et al. 1992), and (d) each colony can produce up to 5,000 reproductives per year (Markin et al. 1973) that disperse via mating flights about 300 m in the air (Markin et al. 1971). Fire ants thrive in the disturbed habitats created by humans.

The fire ant queen produces a variety of pheromones that suppress reproductive competition within her nest. For example, *S. invicta* queens produce primer pheromones that inhibit the development of sexual larvae and reproductive activity in other colony members (Vargo 1998). Distribution of these pheromones is facilitated by releaser pheromones produced in the poison gland of the queen that attract workers (Vander Meer et al. 1980). Of particular importance to the work presented here is the dealation inhibitory primer pheromone, which prevents female alates from shedding their wings (dealation) within their colony (Fletcher & Blum 1981a, b, 1983; Vargo 1998).

When weather conditions are favorable (e.g., low wind, recent rain, warm temperature), male and female sexuals will participate in a population wide mating flight. Newly-mated queens fly to the ground, land, and almost immediately proceed to break off their wings, then search for a suitable place to form a nuptial chamber. The time from mating flight to dealation is generally less than 1 h (Markin et al. 1971). The process of dealation initiates a complex series of physiological changes that are typically associated with newly-mated queens, e.g., ovariole development (Fletcher & Blum 1981a, b, c), wing muscle histolysis (Toom et al. 1976), and pheromone production (Glancey et al. 1981; Vargo 1999). In the laboratory the wings of female alates can be artificially removed and the physiological changes associated with mating flights also occur. Similarly, female alates will shed their wings within a few days after they are physically removed from the influence of their queen. These dealates are not mated, but lay unfertilized eggs that develop into males. These males have some capacity to participate in mating flights and pass on at least the maternal part of the colony's genetic material. The colony itself eventually dies because the worker force is not replaced. The dealation inhibitory primer pheromone effectively prevents female alates from competing with the queen. Its main function is to keep female alates "flight-ready" until environmental conditions stimulate the alates and other colony members into a mating flight activity (Obin & Vander Meer 1994; Alonso & Vander Meer 1997).

Results from studies involving allatectomy (Barker 1978, 1979) and topical treatments of synthetic juvenile hormone (JH) I, II, and III (Kearney et al. 1977) and insect growth regulators (Barker 1978, 1979; Vargo & Laurel 1994) demonstrated the importance of JH in regulating dealation and ovary development in female sexuals. Vargo and Laurel (1994) reported that methoprene-treated alates shed their wings and develop ovaries in the presence of the queen. These data suggest that the queen primer pheromone suppresses JH levels in alates.

Female alates can be released from the dealation inhibitory primer pheromone if the colony queen dies or is separated through physical disturbances. However, the most typical method of queen/alate separation is through mating flights. The two possibilities appear to be the result of distinct physiological processes, because dealation within the mother colony may take several days, whereas the time from mating flight to dealation is usually within 1 h (Markin et al. 1971).

This study investigated the rate of the dealation process in the context of pheromone disinhibition within the colony as related to female alate maturity and the influence of workers on the rate of dealation.

MATERIALS AND METHODS

Source Colonies

Solenopsis invicta colonies producing sexual brood were collected from the Gainesville, Florida area. Field collection sites and colonies were determined to be monogyne based upon the following characteristics: (1) the fire ant population had low mound density and large well-developed nests; (2) colony workers were polymorphic (Greenberg et al. 1985); (3) collected colonies had only a single physogastric queen; and (4) colony workers displayed a high degree of conspecific aggression (Morel et al. 1990). Each colony was separated from the soil by slowly flooding the collection bucket (Jouvenaz et al. 1977) and placed in a large tray (52 cm long × 39 cm wide × 7.5 cm deep) with inner sides coated with Fluon® (ICI Americas, Inc., Exton, PA) to prevent ants from escaping. Nest cells consisted of a Petri-dish (14 cm diameter) with a Castone® (Dentsply Trubyte, York, PA) bottom and three equally-spaced holes drilled into the sides of the dish to permit movement of ants in and out of the cell. The Castone® bottom was moistened with water to increase humidity in the nest cell (Drees & Ellison 1998). Colonies were provided with four nest cells covered with red cellophane to simulate dark nest conditions. Colonies were fed a copious diet of crickets, 10% sugar water absorbed on tissue wads, and tap water contained in test tubes (15 cm long × 2.2 cm diameter) plugged with cotton balls (Obin, 1986). Ants were maintained in the laboratory at 27°C and 47% humidity.

Colony Subunits and Source of Alates

Each source colony (see above) was divided into queenright and queenless subunits, each containing 6 g of worker adults, 1 g of brood, and between 30 and 40 highly sclerotized female sexual pupae. Additional field-collected female sexual pupae were introduced into subunits as required. Non-nestmate sex brood were readily adopted into colonies already producing sex brood (see Vander Meer & Morel 1988). Each colony subunit was placed in a porcelain tray (29 cm long × 18 cm wide × 5 cm deep) lined with Fluon®. Each subunit was provided with one nest cell (10 cm diameter Petri-dish) and fed crickets, sugar water, and tap water. These subunits provided the test condition (queenright and queenless) and the alate test subjects for the following experiments.

Antennectomy

The queen-produced dealation inhibitory primer pheromone is detected by the female alate antennae (Vargo & Laurel 1994), therefore antennectomy is used here to determine if immature

female alates are influenced by the primer pheromone as has been shown for mature female alates. In both queenless and queenright subunits, the antennae of sexually immature or mature alates of an age specified below were removed at the scape, close to the insertion point, with iridectomy scissors. Controls consisted of alates who had a middle leg amputated. This simulates the trauma of antennae-loss and has been reported previously by Vargo and Laurel (1994).

Sexually Immature and Mature Alates

Female alates undergo considerable weight increase from eclosion to time of mating flight. Weight was used as a measure of maturity. Field-collected female sexual pupae were placed in each queenright subunit and were monitored every 12 h for newly-eclosed female alates. The newly-eclosed alates were weighed and marked on the thorax with ballpoint industrial pens (Mark-Tex Corp., Englewood, NJ) to facilitate identification within subunits. The newly-eclosed female sexuals were classified as sexually immature. Two groups of sexually-mature alates were maintained within their colonies. Alates were removed and weighed at 7 and 14 days post-eclosion (Glancey, unpublished data, cited in Lofgren et al. 1975; Fletcher et al. 1983). For weight comparison, newly-mated queens were collected immediately after their mating flight from a predominantly monogyne area in Gainesville, FL, and weighed the same day. Prior to experiments with queenright subunits, all female alate pupae were removed to avoid possible confusion from the eclosion of non-treatment female alates. Alates were either antennectomized (described above) and returned to their queenright subunit or transferred to queenless units. Alates were observed every 12 h for dealation, defined as the removal of at least three of four wings (Vargo & Laurel 1994). Dealates found at each observation period were removed. Observations were stopped after all alates had dealated.

Dealation in the Absence of Workers

The above experiments were carried out in the presence of workers and brood. This experiment measures dealation rates in the absence of workers and brood and simulates what the alates would experience after a mating flight. Sexually mature alates were isolated individually and in groups, consisting of three alates per group. Dealation was observed in test tube (70 ml) holding chambers. Each test tube chamber was made by filling half the tube with water and plugging the tube to the water level with cotton balls. This left an area for the alate(s) to move within the tube. The alate(s) were placed in the tube, and another cotton ball was placed in the mouth of the tube to keep the alate(s) inside. The portion of the holding chamber housing the alate(s) was wrapped with red cellophane to simulate darkness. Alates were observed every 12 h for dealation. Dealates were removed at the end of each observation period. The rates of dealation of isolated alates were compared with those of mature alates in queenless colony subunits (with workers) as described above.

Statistical Analyses

To linearize the relationship between percent dealation and time of dealation, percents were converted to probits. Data were then analyzed by Pearson chi-square goodness-of-fit tests. Other statistical tests are indicated in the text.

RESULTS

Dealation Following Queen Loss

The Maturity of Female Alates

Newly-eclosed female alates (less than 12 h old) had a mean wet weight (±SD) of 11.8 ± 2.1 mg (n = 70). Seven days after eclosion female alate weights were significantly higher (mean ± SD, 15.3 ± 1.3 mg, n = 70; df = 138, t = 11.9, $P <$ 0.0001). After another seven days the 14-d-old female alates had increased their weight (mean ± SD, 16.2 ± 0.9 mg n = 76; df = 144, t = -4.52, $P <$ 0.0001) from that of the 7-d-old female alates. The weights of 7-d-old female alates were not different from the weights of newly-mated queens (mean weight fits the monogyne-derived category; Keller & Ross 1993, 1995) collected directly after their mating flight (mean ± SD, 15.4 ± 0.95 mg, n = 85; df = 153, t = -0.099, P = 0.921). However, the weights of 14-d-old alates were significantly higher than the weights of newly-mated queens (df = 159, t = 5.52, $P <$ 0.0001).

The rates of dealation were observed for both antennectomized and leg-amputated control female sexuals from each of the three age categories (newly-eclosed, 7-d-old, and 14-d-old). Over a 108-h observation period, leg-amputated control alates from the three age categories did not shed their wings in the presence of the queen (Fig. 1A-C). However, within each age category, 100% of alates that were liberated from the influence of queen pheromones, either by removing the queen, antennectomizing the female alates, or both, dealated by 108 h (Fig. 1A-C). Comparison of probit slopes showed that within each age category there were no significant differences ($P >$ 0.05) in the rates of dealation among antennectomized alates in the presence of the queen, antennectomized alates in the absence of the queen, and non-antennectomized alates in the absence of the queen. Comparison of dealation rates (probit slopes) of sexually
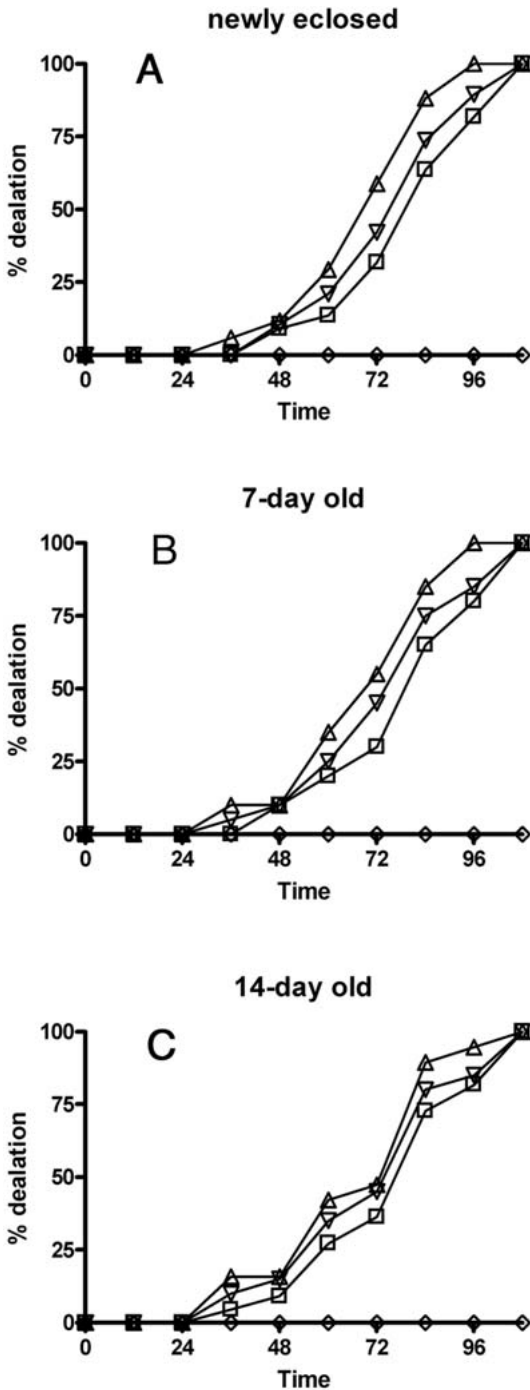
newly eclosed

7-day old

14-day old

Fig. 1. Rates of dealation of newly-eclosed (A), 7-d-old (B), and 14-d-old (C) female alates under four conditions: □-without queen ($n = 22$, newly-eclosed; $n = 20$, 7-d-old; $n = 22$, 14-d-old), ◇—with queen ($n = 12$, newly-eclosed; $n = 15$, 7-d-old; $n = 15$, 14-d-old), △—antennectomized with queen ($n = 17$, newly-eclosed; $n = 20$, 7-d-old; $n = 19$, 14-d-old), and ▽—antennectomized without queen ($n = 19$, newly-eclosed; $n = 19$, 7-d-old; $n = 20$, 14-d-old).

immature and mature females showed no significant differences ($P > 0.05$). Likewise, dealation rates of antennectomized newly-eclosed, 7-d-old, and 14-d-old alates in the presence of the queen were not significantly different ($P > 0.05$). Additionally, there were no significant differences ($P > 0.05$) in the rate of dealation among either antennectomized or non-antennectomized alates in the absence of the queen (Fig. 1A-C).

Dealation in the Absence of Workers

The dealation rate of alates decreased (comparison of probit slopes, $P < 0.05$) when workers were removed. Within 156 h, 100% dealation occurred in both alates isolated and grouped. There was no difference (comparison of probit slopes, $P > 0.05$) between dealation rates for the two sets of alates (Fig. 2). One hundred percent of alates placed individually or in groups with workers and brood dealated within 108 h, and dealation rates between the two groups of alates did not differ (comparison of probit slopes, $P > 0.05$, Fig. 2).

DISCUSSION

Prevention of dealation by a queen primer pheromone appears to be an example of pheromonal control by queens of potentially competing reproductives. This process implies that queens are manipulating workers and female alates to her advantage and their disadvantage. This system in large colony species has been argued against (Keller & Nonacs 1993) on the grounds that it would create a costly evolutionary arms race between the queen and other colony members. Pheromonal queen signal may be a better
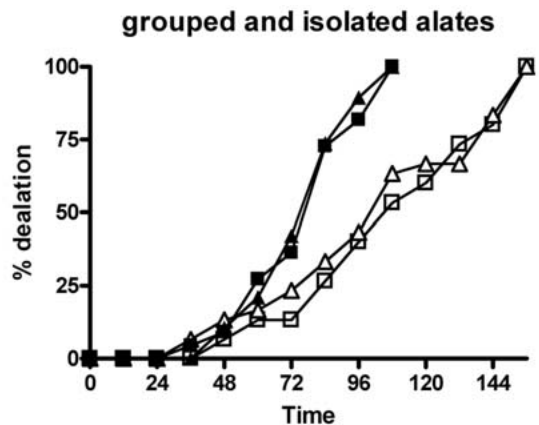
grouped and isolated alates

Fig. 2. Rates of dealation of isolated and grouped female alates: □—grouped alates, $n = 30$; ■-isolated alate, $n = 15$; △—grouped alates with workers and brood, $n = 30$; and ▲—single alate with workers and brood, $n = 15$.

terminology, where the queen pheromone increases the fitness of workers, and in the case of fire ants, sexual alates (Keller & Nonacs 1993). It is in the interest of female alates not to dealate prematurely, and to remain in the colony until environmental conditions induce a mating flight where they can have an opportunity to mate and found their own colony. The source of the dealation inhibitory primer pheromone is reported to be the queen poison gland (Vargo 1997). In addition, the poison gland produces a releaser pheromone that is an attractant to workers (Vander Meer et al. 1980) and has been shown to be released by the queen via the sting apparatus virtually every time the queen lays an egg (Vander Meer & Morel 1995). The two pheromones can be viewed as acting in concert with each other; the volatile releaser pheromone attracts workers to the queen, and then they are stimulated to feed and groom the queen and to remove eggs laid by the queen. The worker/queen/egg interactions ensure that the non-volatile dealation inhibitory primer pheromone is distributed throughout the colony. Again the queen is releasing pheromonal signals that appear to benefit all parties. Since release of the worker attractant pheromone is linked to the queen's egg-laying rate (Vander Meer & Morel 1995), it can be envisioned as a self-regulating behavior modification mechanism. If the queen stops laying eggs for some reason, then the stimuli stops, distribution of dealation inhibitory primer pheromone stops and female alates dealate, which normally portends the demise of that colony. Disinhibition and dealation most commonly occur through the mating flight, mating, colony foundation process. Disinhibition followed by dealation within the colony due to queen loss is important to understand because similar physiological changes take place in both processes (Glancey et al. 1981). In addition, disinhibition and dealation are readily manipulated in the laboratory and may contribute to deciphering the many physiological triggers activated after mating and the isolation of the primer pheromones themselves (Fletcher & Blum 1981).

Under our experimental protocol there were no differences in the dealation rates of sexually immature and mature alates placed in queenless colony subunits. However, rates of dealation were slower when alates were set up without workers or brood, simulating a claustral-colony founding situation after a mating flight. Earlier work (Fletcher et al. 1983) also found that the presence of workers increased the rate of dealation but that disinhibited mature alates dealated faster than immature female alates. This difference probably reflects differences in protocol. Female alate dealation that occurs soon after mating is completely independent of workers, which further supports the hypothesis that the mechanism of dealation is different for within colony and after mating flight situations.

The dealation inhibitory primer pheromone has been postulated to slow but not stop JH build-up in nestmate alates (Fletcher & Blum 1983; Vargo & Laurel 1994). This is supported by correlative evidence that the rate of dealation can be accelerated by topical JH applications (Kearney et al. 1977); however, regardless of applied JH concentrations, the time to dealation after mating could not be duplicated (Burns et al. 2002). That dealation rates for immature and mature alates were indistinguishable implies that JH quantities in female alates do not increase with age to a level sufficient to affect dealation rates. This also suggests that the dealation inhibitory primer pheromone is detected and acts on immature and mature female alates equally well. We clearly demonstrated detection by showing that immature alates were released from queen pheromone influence when their antennae were amputated (see also Vargo & Laurel 1994). Vargo & Laurel (1994) found that antennectomized alates shed their wings in the presence of the queen, suggesting that the queen primer pheromone is detected by sensory cells in the antennae. However, once released from pheromonal control, even immature alates appear capable of producing JH or other agents to promote dealation.

When female alates leave the colony to engage in a nuptial flight, they leave behind both the colony queen and workers. Under these conditions newly-inseminated females shed their wings soon after landing (Markin et al. 1971). Future investigations will examine the influence of mating and/or behaviors associated with a nuptial flight on the physiological changes that induce rapid dealation in newly-inseminated females.

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