

HERMETISM VARIATION IN *Camponotus morosus* (Hymenoptera: Formicidae) WITH THE AGE OF HOMOSPECIFIC INTRUDING ANTS

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ABSTRACT

Ants present hermetism, that is, they recognize and discriminate individuals alien to the colony, even at a homospecific level, which results in aggressive reactions against intruders, varying with their age. To evaluate the importance of this factor, transfers of homospecific larvae, pupae and 2- and 8-h-old adults of *Camponotus morosus* Smith were carried out. All the transferred larvae developed into pupae, and later into adults, but only 20% of these survived 15 d in the receiving nests. The transferred pupae were attacked and killed in 8 d. The transfer of 2-d and 8-h old adults produced 70 and 30% acceptance, respectively. These results indicate that adults begin to develop their own odor earlier than 2-d of age. The age of the intruder was determinant in its acceptance of *C. morosus* homospecific resident ants, as indicated in a 1-way ANOVA ($p = 0.0001$). The adults that survived the transfer of larvae were later reintroduced into their original nests; 37.5% of them were accepted, compared with 65% acceptance for 2- and 8-h old adults reintroduced, indicating that there is a strong genetic influence in the development of their own smell, that would allow adults to be recognized as belonging to the nest. The fact that not all the males were accepted can be explained by the influence of the odor acquired in the receiving nest.

Key words: Ant hermetism, homospecific hermetism.

INTRODUCTION

Ants present hermetism, that is, they do not accept individuals from another nest because of their odor, due to genetic, physical, and environmental factors, or because of the particular smell of the queen (Errard et Jaisson, 1984; Hefetz et al., 1994), emitted by hydrocarbons in the epicuticle. The odor of the nest average the individual one of each ant through trophalaxis, and allows the members to discriminate, in degrees varying according to the species, between the nest ants and those intruder ants (Ipinza-Regla et al., 1994). A little-studied aspect of ant hermetism is the influence of the age of the foreign ants. In Chile, *Camponotus morosus* Smith presents great aggressiveness, which varies with the age of these intruder ants, as it was investigated in this paper.

MATERIALS AND METHODS

Two donor and four receiving *C. morosus* nests containing ~150 workers were used (the donor nests had a variable number of larvae and pupae), to reduce possible variations in the acceptance or rejection responses. Nests were at least 100 m apart to avoid interferences, and were collected in shrubs found in the pre-Andean hills in San Carlos de Apoquindo (33°23'27.25" S; 70°30'1.39" W) and the Río Clarillo National Reserve (33°46'00" S; 70°27'00" W), Metropolitan Region, Santiago, Chile. These nests were taken to the Zoology and Ethology Laboratory, College of Agroforestry, Universidad Mayor, Santiago, Chile, where they were left undisturbed for acclimation, in 24 x 34 x 12 cm plastic containers, at 20 ± 2°C, 45-50% RH, and exposed to 12 h light from fluorescent tubes (Cosens and Toussaint, 1985). A diet of apple

pure mixed with bee honey and ground chicken meat (Ipinza-Regla et al., 1991) was provided; drinking water was also provided through cotton plugs. After the 3 wk acclimation, larvae, pupae, and 2- and 8 h-old adults from donor nests were transferred to receiving nests, where the behavior parameters were observed and registered. The resident ants were marked with color pigments to differentiate them from the arriving ants.

To carry out this study, ten larvae, pupae, 2- or 8-h-old adults were transferred separately. The receiving ants were observed 10 min three times a day (at 08:00, 18:00, and 00:00 h) from the first day through day 15 after egg hatching for larvae and pupae (all transfers were simultaneous). Transfers of 2- and 8-h-old adults were done as they emerged; thus, they were done in 5-12 days. Antennal examination (AE), mandible opening (MO), biting (BI), abdomen flexed dorsally (AFD), abdomen flexed ventrally (AFV), fighting (FI), isolation of the intruder (II), marginalization (MA), trophallaxis (TR), grooming (GR), transportation of the intruder (TI), indifference (IN), and death (DE) were recorded in all transfers. A male surviving the 15 d study was considered accepted (AC). After this period, the surviving adults were taken to their original donor nest, where the same behavior parameters were recorded during 10-min observation periods. The first appearance and frequency of each parameter were also registered.

The parameters recorded, particularly acceptance and rejection conducts were analyzed through a 1-way ANOVA to determine differences in the acceptance of the resident ants to the transfer of homospecific larvae, pupae, and 2- and 8-h-old-adults. The non-parametric Kruskal-Wallis test was used to verify the first appearance in sec of the behavior events observed when reintroducing the individuals to their original donor nest.

RESULTS AND DISCUSSION

In this study, 100% of the larvae introduced into a receiving nest were collected, transported and fed in a nest gallery by the resident workers, as also described in some previous studies (e.g.

Carlin and Hölldobler, 1983; Errard et Jaisson, 1984; Nowbahari and Lenoir, 1984; Aldea, 2001). One week after their transfer, these larvae began to pupate. All of them reached this stage in ca. 3 weeks, during which they were cared for, protected and transported; 45-60 d later, adults emerged from these pupae, which gradually began to be attacked by the resident ants, so that only 20% of these adults from introduced larvae survived the 15 d study in the receiving nests. The remaining 80% was killed, some hours after emergence and others in a few days; only 1, 0, 2 and 5 adults in nests 1-4, respectively, survived the entire study (Table 1).

After their 15 d survival, these adults were returned to the original nests. Their most marked behavior parameter was Antennal Exploration (AE), which occurred in all of them, with a 94 sec mean appearance period (Table 2). Mandible opening (MO) presented a 20% frequency, and occurred in 2 of the 8 reintroductions, with a 442 sec mean appearance period. Biting (BI) appeared on average in 87 sec, with a 50% frequency. Abdomen flexed dorsally (AFD) occurred after a mean of 185 sec, only in two ants in nest 4. Abdomen flexed ventrally (AFV) occurred in a frequency of 37.5%, with a 167 sec mean. Fighting (FI) varied greatly (4 to 267 sec), and occurred with a frequency of 50%. Trophallaxis (TR) and acceptance (AC) had both 25% frequency, with appearance periods of 278 and 225 sec, respectively. Marginalization (MA) and indifference (IN) occurred only once. Grooming occurred in 25% of the adults. The period of appearance of IN was 525 sec, and MA was attempted since sec 2 of reintroduction, but the adults affected escaped constantly. Transportation of the intruder (TI) occurred in none of these reintroductions.

After 24 h reintroduction of the adults, 37.5% was accepted, and the remaining 62.5% was killed by the original nest workers (Table 3).

Because of the small survival of the adults reintroduced, and the little frequency of the parameters observed, the results obtained allowed the Kruskal-Wallis test only for AE (Table 4), with a value of 4.752 ($p = 1$).

These results differ from Nowbahari and Lenoir (1989) with *Cataglyphis cursor*. These

Table 1. Adults surviving after 15 d in receiving nests from larvae transferred from donor colonies.

Receiving nests	Emerged adults used	Adults alive after 15 d	% survival
1	10	1	10
2	10	0	0
3	10	2	20
4	10	5	50
Total	40	8	20

Table 2. Behavior events observed in nests 1, 3, and 4 (no survival in nest 2), and appearance frequency (%).

Behavior parameters	Nest 1	Nest 3	Nest 4	Means	Frequency appearing (%)
Antennal examination (AE)	2	5	149	94	100.0
Mandibles opening (MO)	---	---	442	442	25.0
Biting (BI)	4	---	144	87	50.0
Abdomen flexed dorsally (AFD)	---	---	185	185	25.0
Abdomen flexed ventrally (AFV)	4	---	248	167	37.5
Fighting (FI)	4	---	267	202	50.0
Transportation of intruder (TI)	---	---	---	---	---
Trophalaxis (TR)	---	---	278	278	25.0
Grooming (GR)	---	225	---	225	25.0
Indifference (IN)	---	---	525	525	12.5
Marginalization (MA)	---	---	1	1	12.5

Table 3. Survival of adults 24 h after reintroducing them on their original nests.

Nests	Adults alive	% survival
1	0	0.0
2	---	---
3	2	100.0
4	1	37.5

authors reported that all adults reintroduced were accepted in their original nests, with only minor events of aggression.

The odor pattern of ants is determined by environmental and genetic factors (Bagnères and Morgan, 1990; Hefetz et al., 1994, 1998; Obin and Vander Meer, 1988, 1989; Boulay et al., 2000); grooming and trophalaxis, and early contact with other ants would influence greatly in mixing the individual odors of the ants in a colony and thus each member (Hefetz et al., 1994; Soroker et al., 1998; Cerdá et al., 1999; Boulay et al., 2000). The data obtained in this study leads to think that the influence of genes in *C. morosus* would be greater on individual odor than on environmental odor and early contact with nest workers. In fact, the adults developed from larvae transferred, accepted and taken care of up to their emergence, were killed later (after 4 h). This occurred once they began to develop their own odor, as been described by Ipinza-Regla et al. (2005).

All the larvae transferred developed into pupae, and later into adults, but only 20% of these survived 15 d in the receiving nests. The pupae transferred were attacked and killed in 8 d. Unlike the larvae transferred, all the pupae transferred were killed. Most of these were killed by soldier ants (some of them were killed in minutes), and had a mean survival period of only 2 d (Table 5). Those few pupae that were not killed immediately, were transported and bitten

occasionally, and then the resident ants remained indifferent.

Our results do not coincide with those reported by other authors for *Cataglyphis cursor* (Fonscolombe), *Formica lugubris* Zetterstedt, *Camponotus vagus* Scopoli, *Solenopsis invicta* Buren, and *Pseudomyrmex ferruginae* Smith, as they reported that all larvae or pupae transferred to a conspecific nest were always accepted and taken care of as belonging to the corresponding species nest (Carlin and Hölldobler, 1983; Errard et Jaisson, 1984; Nowbahari and Lenoir, 1989). It is possible that their pupae present the colony odor in the cocoons, making them recognizable and thus not attacked by their sisters, as herein.

The acceptance of 2- and 8-h-old *C. morosus* adults in the receiving nests is presented in Table 6.

The behavior parameters of *C. morosus* observed in four nests receiving 2- and 8-h-old adults from a donor nest are presented in Table 7.

The transfer of 2-d and 8-h-old adults produced 70 and 30% acceptance, respectively. These results indicate that the adults begin to develop their own odor earlier than 2-d of age. The age of the intruder was determinant in its acceptance of *C. morosus* homospecific resident ants, as indicated in a 1-way Anova ($p = 0.0001$). The adults that survived the transfer of larvae were later reintroduced into their original nests; 37.5% of them were accepted, compared with 65% acceptance for 2- and 8-h-old adults

Table 4. Behavioral events (n ± SD) observed in the adults of four nests after reintroducing them on their original nests.

Behavior parameters	Nest 1		Nest 2		Nest 3		Nest 4		Kruskal-Wallis
Antennal examination (AE)	1	6	0	---	2	5 ± 1.4	5	143 ± 104.0	4.752
Mandibles opening (MO)	1	---	0	---	1	1	2	421 ± 166.2	p=1
Biting (BI)	1	4	0	---	0	---	3	114 ± 64.2	CNP
Abdomen flexed dorsally (AFD)	0	---	0	---	0	---	2	185 ± 113.1	CNP
Abdomen flexed ventrally (AFV)	1	4	0	---	0	---	3	201 ± 119.2	CNP
Fighting (FI)	1	4	0	---	0	---	3	267 ± 112.3	CNP
Transportation of intruder (TI)	0	---	0	---	0	...	0	---	CNP
Trofalaxis (TR)	0	---	0	---	0	...	2	277 ± 67.2	CNP
Grooming (GR)	0	---	0	---	2	225 ± 216.4	0	---	CNP
Indifference (IN)	1	5	0	---	0	---	1	525	CNP

Means ± SD only when observed in nests 3 and 4. CNP: Calculation not possible.

Table 5. Survival of pupae (d; n = 10) in the receiving nests.

Nests	Surviving days
1	3.3
2	3.6
3	2.3
4	1.5
Mean	2.2

Table 6. Acceptance of 2- and 8-h-old *C. morosus* adults in homospecific receiving nests.

Nests	2 h-old (%)	8 h-old (%)
1	70	20
2	60	30
3	60	40
4	90	30
Means	70	30

reintroduced, indicating that there is a strong genetic influence in the development of their own smell, that would allow adults to be recognized as belonging to the nest, and also some influence of the environment of the smell acquired in the receiving nest, responsible for not all the males were accepted.

The acceptance of 2- and 8-h-old adults that survived in the receiving nests and were reintroduced in the donor nests are presented in Table 8. The first appearance (sec) and observation frequency of behavior parameters (%) are shown in Table 9.

The frequencies of appearance (%) of automarginalization, death, and acceptance of ants reintroduced after 24 h to their original nests from receiving nests are presented in Table 10, and the occurrence of the first appearance (sec)

of the behavior parameters observed in 2- and 8 h old adults after reintroduction to their original nests in Table 11.

CONCLUSIONS

A marked trend was observed in the influence of the age of the intruding ant on the level of hermetism of the resident ants. The greater the age of the intruder the more intense will be the aggressiveness and rejection of resident ants of the same species.

All the larvae transferred from donor to receiving nests were accepted and developed into pupae and later to adults. However, only 20% of these adults survived after 15 d in the receiving nests.

All the pupae transferred from donor to

Table 7. Behavior parameters of 2- and 8-h-old *C. morosus* ants in four nests receiving 2- and 8-h-old adults from a donor nest.

2 h-old	Behavior parameters observed	Final results
Nest 1		
1	AE, BI, AFV, FI, death before the end of the day	Death
2	AE, BI, AFV, FI, death before the end of the day	Death
3	AE, MO, AFD, TI, BI sporadic, FI with 2 workers, death at the end of the day	Death
4	AE frequent, MO, BI sporadic, IN	Acceptance
5	AE, TI	Acceptance
6	AE, TI	Acceptance
7	AE frequent, BI sporadic	Acceptance
8	AE frequent, BI, MO	Acceptance
9	AE, IN	Acceptance
10	AE, MO, IN	Acceptance
Nest 2		
1	AE, MO, BI, AFD, AFV, FI, death before the end of the day	Death
2	AE frequent, MO, BI sporadic, death before the end of the day	Death
3	AE frequent, MA, BI, IN, death before the end of the day	Death
4	BI, AE frequent, death before the end of the day	Death
5	BI, AE frequent	Acceptance
6	EA, BI sporadic, IN	Acceptance
7	EA, BI sporadic, IN	Acceptance
8	EA, IN	Acceptance
9	IN	Acceptance
10	EA, TI	Acceptance
Nest 3		
1	AE, MO, BI, AFD, AFV, FI, death before the end of the day	Death
2	MO, BI, AFD, AFV, death before the end of the day	Death
3	BI, AFV, FI, death before the end of the day	Death
4	BI, AFV, FI, death before the end of the day	Death
5	AE frequent, BI sporadic, IN	Acceptance
6	IN	Acceptance
7	AE, IN	Acceptance
8	AE, IN	Acceptance
9	AE, IN	Acceptance
10	AE, IN	Acceptance
Nest 4		
1	MO, AFD, death before the end of the day	Death
2	AE, MO sporadic	Acceptance
3	AE, IN, MO sporadic	Acceptance
4	AE, MO, IN	Acceptance
5	AE, OM, IN, BI sporadic	Acceptance
6	EA, MO, BI	Acceptance
7	EA, TI	Acceptance
8	EA, MO, IN	Acceptance
9	EA, MO, BI, IN	Acceptance
10	EA, TI	Acceptance
8 h-old	Behavior parameters observed	Final results
Nest 1		
1	AE, MO, BI, marginalization during 3 d	Death
2	AE, MO, BI, FI, death before the end of the day	Death
3	AE, MO, BI, FI, death before the end of the day	Death
4	BI, AFD, AFV, FI, death before the end of the day	Death
5	AE, MO, BI, TI	Death
6	AE, MO, BI, TI	Death
7	AE, MO, BI sporadic, FI, death before the end of the day	Death

8	AE, BI sporadic, FI, death before the end of the day	Death
9	AE, BI	Acceptance
10	AE, BI, TI	Acceptance
Nest 2		
1	FI, death before the end of the day	Death
2	FI, death before the end of the day	Death
3	AE, MO, BI, TI	Death
4	AE, TI constantly to the honey	Death
5	AE, TI	Acceptance
6	AE, MO, BI, TI, death before the end of the day	Death
7	AE, BI, MO, IN	Acceptance
8	AE, BI, MO, IN	Acceptance
9	AE, MO, BI, DFA, VFA, FI	Death
10	AE, MO, TI, death and following day	Death
Nest 3		
1	AE, MO, BI, AFD, AFV, FI, death before the end of the day	Death
2	AE, BI, AFD, AFV, FI, death before the end of the day	Death
3	MO	Death
4	AE, BI, TI	Death
5	AE, BI, IN	Acceptance
6	AE, MO, BI sporadic, TI	Death
7	AE, MO, BI sporadic, TI	Acceptance
8	AE, MO, BI, DFA, TI	Death
9	BI sporadic	Acceptance
10	IN	Acceptance
Nest 4		
1	BI, FI, death before the end of the day	Death
2	BI, FI, death before the end of the day	Death
3	AE, MO, BI, MO, AFD, AFV, FI, death before the end of the day	Death
4	AE, AM, marginalization, BI, death before the end of the day	Death
5	AE, BI, MO, death before the end of the day	Death
6	AE, IN, FI, death before the end of the day	Death
7	AE, IN	Acceptance
8	AE, BI, IN	Death
9	AE, BI, IN	Acceptance
10	AE, IN	Acceptance

AE: Antennal examination; MO: Mandibles opening; BI: Biting; AFD: Abdomen flexed dorsally; AFV: Abdomen flexed ventrally; FI: Fighting; TI: Transportation of intruder; IN: Indifference.

Table 8. Acceptance of 2- and 8-h-old adults that survive in the receiving nests and were reintroduced at the donor nests.

Nests	2 h-old	8 h-old	Total
1	70	20	9
2	60	30	9
3	60	40	10
4	90	30	12
Total	28	12	40

Table 9. First appearance (sec) and observation frequency of behavior parameters (%) after reintroducing 2- and 8-h-old adults to their original nests from their receiving nests.

Parameters	Nest 1	Nest 2	Nest 3	Nest 4	Means	Frequency (%)
AE	59	25	25	13	36	92.5
MO	15	43	138	15	17	42.5
BI	80	73	53	81	75	47.5
AFD	149	---	---	22	64	7.5
AFV	139	119	---	143	138	35.0
FI	157	170	119	32	164	45.0
TI	---	2	---	---	2	2.5
TR	---	198	204	150	194	15.0
GR	---	125	241	---	195	12.5
IN	162	129	113	43	111	27.5

AE: Antennal exploration; MO: Mandibles opening; BI: Biting; AFD: Abdomen flexed dorsally; AFV: Abdomen flexed ventrally; FI: Fighting; TI: Transportation of intruder; TR: Trophalaxis; GR: Grooming; IN: Indifference.

Table 10. Frequencies of appearance (%) of automarginalization, death, and acceptance of ants reintroduced after 24 h to their original nests from receiving nests.

Parameters	Nest 1	Nest 2	Nest 3	Nest 4	Means
Automarginalization	0.0	11.1	20.0	0.0	7.5
Death	66.7	33.3	0.0	41.7	35.0
Acceptance	33.3	66.7	100.0	58.3	65.0

Table 11. Comparison of the first appearance (sec) of the behavior parameters observed in 2- and 8-h-old adults after reintroduction to their original nests.

Parameters	Nest 1 ¹	Nest 2 ¹	Nest 3 ¹	Nest 4 ¹	KW ²
AE	n = 8 59 ± 123.9	n = 9 25 ± 21.3	n = 10 25 ± 21.7	n = 11 12 ± 5.0	1.299 p = 0.73
MO	n = 5 15 ± 7.3	n = 3 43 ± 32.3	n = 2 137 ± 102.5	n = 7 15 ± 1.4	10.011 p = 0.04*
BI	n = 7 80 ± 95.2	n = 2 72 ± 53.0	n = 3 53 ± 37.1	n = 7 80 ± 102.3	0.4881 p = 0.92
AFD	n = 1 149 ± ---	n = 0 --- ± ---	n = 0 --- ± ---	n = 2 22 ± 1.4	Calculation not possible
AFV	n = 6 139 ± 132.8	n = 2 119 ± 4.2	n = 0 --- ± ---	n = 6 143 ± 154.6	0.2529 p = 0.89
FI	n = 7 157 ± 136.3	n = 3 170 ± 86.7	n = 1 119 ± ---	n = 7 32 ± 163.9	0.25 p = 0.97
TI	n = 0 --- ± ---	n = 1 2 ± ---	n = 0 --- ± ---	n = 0 --- ± ---	Calculation not possible
TR	n = 0 --- ± ---	n = 1 198 ± ---	n = 4 204 ± 113.1	n = 1 150 ± ---	0.149 p = 1.00
GR	n = 0 --- ± ---	n = 2 125 ± 56.6	n = 3 241 ± 179.6	n = 0 --- ± ---	2.00 p = 0.8
IN	n = 3 163 ± 233.1	n = 3 129 ± 85.7	n = 2 112 ± 7.5	n = 3 43 ± 63.4	0.25 p = 0.89

¹Means ± SD. ²Test of Kruskal-Wallis. AE: Antennal exploration; MO: Mandibles opening; BI: Biting; AFD: Abdomen flexed dorsally; AFV: Abdomen flexed ventrally; FI: Fighting; TI: Transportation of intruder; TR: Trophalaxis; GR: Grooming; IN: Indifference.

receiving nests were killed in 3 d on average, possibly because they smelt to their original colony, and were recognized as alien and attacked by the receiving ants.

70% of the 8 h old adults transferred from donor to receiving nests were killed. Accordingly, 2-d old adults presented only 30% mortality, possibly because they begin to develop their own odor earlier than 2 h. Because of the same reason, the 2- and 8-h-old adults developed from larvae transferred and then reintroduced to their original nests were accepted in 37.5 and 65.0%, respectively.

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