

Role of Worker Thelytoky in Colonies of the Ant *Cataglyphis cursor* (Hymenoptera: Formicidae)*

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In the laboratory, queenless workers of *Cataglyphis cursor* (Fonscolombe 1846) can lay eggs which develop into workers and queens, and a complete society is finally restored. It is suggested that thelytoky may enable colony foundation in this species by isolated groups of workers which retain occasional contact with the parent nest.

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Im Labor können weisellose Arbeiterinnen von *Cataglyphis cursor* (Fonscolombe 1846) Eier ablegen, die sich zu Arbeiterinnen und Königinnen entwickeln, was schließlich zur Wiederherstellung einer kompletten Sozietät führen kann. Es wird angenommen, daß Thelytokie bei dieser Art eine Koloniegründung durch isolierte Arbeiterinnengruppen ermöglicht, die gelegentlichen Kontakt mit dem Mutternest aufrechterhalten.

Cataglyphis ants inhabit dry regions and live in open areas. They forage individually and collect dead animals, mainly insects. They have a well-developed system of navigating. They are only active during the day and use polarized light to determine direction. Detailed experiments have shown that landmarks are also used near the nest [Harkness & Wehner 1977].

Cataglyphis cursor (Fonscolombe 1846) is a mediterranean species [Cagniant 1976 a, b]. Colonies are always monogynous and contain from some 10–1500 workers [♂♂]. More than a 100 colonies have been dug up, and very generally was found the queen [♀]. In the presence of the ♀, the ♂♂ do not lay eggs. ♂♂ are produced in small numbers and appear in early summer. Mating occurs after a nuptial flight.

The mechanism of colony reproduction is not well understood. Foundation by isolated ♀♀ seems very improbable for 3 reasons:

- (1) Never solitary ♀♀ have been found, even though they are well known in *Lasius* or other species.
- (2) In the field, ♀♀ remain near the entrance of the nest to which they return after mating.
- (3) In the laboratory, inseminated ♀♀ die when they are isolated.

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Therefore, another hypothesis has to be presented: Cagniant [1973] found that orphaned ♀♀ of *C. cursor* produce alate ♀♀ and ♀♀ by parthenogenesis. Impaternate ♀♀ were also reported in several other species, but this information needs to be confirmed. Thelytoky seems to be a minority phenomenon in ants [Crozier 1975] but was recently observed in *Pristomyrmex pungens* Mayr 1886, (Myrmicinae), lacking a reproductive caste [Mizutani 1980]. Both, in *Cataglyphis* and *Pristomyrmex*, ♀♀ lack spermathecae [Suzzoni & Cagniant 1975, Itow et al 1984]. If the productivity of the ♀♀ of the 2 species is compared, it seems to be higher in *Cataglyphis* (Tab 1), but this fact could be related to the different durations of the experiments. In *Cataglyphis*, ♀♀ appear first, then the ♀♀, and then rarely some ♂♂. The biological characteristics of thelytoky in the 2 species are probably rather different.

Tab 1: Productivity of ♀♀ of *Cataglyphis cursor* (Fonscolombe 1846) and *Pristomyrmex pungens* Mayr 1886 [Hymenoptera: Formicidae].

Genus species	Composition of initial group	Production in %	No of replicates
<i>Pristomyrmex pungens</i> [Itow et al 1984] 1–2 months	100 ♀♀	20 %	12
<i>Cataglyphis cursor</i> [Cagniant 1980–83] 4–5 months	100–500 ♀♀	73 % ♀ 4.2 % ♀ 0.5 % ♂	35
	100–500 ♀♀ and ♀	163 % ♀ 1.5 % ♀ 0.5 % ♂	22

The biological signification of thelytoky in *C. cursor* has to be discussed: Is parthenogenesis in this species a laboratory phenomenon? Evidently it could be adaptive if the ♀ dies, for example after a tunnel collapse in the nest. But up to now, orphaned colonies have never been observed in the field!

It can be hypothesised that thelytoky takes place during the propagation of the species. There are possible mechanisms based on fission:

(1) A group of ♀♀ leaves the mother colony with a mated ♀ and starts a new colony. Ledoux [1973] propound this hypothesis with *Aphaenogaster senilis* (Mayr 1853). Observations with other species of *Aphaenogaster* in Morocco strengthen it [Cagniant: unpubl data]. This phenomenon has not been observed yet in *C. cursor*, but cannot be eliminated.

(2) A group of ♀♀ leaves the mother nest; as they have no ♀ they produce ♀♀ by thelytoky. These are inseminated by the ♂♂ of neighbouring colonies. The mating of parthenogenetically-produced ♀♀ has been observed several times in the laboratory [Cagniant 1980, Lenoir: personal observations]. The splitting of a large colony was also observed in the laboratory, but the brood of the orphaned group may have come from the main nest. This needs to be investigated.

Small colonies were observed in the field. Sometimes a hole is occupied for only a few days and then abandoned by the ♀♀ which return to the mother nest. Whichever the situation may be, daughter colonies keep strong links with the mother nest. It is a form of slight polycaly. In *Cataglyphis iberica* (Emery 1906) and *Cataglyphis bicolor* (Fabricius 1793), adjacent nests were also found, but they do not have ♀♀ [De Haro 1984, Wehner et al 1983]. In *C. cursor*, the relations between some nests can be observed in the field.

Tab 2: Example of exchanges between neighbouring colonies of *Cataglyphis cursor* (Fonscolombe 1846) in the field. % of ants marked in 1 nest entering another nest [Hymenoptera: Formicidae].

entering nest n° coming from nest n°	0	1	10	Total No of ♀♀ marked
0	75.4	10.6 %	14 %	236
1	5 %	93.2	1.8 %	163
10	22.6 %	11.8 %	65.6	93

Distance between nests: 1 (1.35 m) 0 (0.55 m) 10

For example in nest 0, 236 foragers were marked with a dot of paint and watched for 5 days. 10.6% of them entered nest 1. In contrast, 5% of the foragers of the nest 1 entered nest 0 (Tab 2). Sometimes the ants transport an adult, a cocoon, or a prey. The 2 colonies were dug up and given the same foraging area in the laboratory. All the ♀♀ were marked with a dot of paint. After 1 week, some ♀♀ were observed to have changed nest. The traffic of ♀♀ could be counted at the 2 entrances. Colony 0 was completely dominated: 41% of the traffic at the entrance of the nest is composed of ♀♀ of colony 1! This % increased during the following weeks, and the colony is expected to die during the winter (Tab 3).

Tab 3: % of total traffic of ants as to original nest at the entrance of 2 adjacent nests of *Cataglyphis cursor* (Fonscolombe 1846) in the laboratory [Hymenoptera: Formicidae].

A ↙ B	IX - 14			IX - 20			IX - 26		
	0	1	N	0	1	N	0	1	N
0 (1500 ♀♀ + ♀)	58.9 %	41.1 %	73	36.4 %	63.6 %	44	27 %	73 %	59
1 (750 ♀♀ + ♀)	20.8 %	79.2 %	77	9.3 %	90.7 %	54	2 %	98 %	54

N = Total No of ants counted for each nest (4 observations of 5 mn for each day at one entrance).

A → B = % of ♀♀ coming from colony A and going to the entrance of colony B.

Tab 4: Thefts between colonies of *Cataglyphis cursor* (Fonscolombe 1846) [Hymenoptera: Formicidae]: Colony dug out and A abandoned at the spot, B transferred 250 m.

Experiment	Composition of colony ♀♀ + Larvae	% Thefts in 1 h
A	1	430
	2	360
	3	450
B	4	450

In the field some colonies were dug up and the ♀♀ and brood were abandoned on the spot. During the time necessary to occupy a new site, a lot of them were immediately carried away by foragers of an adjacent nest. Thus, from 13–22.5% of the individuals of the disturbed colony A can be “stolen” by another colony (Tab 4). In a control test, a foreign colony was transferred 250 m, and no transport was observed. It demonstrated that interactions between nests are possible when they are adjacent and probably related.

Conclusion

At the moment, no definitive conclusion is possible about the biological value of thelytoky in *Cataglyphis cursor*. More field observations are needed.

The phenomenon exists: it is easily shown experimentally: Some years ago a colony was dug up in IX and the ♀ picked up. During the following VI, the nest contained many alate ♂♂ and ♀♀ which could indicate the occurrence of thelytoky [Cagniant: unpubl]. To confirm this possibility, other colonies were dug up and orphaned during the summer 1984 and will be observed in 1985.

From an evolutionary point of view, it can be predicted that, given the dispersal by fission over short distances *C. cursor* should show few differences between colonies in the same area, because they belong to the same general lineage. Within colonies, variability also should be low, and it must be decreased by thelytoky, a problem to be examined in the future. There is an intermediary situation between colony foundation by fission involving inseminated ♀♀ as in many Formicinae, and that in *Pristomyrmex* where alate ♀♀ have disappeared. *C. cursor* could be compared with *Apis mellifera capensis* honeybees, in which orphaned ♀♀ rear new ♀♀ by thelytoky [Moritz 1986].

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Brian, M. V.: **Social Insects, Ecology and Behavioural Biology.** – [X+377 Seiten, 98 Abbildungen, 18 Tafeln, Format 155x232 mm, Paperback (Hard cover)]. – Verlag: Chapman and Hall, London-New York; ISBN: 0-412-22930-7; Preis: £ 12.95 (Hard cover £ 25.00). – – – [EGR-Nr 1037].

Brian ist wohl allen mit sozialen Insekten befaßten Wissenschaftlern durch seine Arbeiten ein Begriff. Ein Buch aus seiner Hand weckt somit gewisse Erwartungen. Leider werden diese von dem vorliegenden Band bei weitem nicht erfüllt. Das Buch beschreibt in 16 Kapiteln Ernährung, Futtersuche, Nestbau, Mikroklima, Verteidigung, Verarbeitung der Nahrung, Populationswachstum, Reife von Sozietäten, Reproduktion, Evolution von Sozialverhalten, Koloniestruktur, Ökologie verwandter Arten, Vergesellschaftungen von Arten in bestimmten Ökosystemen, wobei jeweils direkt Termiten, Ameisen, Bienen und Wespen verglichen werden. Die Einführung bringt eine systematische Einordnung der eusozialen Insekten, ein Schlußkapitel ist den Themen „Mutualistische Beziehungen mit Pflanzen“ und „Soziale Organisation“ gewidmet. Insgesamt könnte das Buch einen wertvollen Führer zu der weitgestreuten und umfangreichen Literatur über die genannten Aspekte darstellen, zumal die Bibliografie nicht weniger als 882 Zitate aufweist. Bedauerlicherweise wurde das Buch jedoch offenbar unter Zeitdruck verfaßt, so daß zahllose Druck- und Schreibfehler, ungenaue, verdrehte oder unreflektiert verallgemeinerte Aussagen seinen Wert erheblich vermindern. Nur wenige Beispiele sollen dies verdeutlichen: P 7: „Ants . . . as have termites . . . , have evoked the capacity to break off their wings once dispersal and copulation are over . . .“ – Bei Termiten findet aber die erste Kopula lange nach dem Flug und dem Flügelabwurf statt. P 10: „This association with plants blossoms out until higher ants . . . eat seeds and green leaves“. – Sicher schneiden Attinen grüne Blätter für ihre Pilzgärten, aber ich kenne keine Ameisenart, die Blätter frißt.

P 63: „*Lasius fuliginosus* is . . . virtually blind“. – Diese Aussage entbehrt jeder Grundlage. P 227: „In this species winged females occur as well but in *H. canadensis* all females are winged (Buschinger 1974).“ – Da ich *Harpagoxenus canadensis* erstmals 1977 untersuchte, wird der Leser diese Aussage sicher nicht in der zitierten Arbeit finden. Auch die Behauptung (p. 260), daß *Formica polyctena* „morphologically indistinguishable“ von *F. rufa* sei, ist so nicht gerechtfertigt; Betrem hat dazu 1960 recht brauchbare Beborstungsunterschiede publiziert, die darauf aufbauende *Formica*-Systematik ist inzwischen generell akzeptiert. P 196 wird berichtet, daß die sklavenhaltende Ameise „*Harpagoxenus sublaevis* . . . has queens that can stop queens of one of its hosts (*Leptothorax muscorum*) laying even though they are inseminated, but not queens of its other host (*L. acervorum*). The parasite thus appears to control its host's sexual

production.“ Dies ist eine reichliche Verdrehung der von Buschinger (1978, *Ins. Soc.* 25, 63–78, – nicht die im Text zitierte Arbeit *Ins. Soc.* 25, 163–172) gegebenen Darstellung: Keine der Wirtsarten reproduziert im *Harpagoxenus*-Nest. *L. acervorum*-♀♀ sind darin zu finden, jedoch stets unbegattet und steril, während *L. muscorum*-♀♀ begattet sein können, aber ebenfalls keine Eier legen. Beide werden als Puppen geraubt, *L. muscorum*-♀♀ können in Nestnähe begattet werden, *L. acervorum*-♀♀ nicht. Es ließe sich eine Fülle weiterer Beispiele anführen, doch sei als letztes nur noch vermerkt, daß Brian p 51–57 die Tanzsprache der Honigbienen abhandelt, ohne K. v. Frisch überhaupt zu erwähnen. Mit Blick auf alle diese Mängel und verfälschten Darstellungen kann man das Buch in der Tat nicht empfehlen, jedenfalls nicht für Studenten und andere, die das Studium sozialer Insekten beginnen wollen. Für erfahrene Wissenschaftler bietet es einen Überblick über einen Großteil der relevanten Literatur, aber es wird dennoch zu oft nötig sein, die Originalarbeiten einzusehen.

Alfred Buschinger (Darmstadt)

Bolis, L., Keynes, R.D., & Maddrell, S.H.P. (Editors): **Comparative Physiology of Sensory Systems**. [XI + 660 pages, numerous figures, tables and photographs, size 160 x 235 mm, balacron hard cover, jacket]. – Publisher: Cambridge University Press, Cambridge - London - New York - New Rochelle - Melbourne - Sydney 1984; ISBN: 0-521-25002-1; price: Brit £ 65.-. – – – [EGR-Nr 880].

The book contains 33 papers from the Sixth International Conference on Comparative Physiology, held at Crans-sur-Sierre, Switzerland, June 1982. – Experts on the sensory nervous system met to report advances made recently in the study of visual, auditory and other senses of cephalopods, insects, cold-blooded vertebrates, birds and mammals. The titles of the contributions selected for this book are as follows. Lateral line systems. Hearing in insects. Auditory function at the receptor level in reptiles. Sound detection and processing by teleost fish: a selectiv review. Spatial receptive fields in the auditory system. Auditory basis of echolocation in bats. Afferent innervation of the mammalian cochlea. Efferent innervation of the cochlea. Effect of ganglioside treatment on hearing loss in experimental diabetes in mice. Hearing mechanisms in caiman and pigeon. Functional organization of the medial geniculate body in cats. Initial events influencing olfactory analysis. Neural basis of olfaction in insects. Olfaction and taste in fish. Biochemical studies of physiological function: olfactory recognition in rainbow trout. Pheromone biology in the Lepidoptera: overview, some recent findings and some generalizations. Comparative study of electrophysiological phenomena in the olfactory bulb of some South American marsupials and edentates. Visual systems of cephalopods. Relative movement and figure-ground discrimination by the visual system of the fly (towards a neuronal circuitry). Local circuits in the distal retina of vertebrates. Infrared and visual senses in snake optic tectum. Neuropeptides in retina: morphological and biochemical aspects. Lack of relations between dopaminergic and GABA-ergic mechanisms in chick-retina. Neuroethological basis for electrocommunication. Neural mechanisms of electrolocation and jamming avoidance behavior in electric fish. Navigation by polarized skylight. Electroreceptor mechanisms in teleost and non-teleost fishes. Theory of electromagnetic orientation: a further analysis. Cellular bases for gravistatic reception by invertebrates and vertebrates. Inertial motion sensors. Topographic and non-topographic mapping of spatial sensory information: Predictions from Boring's formulation. Role of sensory information in the control of locomotion in fishes. Effects of motor commands on sensory inflow, with examples from electric fish. – The individual contributions are in part highly specialized and differ widely, some being basically comparative studies while others focus on the general physiological aspects of this topic. The authors are mostly well-known and currently active in their research fields so that the works presented provide a true picture of the status of research into the comparative physiology of sensory systems to date. Taken alltogether the contributions do indeed cover the broad spectrum of research areas impied by the title of this book.

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