ACTA NEUROBIOL. EXP. 1989, 49: 367-379

CONTROVERSIES ON THE SUBJECT OF SLAVE-RAIDS IN AMAZON ANTS (GENUS *POLYERGUS*)

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Key-words: *Polyergus*, slave-raid

Abstract. The paper contains a polemic with the view expressed by Talbot, Wilson and Topoff and his co-workers, who maintain that the existence of scouts and their leading directing in slave-raids of the American *Polyergus*' species is fully proved. In particular we do not agree with Talbot's and Wilson's argument that following by the amazons of the scent-trail prepared from the crushed bodies of their nestmates indicates that the amazon raids follow the trails of scouts. Considering the results and notions of the above-mentioned authors, we maintain that the mechanism of slave-raids in the American amazons is far from clear.

INTRODUCTION

Ants of the genus *Polyergus* are obligatory social parasites: all works in their nests are performed by slave-workers belonging to other species. The sole function performed by the amazons themselves are slave-raids. According to Heinrich Kutter (13), the nestor of contemporary myrmecology, each raid is a remarkable entomological event. The objects of these raids are nests of ant species suitable for slavery, thereafter referred to as slave-species. The purpose is to seize their brood, usually pupae, which in the raiders' nest will turn into adult slave-workers.

The mechanisms of slave-raids, executed with extraordinary efficiency, has absorbed the minds of scholars for the second consecutive century. The original views on the subject were influenced by the fact, that individual amazon ants leave the nest in the morning (with one recently described exception which will be discussed later) and chaotically walk around the area, as do the foragers of independent non-parasitic species when they investigate the terrain. Seeing that in the colonies of *Polyergus* the supplying of food is the duty of slave-workers, these individuals were taken a priori for scouts who first seek out the target of attack and later lead the raid. The individuals generally return to the nest before the noonday heat. About 4 or 5 p.m., when the soil and air still retain the warmth of day but the sun is weaker, the amazons depart from the nest in a group of 80-100 and start circle about entrance hole. Their circulation speed gradually increases and the circle they form becomes elongated in one direction, turning into an ellipse and subsequently being converted into swinging movement along its axis, which ultimately points the direction of the raid. From time to time one of these individuals rushes back to the nest, to re-emerge shortly with fresh groups of amazons behind. This initial group of circling ants which determine the direction of the raid and arouse their nest-mates to join it, Dobrzańska and Dobrzański (6) called "activators". When the number of aroused amazons on the nest surface reaches a certain optimum, the movement becomes more and more direction oriented and the whole swarm starts to move away from the nest. The ants form a close column 1-1,5 m long and 15-20 cm wide, which moves straight ahead with speed and efficiency (6, 18). When they encounter a nest of the slave-species, the amazons "pour into it at once in a body, seize the brood, rush out again and make for home" (Wheeler) (23).

One thing important for our reasoning should be added to that description: that not every raid ends this way. It happens that the raiders come back without prey, having failed to find the target. That amazon raids are frequently unsuccessful is beyond doubt. It has been reported in European ants *Polyergus rufescens* by Forel (10), Brun (2), Dobrzańska and Dobrzański (6), Köhler (12), and in Siberian amazons *P. nigerrimus* by Zhigulskaya (28). Significantly, the phenomenon has also been confirmed by supporters of the scout thesis. Czechowski (5), while admitting that not all raids of *P. rufescens* are successful, thinks that it may be due to taking a wrong direction by the departing column. According to Talbot (18) the raids of East American amazon *P. lucidus* miss the target in 17.6% (i.e., every sixth raid is a failure). Marlin (14) registered in that species 13 unsuccessful raids out

of 62 he had observed (every fifth), whereas Cool-Kwait and Topoff (4) reported 26% failures in 107 raids (every fourth!).

STUDIES BY DOBRZAŃSKA AND DOBRZAŃSKI AND BY KÖHLER

The generally perceived fact, that the amazon-raids sometimes miss the target induced the Dobrzańskis to start research on the role of the so-called scouts. Starting in the morning, they seized each single amazon *P. rufescens* that was leaving the nest. It turned out that capturing all "scouts", even for several consecutive days, had no effect on the colony's behavior. The course of raids as well as their reaching or missing the target were unchanged in the absence of scouts (6).

By marking with paint the specimens in the forefront of the raiding column, the Dobrzańskis confirmed Brun's suggestion, that the amazons' army has no permanent leaders (2). The circulation motion imparted from the start continues as a swinging movement in the efficiently marching column. Occasionally single amazons turn back and march against the tide, only to join after some moments the stream of the forward-marching swarm. In consequence, all the time there are different ants at the head of the column. Thus, the so-called scouts do not march on the head of the army, in fact it is not headed by anyone in particular. The seizing of the first ranks of ants did not affect the movement of the column, either.

There still remained the possibility that the army follows a scent-trail left earlier by the scout. However, even digging the soil in front of the marching column, which involved total obliteration of the possible trail, failed to disturb the movement of the column, as confirmed by Czechowski, too (5). But the Dobrzańskis had successfully changed the direction of the raid by other means. When the prowling group of activators already pointed out the direction of movement, the experimenters lifted them to the other side of the nest. The activators resumed their circling in the new place selected by the experimenters and soon the whole army was marching in the artificially imposed direction, where there was no question of trails or leadership. The effect of these artificially directed raids was commensurate with that of natural ones (6).

Considering that:

— the amazon colony deprived of scouts for as long as several days still continued to undertake raids;
— the column made no change in the direction and course of their march after the possible scent-trails have been obliterated;
— columns artificially steered in random directions obtained effects commensurate with natural raids —

the Dobrzańskis arrived at a conclusion that the reconnaissance role of the scouts is a misconception and changed their name to "pseudoscouts". They have assumed that the *P. rufescens* army does not march to a target known in advance [1]. It comes across the slaves' nest by pursuing the direction spontaneously set by chaotically circling activators. Most raids find the target within a shorter or longer distance, because the nests of the desired species are densely distributed (6). In our geographic region there are four such species: *Formica fusca, F. rufibarbis, F. cunicularia* and *F. cinerea*. The latter is a polycalic species forming colonies of nests that proliferate by budding. Around each mother nest there frequently spread dozens of daughter nests. In the ecological niche inhabited by these species, an army of amazons marching ahead for distances as long as 100-200 m could hardly miss one of the nests. Moreover, they need not come straight across the nest, it is enough for them to enter the foraging territory of nest inhabitants to be led by scent to the nest.

In later years we found additional facts cotradicting the theory of scouts. Here is the most striking one, quoted after a 1978 publication: "At the distance of 4 m away from the studied *P. rufescens* nest there was a big road belonging to *Formica rufa*. From time to time the slave-making ants went on a raid across that road, which resulted every time in an attack by *F. rufa* ants, who defend their roads with an almost equal ferocity to that with which they defend their nest. Although those ants cannot match the amazons in a duel, and thus many more of them were killed, their practically unlimited quantitative superiority [2] resulted in the slave-making ants being decimated each time. The continual occurrence of such fight led by the end of the summer to such decrease in the amazons' numerical force that the colony ceased to make raids and, in the following year, ceased to exist at all" (8). A scout could not possibly show the amazons that road. She would have no chance to cross and recross it, and, more important, there would be no stimuli to make her investigate so dangerous a direction. This evidences the spontaneous character of the process by which an army of the amazons moves in a randomly chosen direction. The Dobrzańskis (8) observed also normally functioning *P. rufescens'* nest in which pseudo-scouts were not present. The existence of nests without pseudo-scouts is an argument in support of the Dobrzańskis' hypothesis, according to which they are an atavistic group of individuals, and their activity no longer plays a part

[1] This does not concern second or repeated attacks on the same nest where the brood was too numerous to be carried out at one go. In such cases the army departs again without needing to be aroused by activators.

[2] A medium-sized family of *F. rufa* attains the number of 500 thousand workers (16), while *P. rufescens* nest contains at the most 2 thousand amazons (9).

in the life of the community, since the foraging has completely fallen out of the *P. rufescens*' pattern.

The findings obtained by the Dobrzańskis affected the views on the mechanisms of amazons' raids. Wilson stated in 1963 that "Dobrzańska and Dobrzański (1960, 1961) in particular have apparently solved the classic problem of how the raids are organized. There are no scouts or raid leaders, and any individual or small group of individuals can be removed at any time without impairing the raid." (25).

Three years after this statement the Dobrzańskis' conclusions, which were based on a rather indirect evidence, have been confirmed by Köhler's studied (12). He conducted the experiments on artificially directed *P. rufescens*' raids with greater precision. After the activators had pointed out the direction, he planted some pupae of the slave-species on the opposite side of the nest. The activators, attracted by the bait, led the column in the direction chosen by the experimenter. The significant thing was not the raid's change of direction, but the fact that the accuracy and efficiency of the raids artifically controlled by Köhler were of the same order as of those led naturally from control nests. (Experimental and control nests were every time alternately changed). There is no doubt that, were the natural raids led by scouts having previous knowledge of the target, their results would essentially — and favorably — differ from the results of raids artificially led in random direction. The absence of such differences in Köhler's experiments confirms statically the Dobrzańskis' conclusion concerning the spontaneous choice of direction by the armies of *P. rufescens.*

FIRST CONTROVERSIES

Köhler's convincing results apparently closed the question of scouts in *P. rufescens.* Meanwhile the same Wilson, who earlier had unreservedly accepted the Dobrzańskis' conclusions, returns in his 1971 monograph again to "the classic problem of entomology", that is to "the means by which the *Polyergus* workers are able to mobilize themselves within minutes and run in a compact column straight for the target colony." This time his says: "Very recently Mary Talbot (1967) seems to have solved it" (26). This author (18) studied the behavior of East American amazons *Polyergus lucidus* and arrived at a conclusion that they direct the raids by following scent-trails left by the scouts returning to the nest.

Even if Talbot's experiments and findings were faultless, there would be no grounds to extend them — against facts described earlier by the Dobrzańskis and Köhler — on all species of the genus *Polyergus*, and

that is what Wilson has done. There are known cases that even closely related species follow different patterns of behavior. In Europe as examples may serve the combative *Formica rufibarbis* and the timid *F. fusca*, or the polycalic *F. exsecta* and exclusively monocalic *F. pressilabris*. With that in mind, one could admit that the mechanisms of raids in American *P. lucidus* and European *P. rufescens* may differ. But neither Talbot's, nor later Marlin's (14) experiments bring sufficient proof of it. In our opinion, they contain errors, methodological as well as logical.

CRITICAL ESTIMATE OF TALBOT'S EXPERIMENTAL METHODS AND CONCLUSIONS

Using a brush, the author laid on the ground near the amazon nest an artificial scent-trail, prepared from crushed bodies of amazon ants dissolved in dichloromethan. On the strength of the fact that the ants changed their original direction to follow this trail, Talbot formulated a thesis that slave-raids are guided by scent-trails left by returning scouts.

There is a possibility that the investigating scout, having found the target, on return to the nest leaves a scent-trail which is later followed by the raiders. However, the whole-body extract used by Talbot in no way answers that purpose. Each species of ants which takes advantage of the scent-trails for recruitment, uses a concrete, specific pheromone, which cannot be identified with Talbot's extract. At present it is not possible to decide what substances are extracted by dichloromethane from the mixture of pheromones, hormones and other substances present in the ants' bodies, the chemical composition of which is mostly unknown. Studies carried out by Wilson (more information about this subject will be presented in the next subchapter) suggest that the above-mentioned extract is not a concrete communicative signal, but rather a sign of threat. In the absence of any stronger evidence, it is not recommended to treat this extract as a scent-trail recruiting the ants to participate in a typical, natural activity of the robber raids. No doubt Talbot herself is a sharp and objective observer and admits that under the effect of the discussed artificial trail the amazons do not leave the nest in great numbers and do not form a mass formation typical for robber raids. This kind of behavior would be easily understood as a defence reaction provoked by an alarming sign and any other conclusion does not seem possible in this case. And even if *P. lucidus* during raids are directed indeed by scent-trails, their behavior in Talbot's experiments is no evidence of their behavior in a raid.

There seems to be some logical error in Talbot's conclusion. Bringing

about the change of direction of the amazon army, regardless of the method employed, cannot lead to conclusions suggested by Talbot. Köhler, too, brought about a change of direction and the stimulus he used — 25 slave-species pupae — was much weaker. But unlike Talbot's, the one used by him was adequate, for pupae are the object of slave-raids. But a change of direction in effect of the stimulus does not mean that under normal circumstances the amazons would follow the scout's trail. Neither does it prove that raid direction is predetermined. It is the unchangeability of raid direction, the inability to change it that could support the scout theory, that the column has a fixed direction which cannot be changed by any stimulus. Even such evidence, however, would only be circumstantial and not a sufficient proof of the existence of scouts.

The facts obtained by Talbot do not justify her conclusion that the natural slave-raids proceed as in her experiments.

CRITICAL ESTIMATE OF WILSON'S CONCLUSIONS

Any scientist can happen to use a wrong method leading to wrong conclusions. It is less understandable, though, when such conclusions are subsequently accepted by an eminent specialist in the field, such as E. O. Wilson. In his earlier studies on chemical communication in ants (24) Wilson employed an accurate though far more labor-consuming method, using as artificial trail the excretion of one particular gland. In the meantime he accepted Talbot's method to such a degree that he took it over himself. In his monograph (26) he refers to his and Regnier's experiments on the slave-making species *Formica rubicunda* in which, like Talbot, for artificial recruiting trails they used the extract in ether from crushed bodies of ants taken from investigated nest. According to our view, the concrete action (e.g. recruitment action) of the extract from crushed ant bodies should be considered under following conditions: (i) It should be known if the solvent used, dissolves the active substances from the particular gland. (ii) Moreover it is important to know if in obtained extract are present the other active substances of similar solubility but different communicative properties. It seems that at present it is not possible to meet the above-mentioned conditions. Hence, Wilson does not seem to be interested in this problem. Although he has accepted Talbot's method used in her research on *P. lucidus*, he stated (17) that in this species "neither the glandular source nor the chemical identity of the trail pheromone has been identified". And in connection with his own studies of the slave-making species *Formica rubicunda* and *F. subintegra* where he used Talbot's method, he states only (ibidem): "In view of the fact, that hindgut is the source of recruitment odor trails in ot-

her kinds of formicine ants, we conclude that this organ also produced a trail pheromone in *F. subintegra.*" (emphasis by DD). However, it is enough to look through several papers on the subject (e. g., 3, 11, 22) to see that the role of a particular gland may be different in various species. Besides, Regnier and Wilson (17) do not mention the chemical composition of the pheromone in question. It seems that the selection of the solvent by Talbot and Wilson was rather accidental, as it is not possible to foresee its action on pheromones and other substances which are in the ant's body. Consequently, there is no reason to consider the obtained extract as the recruitment pheromone. One may rather expect that the extract contains various components from ant bodies, which may act on the sense organ of the ants as an alarm signal. This view seems to be confirmed by other research of Wilson. He has found that in ants *Pheidole dentata* the pheromone from the poison gland acts in an alarm way, and he wrote (27): "Extracts made from whole bodies of workers (*Ph. dentata* — DD) and their poison gland caused typical following when laid in artificial trails" (emphasis by DD). In this case Wilson associated the effect of whole-bodies' extract with the alarm signal, while the analogical "typical following" by combative slave-making ants *F. rubicunda* and *F. subintegra* he considered as an effect of recruitment to the slave-raid and drew from the elementary fact such a far-going conclusion (26): "The communicative signals that trigger and orient the raids of colonies belonging to the *sanguinea* group of slave-making ants have recently been identified, at least in part, by Fred E. Regnier and myself." This conclusion is probabbly based on the fact that the attacked ants belonged to a slave species, but the authors themselves put this slave-species in the way of the excited workers of *Formica.* Their carrying the prey to their own nest after defeating the enemy is also typical behavior of winners in ant wars, and especially in slave-making species. Wilson said it himself (26): "Alarm communication, which is employed in one form or other throughout the higher social groups, has the effect of drawing workers toward sources of danger.:.". For the purpose of control, it was necessary to repeat the above mentioned experiment putting a different, non-slave species in the way of slave-making ants. The effect would certainly by identical.

CRITICAL ESTIMATE OF TOPOFF AND CO-AUTHORS EXPERIMENTAL METHODS AND CONCLUSIONS

Topoff and his co-authors (19) found irrefutable evidence that neither the "scouts", nor the raids of *P. breviceps* are scent-oriented (as is also the case with *P. rufescens* and that the raid follows a different route

than the one taken by the "scout". This evidence is an additional suggestion against Talbot's method, the latter requiring proof that *P. lucidus* differ from other amazons in olfactory orientation and recruitation. To Talbot, however, (and to Wilson as well) these data were not available, as they were not reported till much later. Symptomatically, the authors of these data were so biased by the scout thesis they had formerly accepted, that they held on to it against their own findings. Besides, their methods were incredible. In part I of their work (19) the authors describe the observation of individual scout-trails, but, they say, "...because the scout was not marked, we cannot be certain that the slave--raid was led by the same individuals. Nevertheless our previous studies with marked scouts (19) indicate that successful scouts of *P. breviceps* typically run (at least intermittently) at the head of raid swarms." The mentioned text runs as follows: "During the raid the scout runs intermittently at the head of the swarm, but frequently traverses the swarm behind its leading edge" (20). In more detail, it was formulated in the other paper in the same year: "Scout ran intermittently at the head of the *Polyergus* swarm; periodically she moved back in the column, weaving in and out among the raiders, but invariably resumed the leading role." (4). We fully agree with this description, but it concerns any amazon freely selected from the front ranks. Further on, these authors write that "in field the scout leader was not always successful in relocating the target colony; indeed on several occasions the scout and slave-raid came within less than 0.5 m of the *Formica* nest." In Topoff at al. (21) it is said outright that "the original scout is frequently not the individual that relocates the target colony." The authors attempt to explain it saying that the scout need not lead the column up to the very nest, but in context with the statement that the scout only "intermittently" is at the head of the column, the argument of the leading role of scouts seems unconvincing.

In part II of the publication under discussion (19) the experimenters removed the "scouts" of *P. breviceps* from the nest, which they artificially surrounded with a fence with four openings. As it was only towards the end of the experiment, which continued for more than ten days, that two slave-raids took place, the authors drew a conclusion that without the scouts the raids do not occur. They did not take into account that fencing the nest created a radically changed situation, which impeded the normal course of the raid, where large space is required for the exit of the circling swarm of amazones. The two raids undertaken, despite the absence of scouts, towards the end of the experiment could be explained in another way: that the "activists", being under the influence of increased motivation, induced by prolonged shortage of prey, after many trials, learned to penetrate through the opening in the fence.

The authors should have continued the experiment to verify such explanation, which would be a fine proof of behavioral plasticity in the amazons. Instead, they ceased to remove the "scouts", at the same time removing the fencing in order to "permit unlimited scouting". They failed to perceive that slave raids were also unlimited with the elimination of fencing and concluded that the raids were resumed because of the return of scouts. So this publication, too, is not acceptable as a proof of the existence of scouts.

CONCLUSIONS

It is our opinion that the studies by Talbot, Marlin and Topoff and his co-workers give no grounds for conclusions concerning the mechanisms of American amazons' slave-raids. To us it is incomprehensible why — as the first step in investigations — none of the researchers had repeated Köhler's simple and convincing experiments on American amazons. Had they done so, they would have obtained one of alternative cases: either the results would agree with those of Köhler, excluding at once the role of scouts and leaving no doubt that the raid marches to un unknown target; or the findings would show that, unlike European amazons, the columns artificially steered in random directions have significantly poorer effects than in natural raids. That would be the reason for further research, including the investigation of the role of scouts.

In our view it is rather not possible to obtain results other than Köhler's. We state this, basing, among other tings, on facts described afterwards by the American scientists, although most of them hold up the thesis on scouts. We have already mentioned numerous unsuccessful raids of *Polyergus lucidus* and *P. breviceps*, referred to by Talbot, Marlin, Topoff and co-authors. Also mentioned was the fact that all earlier and contemporary research confirms the instability of personal make-up of the front ranks in all investigated amazon species.

These facts testify rather to a spontaneous choice of direction by the column than to its being indicated by the scouts. What is more, the known facts correspond with one another only if the scout thesis is abandoned. Finally, the confirmed similarity of raiding behavior in European and American amazons, such as the circulation of "activators", the changing composition of the front ranks, the lack of accuracy in finding the target, also suggest that the entire model of behavior is similar in those species. It should be added that the American amazons use several species as slaves, like *P. rufescens*. According to W. M. Wheeler (23), *P. lucidus* use *Formica schaufussi, F. nitidulus, F. subsericea* and

F. neocinerea. Here again there is likeness to *P. rufescens*, what guarantees dense distribution of nests of the slave-species.

There are still other reasons that make us doubt the reconnaisance role of individuals which we have named "pseudoscouts". To a geater or lesser degree, scent-trails are used for spatial orientation and for recruitment by many ant species, maybe by all, in a certain measure even by those using, as a rule, visual orientation, which refers to the sub-family *Formicinae*, meaning also the genus *Polyergus*. The durability of scent-trails, however, is counted in minutes, since these substances are volatile and when they dry up, the trail disappears. According to Wilson (24), the scent-trail of *Solenopsis saevissima* holds for 2 minutes. Baroni-Urbani (1) reports the same duration for the genus *Crematogaster*. Maschwitz (15) mentions a few minutes' duration of the trail in *Leptogenys ocellifera*. Recruitment trails, naturally need not have identical duration in all species, since it depends on different factors, mainly behavioral. But the volatility of the trail pheromones is general and Wilson explains the biological sense of this rule: owing to it, the trails laid earlier do not lead the ants astray, for only the newly laid, actual ones remain. For that reason we do not think it possible that a recruitment scent-trail left by a single passage of a single individual would hold for a longer time, which is what should have been accepted with regard to scouts in the amazons. We remind that the "scouts" investigate the terrain singly in the morning and their return to the nest is sometimes hours apart from the raid's departure. It has been confirmed for *P. lucidus* by Talbot (18) and Cool-Kwait and Topoff (4). The latter argument does not concern *P. breviceps*, the West-American amazon whose "scouts" depart from the nest in the afternoon hours. Topoff and co-authors (20) attribute it to the ants' wanting to avoid lizards preying on them, who hunt in the morning. Such explanation might be worth thinking over. But perhaps *P. breviceps* actually use scouts who leave the nest immediately before the raid, so that the scent-trail left by them has no time to vanish? This supposition is prevented by the statement of Topoff et al. (19), that the "scouts" and raids are not scent-oriented.

Future studies will show who is in the right. We are sure of one thing: that so far the studies of the American species of genus *Polyergus* have brought no answer to the question of mechanisms of their slave-raids.

This investigation was supported by Project CPBP 04.01 of the Polish Academy of Sciences.

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Accepted 5 June 1989

RESPONSE TO J. DOBRZAŃSKA AND J. DOBRZAŃSKI ON THE RAIDS OF *POLYERGUS*

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The evidence cited by Dobrzańska and Dobrzański has certainly shown that the organization of the *Polyergus* raids is more complicated than mere trail following. They have not eliminated the role of odor trails in the process, however. There is first of all a clear distinction between orientation in *Pheidole dentata* and other ants to broadcast alarm substances and trail recruitment that accompany alarm. Furthermore, these two functions have been traced in experiments to pheromones from separate glandular systems. Also, the experiments by Regnier and myself on *Formica rubicunda* and *F. subnuda* leave no doubt that the workers of these slave-makers were following trails in the manner of recruitment, whatever the glandular source. No one to my knowledge has ever seen *Formica* come out along trails in this fashion just to attack enemies, although such alarm-recruitment occurs in formicine weaver ants of the genus *Oecophylla*. Also, there is no doubt that the *F. rubicunda* and *F. subnuda* workers led to colony fragments of slave species