

All snakes displayed a slight pupillary constriction underwater. However, the response is too weak to support the idea of a mechanism similar to the one in comorants [2]. Although Beer pointed out already in 1898 [11] that *N. tessellata* has a very flexible lens which would be perfectly suited for large amounts of accommodation, the mechanism present in the water snakes (providing more than 100 diopters of accommodative power) remains to be discovered. From ray tracing (personal observation), it can be seen immediately that a mechanism of accommodation typical for terrestrial snakes (moving the lens along the optical axis) is insufficient. Therefore, a deformation of the lens must be involved. In conclusion, similar to an earlier study in North American species, we observed fundamental differences in the ranges of accommodation among the three European water snake species. The results are in agreement with behavioral observations, which show that both *N. tessellata* [12] and *N. maura* (personal observation) are very success-

ful when they are catching fish under water, as opposed to *N. natrix* which can locate a jumping frog in the air at a distance of 1 m, but appears quite disabled under water. Two generalizations emerge from the present study and previous work on *Thamnophis* [5,6,13]. First, the ability to accommodate vision under water can vary greatly between closely related (in these cases, congeneric) species, indicating relatively rapid evolution of this trait. Second, enhanced underwater vision occurs only in species that specialize on aquatic prey. Selection of generalist species that feed both in and out of water is apparently not strong enough (or has not been operating long enough) to result in good underwater vision.

We are grateful to Prof. K. Vogt, Freiburg, for providing a specimen of *Natrix maura*. This work has been supported by a grant from the German Research Council to FS (SFB 307, TP A7).

Received April 18 and June 6, 1991

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Naturwissenschaften 78, 375-377 (1991) © Springer-Verlag 1991
002810429100121Q

Genetic Component to Division of Labor Among Workers of a Leptothoracine Ant

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The ecological success of social insects is often attributed to division of labor within their colonies and the relative efficiency that this confers on the performance of various tasks in comparison to solitary insects [1, 2]. There is a strong reproductive division of labor between highly fertile queens and relatively infertile or sterile workers, and there is a further division of labor among workers for the tasks that they perform [3, 4]. Darwin struggled to explain the evolution of specialized worker traits and suggested that since workers themselves are often nonreproductive, natural selection must act on differ-

ences among colonies (colony-level selection) to produce and further modify worker castes [5]. This idea is generally accepted [3, 4, 6, 7], but a genetic component to division of labor among workers has only recently been demonstrated, and in only a single species, the honeybee [7]. Here, we report evidence for a genetic component to division of labor among workers of the ant, *Leptothorax (Myrafant) rudis* Wheeler. The discovery of this phenomenon in members of two phylogenetically distinct groups of social insects, the ants and the bees, contributes to an emerging view of the importance of

genetic components in explaining individual and colony-level variability in social insect behavior, and provides empirical support for the general applicability of theoretical models explaining the evolution and functional dynamics of division of labor in social insects.

Division of labor among workers (or polyethism) is of two general types [3, 4]. The most common is age or temporal caste polyethism in which workers follow a fairly orderly progression from performing certain tasks within the nest (e.g., brood care) to riskier outside tasks (e.g., foraging). However, details of this progression often vary among individuals, and appear to be responsive to various environmental contingencies. Certain species also display physical caste polyethism in which morphologically specialized workers perform more limited sets of tasks. Recent studies of honeybees have revealed that there are genetic components associated with age polyethism, components which influence the probability that workers

will perform specific tasks and the degree of flexibility that they show in their behavior [7].

L. rudis colonies [8] have a single queen (monogyny) and monomorphic workers, and often form dense, local populations. We tested for a genetic component to division of labor in *L. rudis* by assessing the tendency of workers to forage in artificially constructed laboratory colonies composed of similarly aged, marked workers derived from three pairs of field-collected parental colonies. The six parental colonies were collected 19 June 1990 from rotting wood at a single site near Dutch Flat, Placer County, California, and were part of a collection of 26 nests. The ants were maintained in plastic nests and foraging dishes in the laboratory [9], and fed 2–3 times per week on a uniform diet [10]. The parental colonies contained 125–181 workers (\bar{x} = 153.3, SD = 22.21), were among the largest colonies collected, and were selected for the experiment because they produced large numbers of worker pupae. During the period 11–29 July 1990, we established 23 experimental “subcolonies” from workers that eclosed from pupae during either 1- (n = 16) or 2- (n = 7) day periods. Worker pupae were removed from their parental colonies when the darkness of their pigmentation indicated that they were nearing eclosion, and were placed in separate nests where eclosion could be closely monitored. At eclosion, the ants were immobilized by chilling, and were marked by tying colored polyester fibers around their alitrunk [11]. Each subcolony was formed from an equal number of callow workers from each of two parental colonies. Combining young ants to form artificial mixed colonies in this manner is a common technique used in nestmate recognition experiments [12]. Eight subcolonies were produced from the first pair of parental colonies, seven from the second pair, and eight from the third pair. All subcolonies combined contained a total of 512 workers with individual subcolonies containing 10–50 workers (\bar{x} = 22.3, SD = 10.88). On 27 September 1990, each subcolony was censused and all of the workers that were currently either outside or inside their nests (referred to here as “foragers” and “nonforagers”, respectively) were identified as to colony of origin.

When censused, all subcolonies combined contained a total of 474 live workers, and 17 of the 23 subcolonies contained larvae which had been reared from worker-laid eggs (\bar{x} = 9.6, SD = 11.52, range = 0–44). In queenless nests, *Leptothorax* workers often lay haploid eggs which mature to produce males [13]. Similar behavior occurs in queenright nests of at least some species in this genus [14]. A total of 132 workers were designated foragers. In all three cases, when the data for all subcolonies from each pair of parental colonies were pooled, there was a highly significant difference in the proportion of workers that were foraging from each parental colony (Fig. 1). Two of the subcolonies from the first pair of parental colonies had no current foragers and were omitted from the analysis. The number of foragers within each subcolony was generally small, and there was a significant difference in the proportion of foragers from the two parental nests in only five subcolonies (one from the first pair, two from the second pair, and two from the third pair). All of these significant differences were consistent with the bias shown in the pooled data. Four subcolonies showed a bias in the opposite direction to that in the pooled data (one from the first pair, one from the second pair, and two from the third pair), but these involved a difference of only one or two workers and were not significant. Differences in the magnitude of the for-

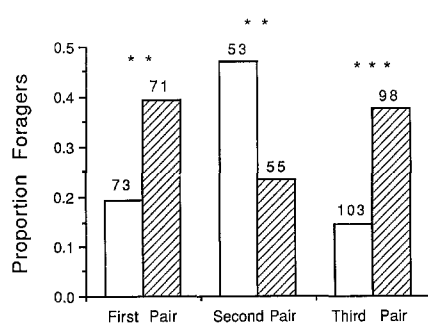


Fig. 1. Proportion of workers foraging in a series of pooled subcolonies derived from each of three pairs of parental colonies. The number above each bar indicates the total number of workers from each parental colony that were present in the subcolonies. Statistical comparison within each pair of parental colonies was based on 2×2 contingency tables and the Log-Likelihood Ratio Test [15]: **, $P < 0.01$; ***, $P < 0.001$

ager biases in the dominant direction and occasional nonsignificant biases in the opposite direction resulted in significant heterogeneity G scores for subcolonies from two of the three pairs of parental colonies (first pair of parental colonies, heterogeneity $G = 11.110$, $df = 5$, $P < 0.05$; second pair of parental colonies, heterogeneity $G = 11.879$, $df = 6$, $P > 0.05$; third pair of parental colonies, heterogeneity $G = 27.417$, $df = 7$, $P < 0.001$ [15]). However, this heterogeneity, a likely result of the small sizes of the subcolonies, does not detract from or invalidate conclusions drawn from the pooled data.

The results of this experiment demonstrate a significant bias in the tendency for foraging among similarly aged workers derived from three different pairs of colonies of the ant, *L. rudis*. Age polyethism has never been demonstrated in *L. rudis*, but is extremely common among ants (only one exception is known [4, 16]) and would be expected to occur in this species as well. The design of the present experiment controlled for any potential age effects by establishing replicate subcolonies with workers that had eclosed within a 1- or 2-day period. Thus, it is unlikely that any uncontrolled age variation influenced the results of this experiment. Environmental variability in the rearing environments of the workers (i.e., different parental colonies) was not controlled but, by choosing parental colonies that were all collected on the same day from the same site, were all similarly large, and contained large numbers of worker pupae, we expect such variability to be minimal and to have had no significant impact on the results of this experiment. For any systematic environmental effect, workers would have to be fated in their tendency to forage during the immature stage of development, and the proportion of similarly aged workers that were fated in this manner would have to differ significantly between the colonies that comprised each pair of parental nests. No environmental effects of this type have yet been documented and would be remarkable in their own right. The most likely explanation for these results is genetic variability among parental colonies and, since we found significant differences for all three pairs of parental colonies tested, this kind of

variability is apparently quite common in this species.

Variability among colonies for genetic components of division of labor is necessary for the continuing evolution of this important aspect of colony organization [6, 7], but exactly how the differences detected in this experiment might manifest themselves within more normally structured colonies is debatable. Recent studies of honeybees have demonstrated several selectable components of division of labor including the probability of workers performing certain tasks, and the rates of changes in behavioral development as a function of changing colony needs [7]. Subtle changes in the response thresholds of workers to various stimuli could have important influences on colony organization and theoretical models have been formulated which utilize these kinds of parameters to simulate the social organization of insect colonies [6]. Recent independent observations using different experimental approaches indicate that genetic components to division of labor also occur in the ant genera *Camponotus*

(N. F. Carlin and S. P. Cover, pers. commun.) and *Formica* (L. E. Snyder, pers. commun.). These results suggest that models of social organization involving genetic components may be universally applicable among social insects.

This research was supported by NSF grant BNS-90-96139.

Received February 25 and April 30, 1991

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Naturwissenschaften

Buchbesprechungen

Farn- und Samenpflanzen in Europa.

Von H. O. Martensen und W. Probst. Stuttgart: G. Fischer 1990. 525 S., 51 Abb., 233 illustr. Bestimmungstabellen, über 2300 Einzeldarstellungen, DM 89, -.

Dieses Bestimmungswerk erhebt große Ansprüche: Alle in Europa vorkommenden Wildpflanzen (gemeint sind Farn- und Samenpflanzen) sollen mit Hilfe dieses Buches bis zu den Gattungen bestimmbar sein. Es ist ein Versuch, das Bestimmen von Pflanzen mit zahlreichen Abbildungen zu erleichtern und gleichzeitig mit einer Einführung in die Systematik der Pflanzen zu verbinden.

Das Buch gliedert sich in zwei Hauptteile. Im ersten – sehr kurzen – allgemeinen Teil wird eine Einführung in die Grundlagen der Systematik der Höheren Pflanzen gegeben. Dieser hervor-
gend arrangierte Abschnitt ist mit detaillierten Abbildungen versehen und fundiert geschrieben. Er verdient großes Lob und ist im universitären Bereich sowohl für Lehrende als auch für Lernende sicherlich ein Gewinn.

Der zweite Teil des Werkes ist der eigentliche Bestimmungsteil. Die Bestimmung der einzelnen Gattungen beginnt hier immer mit einem allgemeinen Überblick und einer kurzen Charakteristik der übergeordneten Abteilungen, Klassen und Ordnungen. Die Abbildungen der jeweiligen Einführungsteile zeigen das Wesentliche und sind übersichtlich. Selbst an die Blütenformeln der einzelnen Ordnungen ist gedacht. Die Bestimmung der Pflanzen ist mittels einer Sequenz von Bildchen möglich (synoptischer Bestimmungsschlüssel), wobei alternativ und/oder ergänzend auch der bewährte „klassische-di-

chotome“ Bestimmungsschlüssel dann und wann erscheint.

Die Benutzung dieses synoptischen Bestimmungsschlüssels fällt anfänglich nicht leicht, wenn man mit dem „klassisch-dichotomen“ Bestimmungsschlüssel groß geworden ist. Häufig steht man vor dem Problem, aus sieben oder mehr Möglichkeiten die richtige auszuwählen. Hinzu kommt, daß man – wenn man alle Hindernisse genommen hat – eben nur bei der Pflanzengattung herauskommt und dann doch noch einen dichotomen Schlüssel zur Hand nehmen muß, um die Art oder Unterart zu bestimmen. Ein Laie wird meines Erachtens erhebliche Schwierigkeiten haben, die in den synoptischen Tabellen verwendeten Trennkriterien zu verstehen. Allerdings zeigt die Praxis in Bestimmungsbüchern für Studenten, daß ein Anfänger auch bei der Benut-