

Individual and family recognition in subsocial arthropods, in particular in the desert isopod *Hemilepistus reaumuri*

K. E. LINSENMAIR

Zoologisches Institut der Universität Würzburg, F. R. Germany

Abstract

Individual recognition in the non-eusocial arthropods is, according to our present knowledge, predominantly found in the frame of permanent or temporary monogamy. In some cases, e.g. in stomatopods and possibly other marine crustaceans too, individual recognition may serve to allow identification of (i) individuals within dominance hierarchies or (ii) neighbours in territorial species thus helping to avoid the repetition of unnecessary and costly fights. Kin recognition is experimentally proven only in some isopod species (genera *Hemilepistus* and *Porcellio*) and in the primitive cockroach (termite?) *Cryptocercus*. The «signatures» or «discriminators» used in the arthropods are chemical. It is assumed that the identifying substances are mainly genetically determined and in this paper I shall discuss possible evolutionary origins. The main part of this account is devoted to the presentation of some aspects of the highly developed individual and kin identification and recognition system in the desert isopod *Hemilepistus reaumuri* – a pure monogamous species in which pairs together with their progeny form strictly exclusive family units. Amongst other things problems of (i) mate choice, (ii) learning to recognize a partner, (iii) avoiding the unadaptive familiarization with aliens are treated. Monogamy under present conditions is for both sexes the only suitable way of maximizing reproductive success; an extremely strong selection pressure must act against every attempt to abandon monogamy under the given ecological conditions. The family «badges» which are certainly always blends of different discriminator substances are extremely variable. This variability is mainly due to genetical differences and is not environmentally caused. It is to be expected that intra-family variability exists in respect of the production of discriminator substances. Since the common badge of a family is the result of exchanging and mixing individual substances, and since the chemical nature of these discriminators requires direct body contacts in order to acquire those substances which an individual does not produce itself, problems must arise with molting. These difficulties do indeed exist and they are aggravated by the fact that individuals may produce substances which do not show up in the common family badge. An efficient learning capability on the one hand and the use of inhibiting properties of newly molted isopods help to solve these problems. In the final discussion three questions are posed and – partly at least – answered; (i) why are families so strictly exclusive, (ii) how many discriminator substances have to be produced to provide a variability allowing families to remain exclusive under extreme conditions of very high population densities, (iii) what is the structure of the family badge and what does

an individual have to learn apart from the badge in order not to mistake a family member for an alien or vice versa.

1 Introduction

Before animals can reproduce they have to come to numerous decisions requiring special recognition and classification performances. They have to discern self from non-self, their species from others and nearly always different categories within their species: females, males, young etc. Additionally they often have to distinguish between sub-categories, e. g. females in different phases of their reproductive cycle or young of different ages. Under special conditions, still more sophisticated capabilities have been selected, those for individual and for kin recognition. These are the topic of my account, – as far as arthropods are concerned – with the exception of the eusocial species (cf. MICHENER 1985, this Vol.)

Only a very few species within the huge number of non-eusocial arthropod species are known to possess either or both of these abilities, and in most of these few cases our knowledge is still very limited. Therefore I shall only mention a few studies, partly to exemplify which environmental conditions may favour the selection of such capabilities and which their probable present adaptive value is. I shall mainly concentrate on some selected features of the highly developed mechanisms of identification (sensu BEECHER 1982) and recognition of individuals and kin in the desert isopod *Hemilepistus reaumuri* (LINSENMAIR and LINSENMAIR 1971, LINSENMAIR 1972, 1975, 1979, 1984). The first aspect, that of the individual's or kin's identifying cues, will be dealt with predominantly, but not exclusively, since the second aspect, the decoding of the signals provided by individuals or kingroup members about their identity is comprehensively treated and reviewed in this volume by SHERMANN and HOLMES.

Individual recognition requires that, independent of the site of encounter, a single individual can be sorted out of a larger homogeneous group of conspecifics by means of reliable identifying characteristics and that this individual is treated in a way which presupposes earlier experience with it. As far as kin specific recognition is concerned, an analogous definition proves to be true, omitting the final restriction: kin can in some species be recognized without previous direct contact (e. g. BLAUSTEIN and O'HARA 1981, 1982; BUCKLE and GREENBERG 1981; GREENBERG 1979; HOLMES and SHERMAN 1982, 1983; SHERMAN and HOLMES, this Vol.; WALDMANN 1981; WU et al 1980).

2 Individual and kin identification and recognition in non-eusocial arthropods

As far as we know, individual «signature» systems (BEECHER 1982) and recognition mechanisms in the group alluded to are found mostly in connection with temporary or permanent monogamy. Following WICKLER and SEIBT (1981) a distinction is made between a «mate guarding» monogamy and a «shared duty» monogamy.

2.1 Individual identification and recognition of mates in monogamous species

In the *mate guarding monogamy* of the clown shrimp *Hymenocera picta* (SEIBT 1974, 1980; SEIBT and WICKLER 1979; WICKLER and SEIBT 1981) males seem to have considerable difficulties in finding unpaired females. Once a male has found a suitable mate it seems to pay him to stay with his iteroparous female, most probably because leaving her

and searching for a new one would on average be more costly in terms of time expenditure and/or reduction of his probability to survive. The attachment in this case is asymmetric with males being strongly attached to the partner and females much less so. The adaptive value for a male of recognizing his female individually is presumably to be seen in protection against confusion; mistaking a new female for the former one – if this female is still alive and still offers good reproductive prospects – would too often result in uncompensated time losses. The question of why females recognize their male partners too is more difficult to answer, and until now there seems to have been no satisfactory hypothesis to account for this fact. The individual recognition cues are chemical characteristics and are – contrary to conditions in many other species – effective over long distances. Nothing is known about the chemical nature of the compounds used. The cleaner shrimp *Stenopus hispidus* lives in pairs too, the partners being capable of individual recognition (JOHNSON 1977). Possibly the adaptive value of this capability is the same as in the *Hymenocera* mentioned above, but this assumption is not yet proven.

In the *shared duty monogamy* which may originate from a mate guarding monogamy (as I assume has been the case in *Hemilepistus*, cf. LINSENMAIR 1984) resources vital for reproduction cannot – under present ecological conditions – be secured or handled by one individual alone; the cooperation of at least two conspecifics is necessary. In some cases, as in the carrion beetle *Necrophorus vespilloides* (PUKOWSKI 1933), the essential resource must not be left (and has only to be defended against conspecific competitors for a short period). If under such circumstances each partner wards off only consensual rivals – a feature not only of *Necrophorus* but also of the snapping shrimp *Alpheus ornatus* (KNOWLTON 1980) – a monogamous social and mating system may result although partners do not recognize each other individually. In cases such as that of *Hemilepistus*, where the vital burrow has to be defended for a very extended period alternately by one pair partner against competitors of both sexes (also during periods of temporary absence of the mate from the den) an anonymous relation of the partners cannot suffice. Mutual individual recognition of mates is then a necessary precondition for securing this resource reliably.

Besides *Hemilepistus*, *Cryptocercus*, which was formerly considered a primitive cockroach but is more probably a very primitive termite, seems to be the only other non-eusocial arthropod to have reached a level of social evolution which in some respects is comparable to that of the desert isopod *Hemilepistus* (SEELINGER and SEELINGER 1983). *Cryptocercus punctulatus* clearly lives in monogamous pairs or in closed family communities. The animals dwell in the rotten wood of fallen logs and by feeding on the wood they construct in time rather complicated burrows consisting of a number of chambers connected by galleries. In laboratory experiments G. and U. SEELINGER could demonstrate that these burrows are defended – mainly by the adult pair – against alien conspecifics and they assume that they possibly also deter predators (of the young). Foreign adult or juvenile roaches can be discerned from the mate and from the pair's own young – by unknown chemical identifying substances. The question of the adaptive value of the monogamous pair formation in *Cryptocercus* has to be considered still open. One adult alone could probably fulfill all tasks but its chance of surviving the extremely long time of at least 3, possibly 5, years of broodcaring could be too low.

2.2 Individual recognition and rank orders

In many vertebrates rank orders and mutually accepted territory borders are an outcome of aggressive encounters between conspecifics. By individual recognition members of a rank order or «dear neighbours» can avoid repeating already settled disputes. CALDWELL

(1979) has proved that the mantis shrimp *Gonodactylus festai* can potentially learn to recognize conspecifics individually. These highly aggressive stomatopods equipped with potentially lethal weapons fight for scarce holes. Possibly they recognize their neighbours, they certainly recognize and avoid for some time those individuals which have defeated them in a previous battle. Since there is a high risk of severe injuries in fights, the adaptive value of the identification and recognition of individuals in this respect is obvious.

2.3 Kin recognition

Kin recognition, very common in mammals, birds and the eusocial Hymenoptera (cf. e.g. the relevant articles in this Vol.), is experimentally proven in the non-eusocial arthropods besides *Hemilepistus* (see below) and one subsocial Canarian *Porcellio* species (LINSEMAIR 1984 and unpubl.) only in *Cryptocercus* (SEELINGER and SEELINGER 1983). In the latter, trophallaxis with symbiont transfer is of paramount importance for larvae during the first two instars, i.e. during the first year of their life. Which valuable advantages the family offers its members in the following 2–4 years, remains at the moment a matter of speculation; possibly it is defense of the adults against predators on the young.

2.4 Nature and origin of the individual – or kin-specific signatures

Individual and kin recognition in the group of arthropods discussed here seems always to be mediated by chemical means. (The assumption of VANNINI and GHERARDI (1981) that the crab *Potamon fluviatile* might use optical cues to identify conspecific individuals was deduced from results gained under very artificial conditions; confirmation of these results by experiments performed under more natural conditions is required.)

With the exception of *Hemilepistus* we know hardly anything about the chemical properties of the substances used, literally nothing about their degree of variability and their origin. Assuming that these substances are chiefly genetically determined (and not predominantly acquired from the surroundings) which is known to be the case in *Hemilepistus* and which is not improbable in all other species mentioned, the question arises of what the initial variability has been on which selection could have started to work. I can distinguish two main «substrates».

1) Due to variability in their enzymatic equipment, members of a population always differ to some extent in their metabolism. If a repeatedly used vital resource, e.g. a burrow, has to be left temporarily and has to be found again under difficult conditions under which external cues for (i) reorientation to the animal's own (ii) and differentiation between its own and an alien burrow are unreliable or lacking, individual variability in metabolic endproducts (showing up in secretions, faeces and urine, for instance) which had no direct previous value could gain great importance by offering themselves as cheap labels. If those substances were used we could expect a great deal of preadaptation on the decoding side of the system. Many of these compounds could already have gained sign character in connection with e.g. food choice (preference and avoidance) at earlier times. (Furthermore the normally highly developed capacity in arthropods to acquire and process chemical information will always allow the identification of many compounds with no previous biological significance.) Primitive bees and wasps (STEINMANN 1973, 1976) and isopods (*Porcellio* spec., LINSEMAIR 1979) mark their burrow entrances individually, enabling them to find their burrow even under difficult conditions of high dwelling densities. In both groups this could have been a basis for the further development of a signature system.

2) The species-specific signals could represent the other possible starting point (cf. GREENBERG 1979). In order – for example – to find the optimum balance between outbreeding and inbreeding, those individuals will be favoured which are able to use the variability always present within the species-specific features to learn what their near relatives are like, and then, in choosing a mate, to avoid conspecifics which are too similar or too different from the relatives (e. g. BATESON 1980, 1982, 1983). This does not require the ability for individual recognition but to reach it from this level should pose no very difficult evolutionary problems.

3 Individual- and family-specific recognition in the desert isopod *Hemilepistus reaumuri*

3.1 Individual recognition of the mate

3.1.1 *The monogamous pair: formation and behavior*

Hemilepistus family groups stay together for 9 to 10 months after the birth of the young. By the end of the two- to four-month hibernation period the previous bonding of the family members to one another and to their burrow has been dissolved. As soon as they appear above ground, most of the animals leave their birthplace forever, maintaining (by astromenotaxis) constant walking directions for considerable distances (LINSENMAIR in prep. (I)). These directions are chosen at random. This has been demonstrated by marking > 3500 isopods. The distribution of the sites of recovery revealed neither indications of a family-specific nor a population-specific directional bias. Before attempting to set up a new den, the animals travel at least several tens of meters, and sometimes more than a kilometer.

About 8 days after leaving their family burrow, at the earliest, the first emigrants settle down. Sometimes they take over an empty burrow or succeed in evicting a previous occupant, usually they construct a burrow (for details see LINSENMAIR and LINSENMAIR, 1971; LINSENMAIR, 1979, 1984). In most cases (87 %, n=63) the builders of new burrows are females; they dig a tunnel 2–4 cm long and then guard it continuously. In a procedure that usually lasts for hours, a conspecific of the other sex is allowed to enter. By marking the partners in these pairs and observing them for long periods, an observer will notice the following points:

- (a) After the first 48 hours of their life together the two partners were in no cases (apart from experimental intervention) found to separate «voluntarily». If a pair does break up it is because one of the partners fails to molt properly, dies, or is driven away by a competitor.
- (b) The two partners cooperate in many activities – construction, cleaning and defense of the burrow, providing food (to some extent), and later the care of the young.
- (c) In the 9–13 weeks from pair formation to the birth of the young, the burrow is always guarded by one of the partners.
- (d) Beginning the second day after pair formation, at the latest, the guard drives away all conspecifics other than its partner, as long as it has had direct contact with its mate within the last 3–12 hours. When the partner demands admittance – e. g. upon its return from foraging – the guard first examines it by touching it with the apical cones of the 2nd antennae, which bear chiefly contact chemoreceptive sensilla (SEELINGER 1977; KREMPIEN 1983), and then as a rule immediately allows it to enter. This special, peaceful treatment of the partner is not site- or situation-specific, and it does

- not require special behavior on the part of the mate. All that is needed is that the guard is able to touch the returning isopod somewhere on its cuticular surface.
- (e) The forager finds its way back to the burrow by means of allo- and idiothetic information, in some cases using an effective search behavior (HOFFMANN 1978, 1983a–c, 1984). Having returned, however, it attempts to enter only if it has identified the burrow as its own. The decisive criteria for this identification in the first days after pair formation, are provided by the individual chemical characteristics (see below) of the partner itself – perceived chemotactically.
 - (f) When a foreign conspecific is – e.g. following experimental manipulation of the guard – allowed direct entry (i. e. entry without the admittance routine) to a burrow, the intruder usually (in 70–90 % of cases, depending on conditions; $n > 100$; details in LINSEMAIR in prep. (I)) ejects the guard from the burrow, letting it back in only after a normal admittance procedure. A paired woodlouse admitted by its partner unimpeded to its burrow never behaves in such way, even if it has been experimentally separated from its mate for several days.
 - (g) Under the climatic conditions prevailing in the normal pair formation season, the female permits copulation only at or in her own burrow and only with her – individually known – male.
 - (h) After the parturial molt the gravid female accepts only her own male. Conversely, the male behaves peacefully only towards his own female during and after the parturial molt.

3.1.2 Discussion: pair bonding in *H. reaumuri*

It is evident from the above points (a–h) that *H. reaumuri* forms monogamous pairs. There are two criteria, each of which in itself is regarded as sufficient to categorize a relationship between two heterosexual conspecifics as monogamy (WICKLER and SEIBT 1981, p. 215), and both are satisfied here:

1. «... the togetherness of two heterosexual adults as a social system».
2. «... a mating system in which an individual reproduces sexually with only one partner of the opposite sex».

The partnership is not simply an association of each member with the burrow, or any other kind of an anonymous monogamy rather the pair is kept together by a mutual attachment of the two individuals – each individually recognized by the other – supplemented by a bonding of the two together to their burrow. The latter bond always proves to be the weaker in conflict experiments. The great significance of the burrow with regard to the cohesion of the pair is that it is the meeting point of the partners, which can notice and identify one another only by direct contact, for they have no mechanisms for long-distance observation of and communication with conspecifics. Without such a meeting point they would quickly lose contact with each other and they never could establish a prolonged pair bond.

The mutual attachment of the partners to one another is evident in

- (a) the prolonged cohabitation in very close proximity; after pair formation each member seeks frequent direct antennal and body contact with its partner (and later with its own young), whereas alien isopods are avoided or attacked.
- (b) the many behavior patterns related only to the mate (and not to other potential sexual partners), only some of which have been listed above; (see LAMPRECHT 1973; WICKLER 1976).

The partner is individually identified on the basis of extremely varied chemotactically detected characteristics («discriminators»: HÖLLDOBLER and MICHENER 1980) (see below).

3.1.3 Individual recognition: a few selected problems

Of the many questions raised by the existence of monogamy and the ability to identify the partner individually, only a very few can be considered here – and these answered only in broad outline.

3.1.3.1 Do the partners learn to recognize each other in the initial admittance ceremony?

The procedure by which the occupant of a burrow in the field first allows a sexual partner to enter the burrow lasts, depending on different conditions, from ca. 1.5 to more than 48 hours. Here we are concerned only with the question of whether the occupant and the applicant for admission get to know one another during this prolonged interaction. The intensity of the mutual touching during this procedure suggested that they do. The possibility was tested by exchanging conspecifics with the same previous histories, involved in identical parallel experiments, but belonging to different families.

Table I:

A Is admittance time prolonged by exchange of intruders (females = burrow owners)?	
Males exchanged ¹ every 45 min	Males not exchanged
Time until admission ² in min	
122 ± 94 (n = 25)	126 ± 123 (n = 40)
B Are males individually recognized 60–120 min after 1. admission	
Males replaced to original female ³	Males crosswise exchanged ^{1 3}
Time until 2. admission in min	
19,5 ± 18 (n = 20)	17 ± 8 (n = 15)

¹ Exchanged males originated from different families.

² Admission is characterized by females allowing males (i) to assume normal guard position within the burrow without pushing them out again for at least a quarter of an hour or (ii) letting them pass into the underneath position.

³ In experiment B males were replaced 10 min after removal.

In most of the situations tested (see Table I) individual recognition could not be demonstrated. When one of the two interacting animals was exchanged for an alien 1) no delay of the overall process was detectable and 2) at the time of admittance the intruder is not recognizably distinguished from a foreigner by the burrow owner. The only effect observed was that some of the females in the role of intruders, when shifted to another burrow began search behavior after making contact with the alien occupant (see below). The fact that individual recognition was not normally developed in the admittance process, raised the following question.

3.1.3.2 What is the function of the prolonged admittance procedure in pair formation?

Under natural conditions, female *H. reaumuri* are strictly semelparous. Even after the earliest possible loss of the offspring – directly after birth ($n > 250$), or when the eggs were removed experimentally without ($n=15$) or with damage to the brood pouches ($n=20$) – in no case was a new clutch produced. With only a single chance for reproduction, and being extremely dependent on her mate for realizing this chance (cf. p. 422), the female can be expected to choose her male with great care. I assume that it is because this choice is so important that the female usually starts to dig a burrow; thereby being in a position to decide whom to admit. How does a female choose? She could evaluate the male directly – for example, by means of the duration and intensity of its striving for admission (for details of the behavior see LINSSENMAIR and LINSSENMAIR 1971). However, all results contradict this presumption. First, in a direct evaluation one would have expected the male not to be admitted solely according to a time program but depending on the result of an examination of the applicant's performances. In that case, however, (i) individual recognition should be established during the admittance procedure and (ii) exchange of applicants should prolong the overall admittance time; as was shown above, neither assumption proved to be true. Second, in laboratory experiments female burrow occupants were presented with males that were (i) greatly handicapped by amputation of the first two pairs of pereopods, (ii) obviously sick (dying a few days later), or (iii) too small to defend effectively the burrow, dug by a larger female ($n \geq 25$ in each case). Choice behavior by direct evaluation should have resulted in the rejection of at least some of these males. The actual result, however, was that all the males that persisted long enough at the entrance were admitted, the times required being not prolonged greatly (Table II).

Table II: Are hampered males refused by female burrow owners?

Admittance time (in hours)	
4 legs amputated	Intact males
16,01 ± 13,2 (n = 28)	12,56 ± 16,25 (n = 30)
No admittance in 48 h	
2	2
Admittance rate	
93%	94%

The experiments were performed only 8 days after termination of hibernation, therefore overall admittance times are rather prolonged. As in all comparable experiments the experimental and the control group consisted of sisters and brothers which all had exactly the same previous history.

Field observations have shown that during the first weeks of the pair-formation phase, everywhere but in the sparsely-inhabited peripheral regions, males – being forced to wait for hours during the admittance procedure – must in this time engage in multiple fights with other males – partly vigorous battles that are very often repeated at intervals of only a few minutes, due to a large number of competitors. Ordinarily the winner is the larger

Table III: Aggressive encounters in the field: weights of winners and losers

A Males			
	Heavier	Lighter	Significance
Winner	68 (284 ± 28 mg)	23 (266 ± 29)	$P \ll 0,001\%$
Loser	25 (290 ± 20)	73 (244 ± 39)	χ^2
B Females			
Winner	17 (246 ± 19)	9 (237 ± 10)	$P = 0,03$
Loser	9 (259 ± 15)	19 (204 ± 22)	χ^2

All fights took place without experimental interference at natural burrows. In most cases winners and losers – after reaching a definite decision – were put individually in small containers. They were weighed on a microbalance 1–4 hours later. In a few cases single winners started a new fight immediately after the first one observed. Therefore the number of losers in A exceeds that of winners. The fact that the average weight of those losers which are heavier is slightly higher than the weight of heavier winners is mainly caused by the participation in the aggressive encounters of old parents surviving their first breeding cycle. They are the heaviest but usually are somewhat clumsy and weakened and therefore lose nearly all fights. (They have never been observed surviving until a second pregnancy).

male (see Table III). As a result, during an admittance procedure one male applicant is often replaced by another, sometimes repeatedly. Weakened or small animals usually have no chance of keeping their places long enough to gain entry.

Conclusion. These observations gave rise to the hypothesis that the admittance procedure does indeed serve as a test of the future partner – in an indirect, very effective way that automatically takes into account whether a selection procedure is possible among applicants. In the light of this hypothesis, the results summarized in Table I are not surprising. Even if a conspecific were to become individually identifiable during an admittance procedure, the owner of the burrow should not reject an animal that replaces this already recognized potential sexual partner, because each such change can be expected to bring an improvement. It is also not surprising – indeed, it follows compellingly from the hypothesis – that any applicant (cf. Table II) will eventually be admitted if it persists long enough. After all, if there is no alternative any partner is better than none, and it would be a disadvantage to adhere to absolute criteria. Moreover, after pair formation there is another, indirect test of suitability; an animal that cannot effectively defend its burrow is very likely – if it encounters a superior opponent – to be forcibly expelled. Burrow owners, as just demonstrated, seem not to get acquainted with a potential future sexual partner during the admittance ceremony. But, as already mentioned, females in the role of applicants partly notice an exchange of the burrow owner opposite. (Table IV).

3.1.3.3 Why do about 50% of female applicants give clear indications of recognizing the guard, whereas male applicants do not?

Only to a very limited extent do intruders seem to be able to tell – from the intensity, form and duration of the defense behavior of the guard (and not by chemical cues) –

Table IV: Reactions after transferring intruders to a second burrow with an alien owner

Sex of intruder	Leaving burrow entrance "searching"	Uninterrupted intruding behavior	Significance
Males	1	20	P = 0,002
Females	10 (controls: 1) ¹	12 (controls: 15)	

After striving for admission for 1–2 hours the intruders were cautiously seized with a forceps and immediately transferred to the entrance of another burrow, identical with the first with the exception that its guard originated from another family (i.e. neither from the intruder's nor the first burrow owner's family).

¹ controls: identically treated but replaced to the first burrow

² FEt: Fischer's Exact test

whether the latter is paired or not. For a male intruder the problem of determining that a female burrow guard has no partner is not very difficult; when a burrow is occupied by a pair, the male is almost always present during the activity phase of intruders, and in a series of field observations during 14 activity phases in 86 % (n= 154 pairs) the male was the guard. In these cases brief touching provides the necessary information. When a female with a partner is on guard duty and cannot rapidly drive away an alien male, she will often creep backward into the burrow past her male, «handing over» the task of guard to him. For these reasons, male intruders waste little time in applying to females that already have a partner.

Once a male has found a single female and stays striving for admittance, he loses contact with the burrow only during fights with other males. If, in trying to find his way back after a fight, such a male were often in danger of encountering another single female instead, which would require him to invest more time before being admitted, it would be an advantage to the male to be able to detect his mistake. However, all field observations have indicated that such a situation is so rare and therefore this danger is so uncommon that a special adaptation is not to be expected.

Females seeking admission to a burrow have much more difficulty in finding a single sexual partner. A high percentage of their approaches are likely to be futile (30–60 % depending on how much of the pair-formation phase has elapsed, and if striving for admission for more than 15 minutes is taken as the criterion). Females that have succeeded in locating an unmated male but are distracted by a fight and must then find their way back to his burrow are in great danger of encountering the wrong burrows, occupied by paired males, for these are always much more numerous (the maximal density can reach up to 20 occupied burrows per m² during the mating season). Females capable of identifying males individually (and not only by behavioral criteria, which are relatively unreliable) in this situation could often save themselves time-consuming mistakes.

Discussion. In the situation just described, rapid familiarization with an unknown individual would be advantageous to a female. Otherwise, however, it would be more of a disadvantage, and should be suppressed. The social partner is distinguishable from all conspecifics comparable in sex, age, physiological state and so on solely in that it has a familiar badge. By prolonged experimentally enforced tactile contacts an isopod cannot help but get acquainted with an alien conspecific who, in most situations, is then automatically converted to a social partner. Exclusivity of the social units (see p. 431), which is

necessary for various reasons, is guaranteed only as long as the learning of another animal's discriminators is limited to the situation of monogamous pair formation (and of contact with one's own young after their birth; cf. LINSENMAIR 1984 and in prep. (II)). But just during the pair-formation phase it is often impossible to avoid prolonged contact with conspecifics that should remain strangers. The simplest way to prevent such familiarization, with a general method that does not require analysis of the specific situation, is to set the frequency of contact required for familiarization so high that only the partners in a pair can achieve it. This assumption could explain why – although the partners in a newly formed pair touch one another often and extensively – 12–24 hours must elapse after admittance before both are demonstrably capable of recognizing one another reliably, whereas in other situations they learn much faster. Of course behavioral variables can play an important role in this process; a paired guard touches an intruder much more rarely than does a single guard, which is in principle prepared to allow entry. (It is not clear whether male and female intruders vary in this regard which then could explain the sex-specific differences of Table IV).

3.1.3.4 *Is the pair bond endangered by unavoidable contamination with foreign discriminators?*

The discriminators of the desert isopods are strongly polar, practically non-volatile compounds of low molecular weight (LINSENMAIR, SCHILDKNECHT and ESSWEIN, in prep.). They can easily be transferred from one individual to another by direct contact, the individual thereby becoming – depending on the intensity of contact – more or less strongly and long-lasting alienated (LINSENMAIR 1972, 1984, and in prep. (III); see p.425). Paired guards cannot avoid direct body contact with foreigners during the pair formation period while defending their burrows against alien intruders. When such a guard goes out to forage, in a few cases it is rejected by its partner on its return. In this situation, and this situation alone, 15 of 20 animals responded to the defensive blows of their partners with a very effective behavior: they turned around and presented their hind ends to the guards. This part of the body always remains uncontaminated during defense of the burrow. After it had been touched by the guard's antennae, all individuals were immediately admitted.

In experiments aimed at alienating adult, mated individuals it became apparent that when one member of a pair is forced into body contact with adult foreigners – to an extent that if solely young animals had been involved the contamination would have caused long-lasting rejections by their respective families – its partner guarding the burrow sometimes reacted by no, sometimes by only brief defense. It seemed possible either that the adults are less sensitive than juveniles to foreign discriminators or that they produce less substances which are easily transferable. To test these possibilities, reciprocal contamination experiments were done with adults after hibernation and with almost full-grown (5-month-old) juveniles.

The results of these laboratory experiments are summarized in Table V. They show that the adults (i) transfer less substance than do juveniles under otherwise identical conditions, and (ii) respond less aggressively to foreign substances encountered when examining their partners than do members of families to equally intense contamination of their kin. (Other possible interpretations – that the foreign substances might be less well adsorbed by adults because of differences in the surface properties of the cuticle, and that the adults produce substances less effective in eliciting aggression – have been ruled out by experimental tests outside the scope of the present discussion.)

Conclusions: Our above question can be clearly answered: pair maintenance is not endangered by the unavoidable close contacts with aliens in burrow defense. This poten-

Table V: Alienation of adult pair partners and young family members by direct contact with alien individuals of different age

	Alienated	by	Time of contact	Admittance time		Significance
				≤ 5 min	> 5 min	
I	Adults	30 Young	1 min	4	13	I : II P < 0,02
II	Adults	30 Adults	1 min	16	8	χ^2
				Admittance time		
				≤ 1 hour	> 1 hour	
III	Young	30 Young	1 min	4	18	III : IV P < 0,001
IV	Adults	30 Young	1 min	14	3	χ^2

The individual to be alienated was placed into a small glass vial and then the thirty unrelated conspecifics of different age (see text) were added.

The isopods could not avoid closest contact which was additionally intensified by shaking the group up very often thus taking care that the test animal was during this procedure permanently amidst the aliens.

tial weak spot is multiply ensured against possible disturbances by suitable adjusted behavior, reduced production of exchangeable badge substances, and altered – lowered – sensitivity to contamination.

3.1.4 What are the adaptive values of monogamy and individual recognition under present-day conditions?

a) To acquire a burrow without undue delay and then to hold it against all competition are absolute prerequisites for the survival and reproduction of a desert isopod. Since these animals have no adaptations for efficient digging, construction of a new burrow is a laborious process which – because of climatic conditions – must begin in spring. The very strong intraspecific (to a lesser extent also interspecific) competition for this vital resource makes it necessary to keep constant guard over it. Adequate food can normally only be found outside the burrow, and a single woodlouse cannot simultaneously guard and forage. In the present situation a burrow can be permanently defended only by the cooperation of at least two adults. These should be able to tell one another apart from foreign invaders. Learning to recognize the partner's individual characteristics is certainly the most reliable solution to this problem (LINSENMAIR and LINSENMAIR 1971; LINSENMAIR 1979, 1984).

b) Even if there were no foraging problem and a desert isopod could stay indefinitely in its burrow, a female during the parturial molt and pregnancy would mostly lose its den to competitors since she cannot defend her burrow effectively enough if at all. Only if she lives together with a male during this critical time does the female have a good chance of reproduction. As a proximate cause, the individual attachment of the male to his female ensures that the pair remains together even after the parturial molt, in which the female loses her sexual attractiveness.

c) For reasons as yet unknown, single gravid females (at least under laboratory conditions) have a very small chance of survival even if all competitors are excluded. We had noticed this phenomenon in our laboratory breeds for some time; in an experiment to study it (LINSENMAIR 1984) 20 females were isolated from their males after the parturial molt, 18 of these females died, either before the birth of the young or before the time when the young would have had a chance to survive alone. In the control group with pairs kept under otherwise identical conditions, 19 of 20 sisters of the females in the experimental group survived the critical period. It seems very unlikely that these results are pure laboratory artifacts with no relevance to the situation in the field.

d) Moreover, loss of either partner (regardless of sex) within the first two weeks after the birth of the young reduces the mean number of young that survive. In the experimental group there were 23 ± 28 survivors ($n = 38$ families), 40% (a significant difference) of the average in the control group, with 40 ± 28 survivors ($n=47$); there was a particularly large increase in the incidence of total-brood mortality, with 21% in the control group as compared with 50% in the experimental group (LINSENMAIR 1979).

3.1.5 Discussion: what makes monogamy the best reproductive method for both sexes?

For females the advantages are so obvious, as the preceding section has shown, that a further discussion seems unnecessary. Males deserve closer consideration in this regard – both in general and among the Peracarida in particular, because their direct parental investment in the young is usually so much less than that of the females. In all such cases one would expect to find a polygamous mating system, relinquished only when conditions select strongly against it (cf. TRIVERS 1972; LINSENMAIR 1979, 1984; WICKLER and SEIBT 1981). Because Hemilepistus males in all our extensive experiments never seem to «play the field», it must be inferred that an attempt to do so would incur risks that would not, on average, be compensated by success with one or more additional females. As analyzed in detail elsewhere (LINSENMAIR 1979, 1984), there are only two situations worth considering in which a male could – theoretically – leave his female without a nearly 100% risk of losing the investment he had made up to that time, which on average could never be compensated in the future. These situations are as follows:

(a) The male could leave his female immediately after the regular copulation phase, so soon before parturial molt that the female could find another partner but – because she cannot prolong the brief time until parturial molt – has no opportunity for frequent copulation with him. Results so far, though still preliminary, indicate that there is no sperm clumping (LINSENMAIR 1984), so that eggs would always be partly fertilized by sperm from the first male. A method of this sort would require (i) that the males be capable of judging the point of time within the reproductive phase of the population and hence of knowing whether there is enough time left for them to be likely to find an unmated female offering an adequate opportunity for reproduction, and (ii) that the males be very well informed as to the condition of their females, in order to choose the right time to leave them. The requirement in (ii), at least, is certainly not met; the females «withhold» all relevant information from the males (LINSENMAIR 1979, 1984). Still more important, however, is a third point; males forming a pair with a new female should be able to more than compensate the losses they incur by their infidelity towards their first female. Our first results indicate that males choosing the best time to desert their female «had to reckon» that about 50% of their first females' eggs will be fertilized by the second male. In order to allow for a positive selection of a deserting behavior one basic requirement – besides others left out of consideration here – would be that the new pair's chances for survival (until the male reaches the end of the regular copulation phase for a second time)

should exceed 50 %, but this on average is not the case (SHACHAK 1980; LINSENMAIR 1984), often their chance does not even reach 10 %.

(b) The second opportunity would arise only some weeks after the birth of the young. But because the climatic and other ecological conditions make it essential to time reproduction accurately with respect to the annual cycle, the females are too well synchronized with one another, thus a male leaving his family at that time would have no chance of finding a female still in a suitable state.

In the present-day situation the desert woodlice have good chances of reproduction only as monogamous pairs. Current conditions of selection certainly stabilize this form of a social and mating system. However, they tell us nothing about the evolution of this highly differentiated and certainly very derivative behavior. The special construction and defense of a permanent burrow in a firm substrate, the formation of pairs in which the partners individually recognize one another, brood care with family-specific recognition of the young – all are crucial adaptations to the ecological conditions of the present biotope and hence prerequisites for inhabiting it. Therefore they cannot have been formed by the selection factors prevailing at present. The early steps must have been taken under other selection pressures, under less severe abiotic ecological conditions (cf. LINSENMAIR 1984).

3.2 Kin recognition in *H. reaumuri*

The parental pair together with their young – up to 140 of them – constitute a strictly closed community. Foreign conspecifics that appear at the burrow entrance (or within the area around it bounded by the fecal wall) are always attacked by the parents and juveniles (6 weeks of age or older), and outside this boundary they are either attacked or avoided. The members of the cooperative community never behave aggressively to one another «intentionally» (i. e., after tactile examination) until the family group dissolves, unless too close contact has been made with alien conspecifics. This behavior shows that the desert woodlice are not only capable of identifying individuals, but can also distinguish kin from non-kin.

3.2.1 Interfamily variability

In the field, hundreds of experiments and very many more observations have produced no evidence of mistaken identification, despite the fact that at times *H. reaumuri* can live in very dense local populations (up to 14 families with young per m²). The radius within which the family members forage can be as great as 6 m and is usually 1,5–4 m. Given a foraging radius of 2,5 m, with 5 families per m² it is to be expected that members of about a 100 families will come into the vicinity of any particular burrow. Since families in the field remain exclusive even at highest densities, it follows that the variability of the characteristics used for kin identification must be very great.

Well over 50,000 tests involving reciprocal exchange of the juveniles of two families have been carried out, and no two families have ever been found to tolerate one another. Unilateral toleration has been observed. In a systematic cross-exchange test 70 families collected in the field from an area of 50 × 50 m were examined for discriminator coincidence. Of the 4830 repetition-free combinations there were 4 in which the young from one family were not attacked by the members of a single other family. In this case a number of conditions (of animal maintenance and experimental procedure) acted to reduce aggressiveness, so that this misidentification rate of 0.1 % is certain to be an overestimate. But it does indicate that very close resemblances can exist in this frequency.

3.2.2 Nature and origin of the family badge

There is no doubt that the characteristics used for kin identification, the «family badge», are chemical in nature. One of the clearest demonstrations of this is that with suitable solvents extracts can be obtained that when applied to a neutral carrier such as a glass rod can elicit aggression (as foreign conspecifics do); when such extracts are applied to individuals the other members of their family treat them as aliens for a long time.

The density of family-occupied burrows and the great overlap of the foraging areas of neighboring families made it *a priori* highly unlikely that the variety and specificity of kin discriminators would reside in body odors acquired from the surroundings. All the relevant early experiments (LINSENMAIR 1972) and later extensions of them confirm this view. Only one finding need be mentioned, as follows. Hundreds of pairs and families collected in the field were kept under constant laboratory conditions on the same substrate, and given the same food, for 5–9 months. Many hundreds of woodlouse families bred from those collected in the field have since been maintained for their whole life cycle under these conditions, some of them now in the 4th generation. Unless inbreeding occurred, none of these animals have given any sign of reduced acuity in making the distinction between kin and non-kin ($n > 500$ cross-tests). Our earlier hypothesis (LINSENMAIR 1972) – that the discriminator substances, with all their diversity and specificity, are genetically controlled secretions, very little influenced by the environment – has now been corroborated by many additional experiments (LINSENMAIR in prep. (III)) and can be regarded as firmly established.

There are several compelling reasons – (i) the degree of variability, (ii) the reproducibly graded aggressive response to members from different alien families (extending in the extreme to unilateral acceptance), and (iii) all the results of mixing experiments (see below) – to conclude that the family badge is always a blend of several components.

3.2.3 Intrafamily variability: individual characteristics

Because emigration of the young (see p.415) thoroughly mixes the population during the pair-formation period, we have to assume that in more than 99 % of all pairs the partners come from different families, with different badges and corresponding genetic differences. There is no evidence for sex-linkage of the genes responsible for production of the identifying substances. With normal autosomal inheritance, however, variability among the progeny of a pair is to be expected. How, then, can there be a common family badge? Does it really exist? Adoption experiments (LINSENMAIR 1972) in which parents are brought into very close contact with half of the young from another family, thereby compelling them to get acquainted with these juveniles, have shown that as a rule the foster parents will then also accept the other half of the young. This outcome refutes an alternative hypothesis to that of the family badge, namely that mutual acceptance within a family could be a matter of individual recognition alone. The results indicate that the variability of discriminator patterns among family members is somehow reduced or adjusted so that a common badge is achieved.

Given a great primary intrafamily variability in the production of individual discriminator sets, one way to achieve a common family badge could be to make a secondary adjustment, e. g. by confining the spectrum of produced substances within the family to the smallest common denominator. Then the individuals would have to match themselves to some extent to their chemical surroundings. Amputation of the apical cones, the sole structure responsible for badge identification, ought then to cause changes in production, but no such changes have been found (LINSENMAIR 1972; KREMPIEN 1983). Furthermore, week- to month-long integration of single individuals into strange families, during which

such individuals soon become fully accepted (and soon «regard themselves as belonging» to the new family; LINSENMAIR in prep. (III)), ought to be accompanied by changes in production. But when such integrated individuals were isolated immediately prior to a molt and afterward tested to see how their natural and adoptive siblings would respond, the results (Table VI) gave convincing evidence against such a hypothesis. The integrated isopods after removal from their foster family and before molting – were treated in their natural families like foreigners. The alienation could have been either the result of the integrated animals' adjustment to its changed chemical environment or an effect of contamination caused through transferred substances by the foster families' members. The fact that after molting in isolation these individuals were accepted without any aggression in 84 % of all encounters by their genetical kin but only in 15 % by members of their former foster family clearly indicates the lack of an adjustment in discriminator production. It rather points to contamination as the reason for the observed alterations after the integration and before molting in isolation.

b) As the previous experiments indicate, and as we know since a long time (LINSENMAIR 1972), badge substances are exchanged between animals during body contacts. Members of a family group, living shoulder-to-shoulder within the burrow, cannot avoid this exchange and the consequent intermingling of their secretions. But if the production of the individual discriminators is under extensive genetic control and the family badge is a product of the mixing of the individual discriminators, then – in the absence of special adaptations – in the course of the (very numerous) molts communication problems must arise.

Table VI: Does integration into an alien family change the production of discriminators?

	Test animals	Where tested	Encounter releasing		Significance
			Attacks	No attacks	
A	Not yet moulted ¹	Genetical family	192 ²	3	A : B P << 0,001 (χ^2)
B	Moulted	Genetical family	164	879	
C	Moulted	Foster family	522	92	B : C P << 0,001 (χ^2)

(N = 22) ↗
↓
(N = 11)³

(N = 17)

Reactions of natural and adaptive siblings towards individuals which had been integrated for 4–8 weeks into foster families and then taken out and tested before and after molting (in complete isolation). The integrated isopods were removed from their adoptive families about 24 hours prior to the beginning of an ecdysis; they were tested 36–60 hours after terminated ecdysis.

¹ Tests immediately after removal from the foster family.

² Number of observed single reactions.

³ Number of tested isopods.

Table VII: Loss of alien substances by molting

Contaminated individuals	Reactions of uncontaminated family members		Significance
	Attacks	No attacks	
A Before molting	180 (n = 15 individuals)	3	A : B
B After molting (24–48 hours after termination)	36 (n = 15 individuals)	420	B : C P \ll 0,001
C Controls: contaminated like A, kept in isolation for the same period as B, but without molts	145 (n = 10 individuals)	6	A : C not significant χ^2

The test animals and the controls were contaminated by close direct body contacts with 10 alien conspecifics for 5 min, in A/B 24–48 hours before a molt. For molting individuals were kept in isolation in single uncontaminated containers.

3.2.4 Does molting create problems in communication because of the mixed character of the family badge?

When it molts, each family member discards along with the exuvium all the discriminators it does not itself produce (cf. Table VII; see also Table VI). Observation of undisturbed families reveals that in far fewer than 0.1 % of molts is there any evidence of the newly molted animal being killed (and even in these cases there could be reasons other than communication problems). Here, again, integration experiments and observation of artificially composed groups are useful means of clarifying the situation. We can – as the results summarized in Table VI have proved – safely assume that the substances produced by an integrated animal (which was severely attacked before its integration) depart considerably and permanently from the norm of the adoptive family. If individuals within mixed groups molt 7 days or more after integration, the group or family (if undisturbed) treats them in 96 % of all cases (see Table VIII) not differently from an unmolted mixed group or family member. But if the integrated foreigners are removed shortly before the onset of molting and replaced when molting is completed for more than 36 hours, they are predominantly (in 85 % as the results summarized in Table VI have shown) treated as aliens. Control animals, which had been integrated into families for an equally long time but which did not molt during the four to five-day-period of removal (n=50), were – after being replaced in their foster families – accepted without aggression in 98 % of cases, proving that in the test animals in fact the molting-caused changes were the reason for the altered responses of the adoptive family.

Animals molting within their foster family or mixed group after an integration time of less than 6 days have only a limited chance of surviving (see Table VIII), and all the animals (n=30), which were integrated as singles into pure foster families and which molted there within 36 hours were killed. This dependence of tolerance on integration time could indicate that learning processes are crucially involved in acceptance. But how are we to interpret the difference in response depending on whether the integrated animal molts within the family or in isolation?

Table VIII: Number of individuals surviving complete molts in mixed groups in dependence of time spent in these groups

Days after group formation	Surviving	Killed	Significance
> 2-6	56	24	$P \ll 0,001$
7-35	1433	56	χ^2

Killing normally occurred during or shortly after shedding the posterior half-exuvium. These animals then were cannibalized.

Preliminary answers to these questions have been given by experiments in which animals – either foreigners integrated into pure families or members of complex or highly complex mixed groups¹ – were removed for molting but returned to the group a shorter time after stripping off the anterior hemiexuvium than was the case in the experiments described above (see Table VI). Animals returned 5–16 hours after the anterior hemiexuvium is shed are attacked only rarely and they hardly ever encounter strong aggression (see Table IX). But if one waits longer, most are attacked. Evidently these early post-molt individuals enjoy temporary protection, which becomes permanent if they are returned to the family or group soon enough.

When a woodlouse is presented an unfamiliar, newly-molted individual, it can easily be seen that the newly-molted half of the body exerts, especially during the first hour after the shedding of the respective hemiexuvium, an inhibitory influence. The results summarized in Table X, however, show clearly that this protection is far from perfect at any time, for in all cases sooner or later (and always within a period of a few minutes only) the foreigner, if placed into an alien family or alien mixed group, is bitten – and the emergence of hemolymph always cancels any inhibition (even that with respect to a normal family

Table IX: Members of mixed groups replaced at different times after molting in isolation into their groups

Time between shedding the anterior hemi-exuvium and test in hours	Reactions of group members		Significance
	Attacks	No attacks	
A 5-16	20	242 (n = 16 individuals)	$P \ll 0,001$
B 22-96	180	100 (n = 16 individuals)	χ^2

The isopods were removed about 12–24 hours before molting; they were kept in isolation during the molt and the exact time of shedding the second half exuvium was determined by direct observation. After having been tested in A the animals were isolated again and used for a second time in B.

¹ In «complex mixed groups», containing between 60–120 individuals never more than 3 individuals originate from the same family, in «highly complex mixed groups», each of the 60–120 individuals was taken from another family.

Table X: Reaction towards alien conspecifics after touching their newly molted body half

Time between shedding an hemiexuvium and test	Reactions in single encounters		Significance
	Attacks	No attacks	
A 1–14 min	124	397 (n = 20 individuals)	A + B : C P << 0,001
B > 14–30 min	171	419 (n = 23 individuals)	C : D P << 0,001
C > 30–60 min	249	331 (n = 23 individuals)	χ^2
D > 60 min–3 h	149	40 (n = 9 individuals)	

The test animals, seized with a forceps, were presented the controls in such a way that these could touch the newly molted body half only. Often clear signs of inhibition could be observed as follows: controls quickly withdrawing their antennae, retreating some steps, etc. (cf. Linsenmair 1984).

member). Under most conditions the protection only becomes perfect when the members of the family or the mixed group have had a chance to live together with the alien animal for a prolonged period before its molt. It is to be assumed that the isopods could therewith become familiar with the special chemical properties of the deviating group member. Before proceeding to further considerations, we should answer the question of how relevant the results obtained with experimentally altered groups may be for pure families. When members of unaltered families were isolated for molting, and not replaced until 24 hours after its termination the results summarized in Table XI were obtained; they show that the same alienation problems can sometimes arise in natural families, which justifies our experimental procedure.

How can this recognition system – which apparently requires the ability to learn to recognize deviant individuals – function, given that the family badge is a mixture of all the individually produced components? Is it simply a matter of learning all the individual components of the family badge, in order to be able to tolerate then any arbitrary partial combination if it is coupled with the signal «newly molted»? The members of highly complex mixed groups with a great (about 90–95 %) but not complete overlap in the spectrum of families from which the single individuals originated, in many cases tolerate

Table XI: Reactions of pure families towards members isolated during molt and replaced 24–48 hours later

Members of	Attacks	No attacks
25 families	27 individuals	99 individuals
family No 78/25	17 individuals	4 individuals

These families collected in the field, were kept free of any experimentally caused contaminations. A few families – family No 78/25 is an example – show an extraordinary high incidence of molting-caused alienations.

one another with no aggressiveness, even though they behave very aggressively toward pure families or differently composed mixed groups. The badges of the similar highly complex mixed groups are evidently not distinguished from one another. When members of these mixed groups are isolated for molting and afterwards returned for brief periods, alternately to their own group and to the second group that does not differ detectably in its group badge, they are much more frequently (and with high statistical significance) attacked in the latter group (Table XII). (Observations similar in principle can often be made in pure families that have been divided for long periods, i. e. > 15 days or in complex groups with complete overlap in respect to the families from which members were taken to compose the two or more experimental units.) Accordingly, two groups can have badges indistinguishable from one another and nevertheless comprise differing members (with regard to their production of individual chemical identifiers).

Here, again, experiments in which groups have been assembled experimentally provide critical evidence. A foreign juvenile brought into close contact with young of the control family can alienate between ca. 5 and 20 individuals (depending on the family combination) to such an extent that when they are returned to their uncontaminated family members they are treated as aggressively as foreigners. But when a single alien mingles with a considerably larger number of sibling juveniles from another family, alienation does not occur even after long-term exposure. A single foreigner can produce and transfer only a limited amount of badge substances. If those components which are not contained in the badge of its foster family are distributed among many adoptive siblings, these are diluted below the effectiveness threshold. That is, in the subset of individually produced substances shared by *all* members of the group, the components with respect to which this foreigner (or a single deviant family member) differs from the norm are lacking. We can now understand that two groups may have the same group-specific badge even without complete agreement between the entire sets of discriminator substances produced by each group.

How is such a deviant animal protected when it molts? The decisive point is that in fact the deviant discriminators do not show up in the common badge but – and this certainly is crucial to the deviant's survival – its individual traits are never lost. The family badge can never completely mask an individual's discriminator complex, a complete glossing over individual chemical properties is – according to many experimental results – (LINSENMAIR in prep. (III)) impossible. The physiological basis of this resistance to complete masking presumably (as other findings indicate) lies in a very firm binding of part of the animal's own secretions to the surface of its cuticle. Whereas the family badge can be perceived by touching any member of the group, even if that member itself produces only some components, the detection of individuals producing discriminator substances not present in the

Table XII: Newly molted individuals originating from one of two highly complex mixed groups with identical badges: Are they treated identically in both groups?

Newly molted tested in	Reactions of group members in single encounters		
	Aggressive	Non-aggressive	Significance
Own group	26	191	$P \ll 0,001$
Alien group	108	72	χ^2

7 individuals were isolated 20 hours or less before a molt and replaced within 6–20 hours after its termination.

family badge requires that they be touched directly. Within a large group it certainly does not happen that each member touches each other member in every activity period, and it is just as certain that many touches are necessary to identify a deviant conspecific reliably; in this light, the fact (documented above) that the development of tolerance requires relatively long integration times becomes rapidly understandable.

Memory plays a central role in all identification responses, and this is not the least of the reasons why it is difficult to judge the extent of intrafamily variability by using the indirect methods of behavioral experiments. It is therefore impossible to estimate the demands individual and kin recognition make on the learning abilities of the family members. We do not yet know how many components the family badges contain and how many other discriminators may be «concealed», to be learned only through direct contacts with the individual concerned. But there is considerable evidence that very complex combinations of characteristics, including many components that do not appear in the group badge, can be learned.

3.2.5 Inter- and intrafamily communication: discussion

a) Why are the family groups so strictly exclusive?

In the light of our present knowledge, being the result of intensive discussions which have received their strongest impetus from the fundamental contributions of HAMILTON (1964a, b, 1972), the basic answer is trivial: in order for the valuable and costly efforts expended within the social unit on behalf of conspecifics to have an adequate reproductive payoff, these must be confined to relatives. The society must protect itself from both intentional and accidental parasitism, by keeping foreigners out. Because a desert woodlouse family still stays together very long after the time when the juveniles pass the stage of «altricial» nestlings – though they remain thereafter for many additional weeks dependent on parental care and for months on mutual assistance among themselves – the problem of discerning foreigners from family members cannot be solved by, for example, site-specific recognition. For family members to be reliably distinguished from non-members in this case, where many families may dwell nearby, a stable but highly variable identification system allowing accurate and reliable discrimination of kin among a very large number of conspecifics is required. Acquired body odors, from the surroundings or via the food, which seem to be used exclusively (?) or at least as the essential components of the discrimination systems of some eusocial Hymenoptera (reviews: RIBBANDS 1965; MICHENER 1974; WILSON 1971; HÖLLDOBLER and MICHENER 1980), cannot meet these requirements (LINSEMAIR 1972). The signature system evolved by *Hemilepistus*, with its extremely diverse secretions – under genetic control and extremely resistant to most possible external influences – is an excellent solution to the problem of kin recognition under especially difficult conditions resulting from temporary very high dwelling densities and a more or less complete overlap of the foraging grounds of neighbouring families. But this method has one very vulnerable feature: during direct contact substances are exchanged between unrelated animals, rapidly causing alienation from their own families. Therefore such contacts must be avoided at all costs, and as long as the family badge is used for identification the community must remain exclusive. This certainly explains, at least in part, the pronounced aggressiveness exhibited toward alien conspecifics in situations in which it is comprehensible on neither ecological nor sociobiological grounds – it serves to prevent -unintended- contacts (LINSEMAIR in prep. (III)). The danger of those contacts should not be underestimated, for it is only by direct touching with the antennae that identification is possible, and in such close proximity «involuntary» contact may easily occur prior to antennal touching. (Where the density of *Hemilepistus* families was very high we always found indications of relatively large contamination problems.)

b) Interfamily variability. At a conservative estimate, in relatively densely populated regions each isopod burrow lies within the foraging radius of at least 100 families (see p. 424). An estimated upper limit, for very high population densities (10–12 families per m^2) and extensive foraging excursions (5–6 m radius) due to food shortage caused by the high numbers of individuals, would be of the order of 1000 families, the members of which could make contact with the inhabitants of a single burrow. Moreover, taking into account that within a complete family, as a rule, there exist at least three distinctly different badges: the male, the female and their progeny differ so greatly from one another that familiarity with the identifying characteristics of one of the three does not result in acceptance of the other two (a result not discussed above; see LINSEMAIR in prep. (III)). It should also be remembered that within the progeny individual variability through «personal» substances not showing up in the family badge is high. Thus the possible number of discriminator sets an individual could encounter at its burrow and mistake for kin may increase by another order, or, as an absolute maximum, another two orders of magnitude.

The estimate of 10^5 different types of identifying characteristics that a family member can encounter, none of which is to be confused with those of its siblings and parents, is probably very high and overestimated. But since we have found not a single case in which two families had the same badge, we can reasonably postulate a discriminator diversity sufficient to ensure that even in the most demanding circumstances misidentifications remain very rare exceptions. The finding of unilateral acceptance in 0.1 % of the cross-combinations in one experiment (i) may well be an overestimate (see p. 424 and LINSEMAIR in prep. (III)) and (ii) offers little threat to exclusivity. That is, a member of a family that cannot distinguish the badge of one other family from its own, so that it «feels at home» when it contacts the marked vicinity of the other family's burrow and may attempt to enter, is recognized as foreign and driven away (presumably because its family badge includes at least one extra component; LINSEMAIR in prep. (III)). Members of the family accepted by the other family never discover this fact, for to them the other family is foreign. Only in exceptional situations – for example, when deprived of their own burrow – might individuals of the more discerning family by a very improbable chance try to enter the burrow that would be «right» for them.

Let us assume, as there are good reasons to do, that badge differences are chiefly or even exclusively qualitative in nature; how many components would then be necessary to produce 10^4 – 10^6 distinct badges? In our chemical analysis, after a number of purification steps (ESSWEIN in prep.), 8 fractions were obtained which differ considerably from each other in the chemical properties of the compounds included. 7 of these fractions proved effective in our bioassay. If we consider these 7 as 7 independent badge dimensions we would expect each of these classes to comprise not more than between 4 and 10 (on average 8) different substances (provided they lead to phenotypic differences) in order to generate the desired number of repetition free permutations. At the genetic level, a system with 7 loci and 4–10 phenotypes associated with each locus (which, depending on gene interaction, would require 3–5 alleles per locus) would be just adequate to meet the requirement. Such a system, involving the production of only 40–70 different suitable badge substances, should be entirely realizable as far as this point of production is concerned. Nor would such a system make excessive demands on the sensory abilities of these animals, arthropods that orient to their surroundings in general chiefly by way of chemoreception.

c) Intrafamily variability and badge structure. Given normal processes of inheritance, the high interfamily variability must necessarily result in a certain amount of intrafamily variability. These differences among family members are partially masked by the intermingling of individual components that occur automatically on contact. A family badge is

thereby produced, a chemical common denominator that is similar enough among at least most if its bearers (apart from the parents) that foreign conspecifics (e. g., adoptive parents) need only become familiar with some larger fraction of the individuals (50–70 % of the progeny) in order subsequently to accept the remainder – animals they have never encountered directly – as members of the group. In this experimental situation the adoptive parents employ a phenotype-matching mechanism (ALEXANDER 1979; HOLMES and SHERMAN 1982, 1983; SHERMAN and HOLMES 1984). This mechanism could also play a role in the intact family; for an animal to remind itself of the family badge and to keep track of any changes of the family badge due e. g. to losses of family members as time goes by, it needs only to touch a few of its siblings.

The family badge has gestalt character (cf. CROZIER and DIX 1979). Each member of a group learns this gestalt independently of its own discriminator production. (The interesting, multi-level problem of how the parents learn to identify their young in the first place and how they avoid eating them, in view of the fact that they always cannibalize young foreign conspecifics, is outside the scope of this discussion; see LINSENMAIR 1984, in prep. (II).) The badge, as would be expected of a gestalt model, is very vulnerable to disturbance, and is more readily made unrecognizable by the addition than by the removal of single components.

The system is greatly complicated by the fact that all members of the *Hemilepistus* families molt at more or less short intervals and in so doing, because of (i) the non-volatility of the discriminators and (ii) their intrafamily variability, alter the badge they bear, sometimes severely. Such alterations must destroy the gestalt character of the badge. A gestalt model alone, then, cannot explain the kin-recognition abilities of *Hemilepistus*.

If molting solely involved the loss of certain components of the common family badge, the family members would – in order to categorize a newly molted individual as belonging to their group or as alien – need to be able to determine whether the discriminators borne by a newly-molted animal amounted to a subset of the family pattern, with no foreign additions. To avoid acceptance of a foreigner that happens to match one of the presumably many possible subsets of the family badge, an additional safety measure would be expected – there must be some sign indicating a recent molt. (Because desert isopods can molt successfully only in burrows, owing to evaporation and other problems, no other assurance would be required.) Although the second part of this scheme does apply to *Hemilepistus* – molting is signalled – the first proposal is too simple. The reason is that the family badge contains only those components that – in a large family – are produced by several individuals. Presumably any component produced by only one or a very few individuals, when distributed among all the family members, is diluted under the threshold of effectiveness and therefore no longer influences behavior. But after such an individual has molted, the deviant substances on its surface become very conspicuous at the same time as more or less large fractions of the common pattern have been lost.

Hemilepistus can and has to learn not only the badge common to the family, but also all those chemical discriminators of deviant individuals which are not represented in the pattern borne by every family member. Such learning is possible only because these substances are bound to the producer's cuticula in a way that reliably prevents their dilution below the detection threshold. It is still not clear what the partial patterns remaining after molting must consist of in order to be acceptable – whether all the single components which are present either as personal or as family discriminators may be freely combined or whether they meet the criterion only in certain combinations, thus restricting the number of possible permutations.

The learning task that a member of a *Hemilepistus* family faces in this context cannot yet be evaluated in detail, but in any case it must be formidable. Although the memory of a

Hemilepistus is very good (LINSENMAIR and LINSENMAIR 1971; LINSENMAIR 1972), it must evidently be continually refreshed, especially in the case of the less common characteristics. Continual learning is probably also necessary because, in the course of time, changes in the badge system develop – owing, for instance, to the death of some family members.

Their permanent capacity for learning makes desert isopods especially suitable subjects for detailed analysis of a differentiated communication system. Because the signals are transmitted by contact chemoreception and not by olfaction (in which case orders of magnitude fewer molecules could be involved), chemical analysis seemed a promising approach, and one that was likely to succeed without the need to extract astronomical numbers of animals. In the event, the chemical properties of the substances have considerably hindered and delayed the analysis (HERING 1981; ESSWEIN 1982), but there are good reasons to believe that we shall soon know the general features of the spectrum of substances employed. This analysis is the most important project currently underway, for there are many questions that can be usefully pursued only after it is completed.

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