Comparative Studies on the Social Behaviour of the Desert Isopod *Hemilepistus reaumuri* and of a *Porcellio* Species

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SYNOPSIS

Behavioural adaptations have made the desert isopod *Hemilepistus reaumuri* the most successful herbivore and detritivore of the macrofauna of many arid areas in North Africa and Asia Minor. For survival and reproduction *Hemilepistus* is dependent on burrows. New burrows can only be dug during spring. With the time-consuming digging of a burrow, *Hemilepistus* has only made the first step towards solving its ecological problems. The burrows are vital and have to be continuously defended against competitors. This requirement is met by co-operation of individuals within the framework of a highly developed social behaviour. In spring adults form monogamous pairs in which partners recognize each other individually and later form, with their progeny, strictly closed family communities. *Hemilepistus* is compared with a *Porcellio* sp. which has developed, convergently, a social behaviour which resembles that of *Hemilepistus* in many respects, but differs essentially in some aspects, partly reflecting differences in ecological requirements. This and a few other *Porcellio* species demonstrate some possible steps in the evolution of the social behaviour of *Hemilepistus*. The female *Hemilepistus* is — in contrast to *Porcellio* sp. — semelparous and the selective advantages of monogamy in its environment are not difficult to recognize. This chapter discusses how this mating system could have evolved and especially why monogamous behaviour is also the best method for the *Hemilepistus* male to maximize its reproductive success. The cohesion of pairs and of family communities in *Hemilepistus* is based on a highly developed chemical communication system. Individual- and family-specific badges owe their specificity to genetically determined discriminating substances. The nature of the badges raises a series of questions: e.g. since alien badges release aggression, how do parents avoid cannibalizing their young? Similar problems arise from the fact that family badges are mixtures of chemical compounds of very low volatility with the consequence that they can only be transferred by direct contact and that during moulting all substances are lost which an individual does not produce itself. It is shown that in solving these problems inhibiting properties (presumably substances) and learning play a dominant role.

INTRODUCTION

Owing to a number of pre-adaptations oniscids have succeeded in becoming the only large crustacean group which is completely terrestrial.

Since most species lack effective protection against desiccation they are
restricted to moist habitats (e.g. Edney, 1968; Warburg, 1968; Warburg,
Linsenmair & Berkovitz, 1984). But some have managed to invade the
particularly terrestrial habitats of semi-deserts, and a few thrive in real
desert. The nine species of the genus *Hemilepistus* (Lincoln, 1970) are
among the most successful (Marikowsky, 1969; Linsenmair &
Linsenmair, 1971; Schneider, 1971; Shachak, 1980; Shachak & Yair,
1984). From the present distribution of these species it is presumed that
the genus evolved in the steppes of Kazakhstan and Turkmenja. The
species we are mainly investigating, *Hemilepistus reaumuri* Audouin &
Savigny, is widely distributed in Asia Minor and North Africa (see
Coenen-Stass, 1984) and is very common: in years and habitats with
peak population densities up to five million individuals can live in an
area $100 \times 100 \, \text{m} \, (500 \, \text{m}^{-2})$.

How do these desert isopods cope with the particularly severe ecological
problems, such as lack of water, low relative humidities, high
temperatures? *Hemilepistus* is — for an isopod — physiologically and
morphologically well adapted to living on land (respiration organs: Hoese,
1982; water balance and temperature resistance: Linsenmair, 1975;
Pretzl, 1976; Coenen-Stass, 1981). But with these remarkable adaptations
alone *Hemilepistus* could not exist in its present biotopes.

The great success of *H. reaumuri* is only to be understood by fully
appreciating its ethological adaptations, in particular its social
(Linsenmair & Linsenmair, 1971; Linsenmair, 1972, 1975, 1979, in
press, in prep.; Shachak, 1980) and orientation behaviour (Hoffmann,
1978, 1983a,b,c, 1984a,b). These behavioural adaptations are — to our
present knowledge — very unusual within the isopods. In trying to
determine the consecutive steps on the evolutionary route to these highly
differentiated performances, some *Porcellio* species in which a less
developed social behaviour has been found could possibly serve as models,
throwing light on the origins of the social behaviour and on some
intermediate stages.

ACQUISITION AND SECURING OF BURROWS IN *HEMILEPISTUS*

Desert isopods depend on burrows they construct themselves. Without
these they could never reproduce and could hardly survive a single day
in summer. As they lack effective digging adaptations the construction
of new burrows is time-consuming and — far more important — limited
by climatic conditions to spring. During the warmer months *Hemilepistus*
would not have the slightest chance of digging a sufficiently deep den
quickly enough in the dry solid soil so characteristic of its habitats.

Therefore the timely acquisition of the burrow is a vital task. But a desert isopod meeting this requirement has not yet solved its main residential problem. Since there is strong intraspecific and, to a lesser extent, interspecific competition for the valuable burrows, these can only be retained by continuous guarding.

Effective organs for remote sensing are lacking. *Hemilepistus* therefore cannot guard its burrow if the entrance is beyond the direct reach of its antennae. Consequently a single *Hemilepistus* could permanently defend its burrow only while fasting: to forage it has to leave its den. *Hemilepistus* has solved this problem in an elegant way: the adults form monogamous co-operative pairs and later, together with their progeny, strictly closed family communities. Entrance to the continuously guarded burrow is only allowed to individuals displaying their community membership by individual- or family-specific chemical badges (Linsenmair & Linsenmair, 1971; Linsenmair, 1972, 1975, 1979, in press, in prep.).

PAIR FORMATION AND PAIR MAINTENANCE

Parental Investment, Mating Systems, and Brood Care in Isopods: General Considerations

Monogamy is, in most taxa, a rare phenomenon due to asymmetries in parental investment (Trivers, 1972). These asymmetries are very pronounced in isopods: the direct investment of males in their progeny is small. Sperm are comparatively cheap, they can be produced in much larger amounts than eggs. Therefore the potential reproductive success of a polygamous male can surpass by far that of a conspecific female. In *Hemilepistus* a female produces a single brood, whereas males — in spite of being forced to spend considerable time until allowed to mate — could fertilize all the eggs of at least eight females during the four months in which they form new pairs if experimentally separated from a previous partner. Only strong counteracting selection pressures can be expected to render the usual polygamous mating system of isopod males unprofitable and to favour a monogamous one.

In contrast to males the direct expense of breeding in females is large. It includes the production of yolk-rich eggs and the development of brood pouches (requiring a parturial moult). Besides these energy investments those of time are necessary too: for production of eggs, moulting, carrying embryos for weeks and marsupial mancas (terminology: see Holdich, Lincoln & Ellis, 1984) for days. Therefore isopod females in general are unable to compensate quickly for reproductive losses. This can be expected to influence their behaviour very strongly. One consequence:

females should choose among males very thoroughly to select the best male(s) available for fathering their precious progeny.

In animals already performing some brood-care, as in the Peracarida, one possible way of coping with increasing reproductive losses under changing ecological conditions could be to improve survival of their young by extending and/or intensifying parental care (see, e.g. Wilson, 1975). In the Oniscidea this evolutionary route has been followed separately at least twice: (1) in the ancestors of *Hemilepistus*; and (2) in some North African and Canarian *Porcellio* species (Linsenmair, 1979, in prep.: Herlein, 1981). It is to be expected that females rather than males will be selected to provide further brood care, since they have the greater difficulties in replacing reproductive losses and they are on the spot when their young are released from the brood pouches, the moment at which any extended brood care has to begin. Considering this last point we have to conclude that for a male to participate in brood care, pair formation — prolonged over the period of receptivity of its female — should be an inescapable condition.

Some Aspects of Pair Maintenance in *Hemilepistus reaumuri*

A prerequisite for pair formation under natural conditions in *Hemilepistus* is that one partner is in possession of a burrow, which has been found empty, taken by force or dug. Usually it is the female in *Hemilepistus* that begins digging (out of 63 desert isopods directly observed starting to dig a new burrow, within the first 15 days of the pair formation phase, 55 (= 87%) have been females). Initially the owner defends its short den against every conspecific. After a prolonged ritual the owner admits a single conspecific of the opposite sex. Partners of such pairs then normally stay together until death or forced separation. They are attached to each other by mutual individual recognition (Linsenmair & Linsenmair, 1971; Linsenmair, in press).

The readiness of females to reproduce depends — under those climatic conditions characteristic of the main pair formation phase — largely upon burrow ownership. This is clearly demonstrated by placing pairs in two sets of containers (at temperatures not exceeding 20°C), one with, the other without burrows (and without the possibility of digging but otherwise being completely identical). The results (Table I) show that continuous and close contacts with a particular male over a prolonged period are not alone sufficient to induce parturial moults. Fewer of the paired females without access to burrows moulted, and those that did took on average longer to do so, than the paired females in possession of burrows in the control experiment.

After pair formation a new burrow will be lengthened from an average

TABLE I
Dependence of parturial moults (PM) on burrow ownership — low temperatures

Burrow	PM performed	No PM	PM: days after pair formation	Significance
Present	25	0	23 ± 5	$p = 0.001$
Absent	9	32	41 ± 4	$(FEt)^a$

Number of paired females performing — at temperatures of 18–20°C — parturial moults and time span between pair formation and parturial moult compared to burrow availability (containers otherwise identical); duration of experiment 100 days. (For elevated temperatures compare Table IV.)
^{a} FEt: Fisher's Exact test.

of 2.5 to 6 cm ($n = 25$) within the first 24–48 h and this digging continues at a slower rate in the days that follow. The male participates in burrowing. The question arises as to whether digging by the male enhances the cohesion of the pair and the readiness of the female to reproduce. If it benefits males to burrow, we should expect females to respond to the burrowing of males with an increased readiness for mating. Females admitted by males owning burrows should allow earlier copulations, releasing earlier parturial moults, than females which acquired their burrows themselves. The results of the relevant experiments (Table II) do not support this hypothesis. Even preventing males completely from digging, by amputation of their first two pairs of pereopods, does not influence pair cohesion negatively and does not significantly prolong the time between pair formation and parturial moult (Table III).

The fact that females in most cases initiate digging and also are the main burrowers after pair formation (Linsenmair, 1979), indicates that either females gain by doing so and/or are in a weak position to "charge males with these duties" (see Discussion below). Since females are

TABLE II
Does male burrow ownership promote females' readiness to reproduce by accelerating parturial moults (PM)?

Burrow owner	PM performed within		PM not (yet) performed within		Significance
	19 days	23 days	19 days	23 days	
Males	9	24	18	3	$p > 0.75$
Females	8	24	21	5	not significant (χ^2)

Males or females were offered artificial burrows which all accepted. Eight days later a partner was placed in the container. Pair formation occurred during the first 24 h. Average temperatures 23°C.

Numbers on day 19 and 23 include females starting their parturial moult within the next 30 h. (In this and all following experiments at temperatures of 23–25°C the very first parturial moults are to be expected between the 18th and 20th day after pair formation.)

TABLE III
Does preventing males from digging delay parturial moult (PM) of their females?

First two pairs of pereopods	PM performed	PM not (yet) performed	Significance
Amputated	20	8	$p > 0.65$
Intact	20	5	not significant (χ^2)

Males were rendered incapable of digging by amputation of their first two pereopods; average temperature 23°C. Figures represent numbers of females moulted or still unmoulted (i.e. also not moulting within the next 30 h) 24 days after pair formation.

TABLE IV
Dependence of parturial moults on burrow ownership — higher temperatures

Burrow	Calcium deposits or moulted	No moult indications	Duration in days	Significance
With	37 (all moulted)	0	35	
Without	29 (19 moulted)	21	35	$p < 0.01$ (FEt)
Without	54 (all moulted)	13	50	

Number of paired females with either calcium deposits, indicating a forthcoming parturial moult, or already completed parturial moult or without recognizable moult signs 35 (50) days after pair formation at temperatures of 26°C. In the first experiment (Table I) 22% of the females without burrows became pregnant within 100 days, whereas in this experiment there were 81% within only 50 days. Apart from temperature all conditions were kept identical in both experiments.

TABLE V
Irreversible induction of parturial moult in paired females in relation to time spent with their males after pair formation

Isolation?	Moulted or calcium deposits	No moult indications	Significance
(a) Controls, partners not separated	20 (all moulted)	0	a:b $p < 0.01$ (FEt)
(b) Females isolated after 5–6 days	7 (2 moulted)	14	a:c $p > 0.13$ not significant (FEt)
(c) Females isolated after 13 days	10 (8 moulted)	2	

After isolation from their males females remained in their original burrow without contact with any conspecific. Figures represent numbers of females with either parturial moult or without moult indications at the 25th day after pair formation; average temperature 25°C.

semelparous, with no possibility of replacing any losses of progeny, and since choosing an early time for breeding is very advantageous in many respects (Linsenmair, in prep.), they should avoid time losses. Their sensitivity to increased mean temperatures points very clearly in this direction: high average temperatures ($> 25 °C$), which would in the field indicate an advanced season, stimulate the females' readiness to reproduce after hibernation so strongly (Table IV) that even the most important prerequisites for the induction of parturial moult at low temperatures — burrow ownership and a male partner — lose their significance greatly. Further loss of time then seems to be more critical than the danger of not finding a burrow and a male within the remaining two to three weeks from induction till actual moulting.

Females dependent on male burrowing would often lose time (Linsenmair, in prep.). Such behaviour could only be selected if the costs of digging were very high in terms of time, energy expenditure or reduction of survival probability. But there are no indications that digging for about half an hour per day in order to lengthen an *already owned* burrow, after timely primary acquisition of the den and after pair formation, is very costly or risky. Female *Hemilepistus* could — before parturial moult — build their burrows alone, but they would be unable to secure them for long. What makes the male partners, recognizing their own female individually, irreplaceable is their function as guards warding off all competitors. Thus, females need to spend little time on guard and can leave burrows for frequent excursions, without losing their vital retreats. Also generally they can stay in that part of the den offering the most favourable microclimate, thus considerably accelerating egg development (K. E. Linsenmair, unpublished).

Early in the breeding season the presence of an accepted male in the den influences the reproductive behaviour of its female positively in shortening the time between burrow acquisition and parturial moult. It seems obvious to expect that the male's presence promotes the female's readiness to copulate and that successful copulations induce the parturial moult, as this is the case in the Canarian *Porcellio* sp. and seems also to be usual in most other oniscids that are comparable to *Hemilepistus* in the timing of copulations within the moult cycle (Mead, 1976; Linsenmair, in prep.).

In pairs formed under laboratory conditions (temperature $21 \pm 1 °C$), five to eight days after terminating hibernation (at $10-12 °C$), first copulations occurred three to six days later. Separating females from their males at different times demonstrated that as little as five to six days after pair formation a third of the females showed irreversible induction of the parturial moult (Table V). But experiments with males

TABLE VI
Are successful copulations necessary prerequisites for the induction of parturial moult in paired females?

| | Females | | |
Gonopods of males	Moulted	Not moulted	Significance
Amputated	70	12	$p > 0.65$
			not significant
Intact	43	5	(χ^2)

Number of females — paired with intact or with gonopod-amputated males — performing parturial moults within 25 days.
All eggs of females paired with gonopod-amputated males were without a single exception unfertilized; average temperature 25°C.

rendered incapable of transmitting sperm by amputating the gonopods yielded no significant differences in regard to time of parturial moult and percentage of pregnancies in their females in comparison with control pairs (Table VI). This shows clearly that successful copulations are not required in order to induce the parturial moult.

The frequent copulations differ considerably in length and are distributed over a long period of time (Fig. 1). The durations of copulations are determined by the females (Linsenmair, 1979). As preparations of females have shown, little or no sperm is transmitted
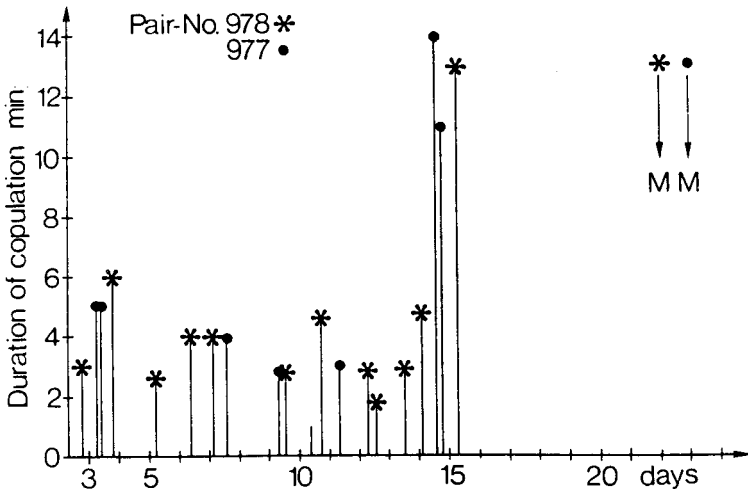

FIG. 1. Temporal distribution (abscissa: days after pair formation) and duration of single copulations (in minutes: ordinate) in two pairs — continuously video-observed — of *Hemilepistus reaumuri*. M: day at which parturial moult started. Average temperature 26°C. (From a total of 43 comparable, permanently observed, pairs in which the partners lived together undisturbed from pair formation until parturial moult, 36 showed a pattern of copulations in accordance with that presented in this Figure. Others showed various deviations, e.g. still allowing short copulations after the long matings, or admitting long ones as early as the first third of the copulation phase and then again at the end, etc.)

in copulations in which the video-recorded mountings of males lasted for less than 2–4 min. Long-lasting copulations are rare. Usually two such copulations in which large amounts of sperm are transferred to the right and left genital tract directly follow each other. After these prolonged matings most females lose their readiness for additional copulations, but only as long as they live together with their *own* males. After separation for 6–12 h a female will accept a new partner (until about one to three days before parturial moult). It then often permits long copulations as soon as 24 h after the new pairing.

Males in the field and in laboratory experiments never differentiate between females previously mated but not yet moulted, that have already permitted long copulations, and virgins, or females paired only for a short period that have no sperm, or only a little amount of sperm, in their receptacula (Table VII). Is this an indication that females only

TABLE VII

Do males discern females according to their stage within the moult and copulation cycle?

Females	Number of females with a new male after 24 h	Females without a new male after 24 h	Significance
4–7 days before parturial moult[a]	27	9	$p > 0.90$ not significant (x^2)
Virgin or recently paired females[b]	31	11	

In this field experiment males were removed from pairs in which the duration of pair living was known. Females remained in their original burrow. Burrows were checked 24 h after separation, new males were removed, and burrows checked again 24 h later. Females of the first group had without exception ended their normal copulation phase.
[a] Indicated by strong calcium deposits; long copulations had already taken place.
[b] Without calcium deposits; long copulations had not yet taken place.

or mainly use sperm from the last copulation (like some insects, cf. Parker, 1970) before the parturial moult, rendering discrimination by males superfluous? In preliminary experiments females paired with X-ray irradiated males (dose: 25Krad) produced only eggs with incomplete development which perished before hatching. Females paired for a part of the time with an irradiated and for the other part with a normal male always had, in their marsupia, a brood containing a fraction of normal developed embryos. Given a more or less perfect sperm clumping, great differences in the quantity of eggs yielding viable young would be expected according to whether females had been paired at first with the normal and then with the sterilized male or vice versa. But such

differences could not be detected. If these first still tentative experimental results (which will be repeated and also checked by using other methods like genetic markers and isoenzymes, cf. Sassaman, 1978) are not misleading (which seems very improbable), a male forming a pair with a female having already intensively copulated with its former male is at a disadvantage: it will raise alien offspring beside its own. Under normal field conditions losses of partners at any time within the reproductive cycle are not rare events and females accept and get new partners until shortly before parturial moult. Males seem, at this point, to be at a disadvantage, in gaining less from pairing with such females than the females themselves (but see below).

Transient Pair Formation in a *Porcellio* * Species from the Canary Islands

The *Porcellio* species have evolved — certainly in convergence with *Hemilepistus* — a social behaviour which parallels that of the desert isopod in many aspects (Linsenmair, 1979, in prep.). But there are also some important differences, e.g. males always try to be polygamous and never participate in brood care. Mating strategies vary according to the size of the male:

(1) Small males (average length: 15.8 mm, range 12–18 mm, $n = 127$) try to copulate forcibly with females which normally resist successfully. But a few of the smaller females allow matings which are long enough for transmission of at least some sperm. These males also enter burrows of unpaired females and try to mate there (with unknown success). Those pairs (in the field) stay together for not more than 24–48 h.

(2) The much rarer large males (average: 21.5 mm, range > 18–28 mm, $n = 37$), mostly form pairs for periods which in the field could not be determined definitely but usually exceed eight days. Under laboratory conditions these pairs stay together for 8–25 days (mean duration: 16 days, $n = 12$). In the field, such pairs live in burrows which are considerably longer (30.3 ± 3 cm, $n = 30$) and deeper (16.3 ± 5.6 cm, $n = 31$) then the usual burrows of this species (see p.437). These holes are normally dug by the males. Females joining these males in the field measured at least 14 mm; they were always at an intermoult stage.

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*The North African *Porcellio albinus* and three other closely related species living on the Canary Island of Fuerteventura show subsocial behaviour. So far these three species have not been formally separated and most probably are still undescribed (Hoese, in prep.). In the following account all statements refer to one very conspicuous, large, highly colour-polymorphic, mainly day-active species distributed over a small area of the Jandia peninsula.

The period of pair-living can be divided into three phases, according to results obtained in the laboratory (temperatures 22°C ± 1; Herlein, 1981; K. E. Linsenmair, unpublished).

In the first phase, (average length nine days)

(a) males carry large amounts of food into the burrow;
(b) males establish antennal or body contact with females for 6–18 h/day;
(c) males attempt to copulate, but females end these trials so quickly (average duration of mountings: 1.3 min, $n = 20$) that sperm transmission can hardly take place (see p.431);
(d) females spend much time outside the burrows to forage.

In the second phase (lasting four to seven days)

(a) males reduce their food collecting and spend more time in guarding the burrow;
(b) the pair copulates frequently (average: six times per day; mean duration: 3.6 min, $n = 50$);
(c) females reduce their outside activity, often to zero.

In the third phase (duration: five to seven days)

(a) males stop guarding the entrance, while females increasingly take over this task, temporarily blocking the entrance against their males too;
(b) direct contacts between male and female are considerably reduced; they are now mainly initiated by the female;
(c) females do not permit copulations but they still remain attractive to males;
(d) later the females lose their attraction to alien males, at which moment their own males desert them (on average four days before parturial moult).

Discussion: Considerations on the Evolution of Pair Formation

Among non-social oniscid species so far investigated, females allow very few copulations and only within a short period of time. Thereafter their attraction to males is quickly lost (Linsenmair & Golla, in prep.). In contrast to this, females of *H. reaumuri* and those of *Porcellio* sp. remain attractive to males for a comparatively long time (which can extend over more than two months in *H. reaumuri* — K. E. Linsenmair, unpublished) and they allow a much higher number of copulations. How have these physiological and behavioural changes been brought about and what could have been their initial adaptive value?

Sex-specific pheromones are usually responsible for sexual attraction in oniscids (e.g. Ducruet, 1976; Linsenmair & Linsenmair, 1971; Mead. 1976). Females starting the production of these pheromones earlier and/or stopping it later in respect to the time over which they admit copulations could attract males for a prolonged period, especially if in addition they were to change their time pattern of copulations (e.g. by shortening each copulation, allowing a higher number and distributing these over a lengthened span of time) as is the case in *Hemilepistus* and *Porcellio*. To develop such methods should pose no particularly difficult evolutionary problems, since nothing really new has to be developed; only time programmes have to be changed.

Hemilepistus females do not, unlike *Porcellio* sp., depend on successful copulations to induce the parturial moult. Hence females alone can determine the moment of induction and they can adjust the temporal pattern of the whole mating phase and the outcome of each single copulation according to their individual needs and conditions. The female "withholds" information about its physiological state, it "conceals" the latest time for successful copulations (Linsenmair, 1979; cf. also Alexander & Noonan, 1979; Strassmann, 1981; Wickler & Seibt, 1981). In a situation in which males lack nearly all relevant information about the physiological state of their female and in which they have little influence on its reproductive behaviour, there are no good choices left to them. The only promising way of attaining maximal reproductive success is waiting to secure all copulations of a particular female. Here females "meet males' wishes halfway" by copulating only at their own burrow and only with an individually known male. A male consorting at the right time with a female in a burrow and staying long enough is guaranteed mating privileges and thereby certainty of paternity as a payoff for its time commitment. The essential question remains: what selection pressures could have favoured such profound alterations from the conditions in non-social oniscids.

Supposing that living in open aggregations is phylogenetically an old behavioural trait of oniscids, we should first take this behaviour into consideration. What concerns the distribution of reproductive success among males within aggregations is unknown. Preliminary investigations (K. E. Linsenmair, unpublished) in several isopod species indicate a high variability of male success, some males copulating very frequently, others not at all. This is most probably the consequence of intrasexual aggressive encounters leading to dominance of a single or a few superior males within an aggregation, preventing the others from mating. Under these conditions there will be hardly any strong selection pressure on females to evolve an elaborate male-choosing behaviour, since choice is made by the males themselves.

If environmental conditions discourage large aggregations then a female cannot any longer "rely on the assumption" that a male, attempting to copulate, has already proved its superiority in many intrasexual disputes. Then the problem of choice arises. If there are no good criteria available, either because the ability to judge is not developed or because the choice is limited or in its scope unpredictable, one way of coping with this situation and trying to diminish the risk of a severe mistake (by admitting a wrong male with a low genetic quality) could be to reduce the share of fertilized eggs of a single male. Allowing many different males to copulate raises the variability within the progeny and therewith reduces the risk of a complete failure. If multipaternal siring of progeny is advantageous, females with a prolonged phase of attractivity and receptivity admitting more copulations should be favoured since their chances to meet different males are thereby improved.

This behaviour of females can be contrary to what is optimal for the reproductive success of males. When circumstances favour males which invest time in guarding a female (thus increasing their share of fertilized eggs compared to those males which use their time to search for new females) we should expect males to be selected to counteract the promiscuous behaviour of females. This could lead then to a new development. But this development could also have been an alternative straightforward route adopted during the assumed change from a gregarious to a more solitary way of life.

If males try to monopolize females this should often lead to competition between males and thus, by indirect means, allow females a choice of the best mate available at that place and time. This could prove better than an unselective promiscuous behaviour. Therefore, given some prerequisites, it is to be expected that those females should be favoured which "take advantage" of this possibility. The main prerequisites are:

(1) Females can only be monopolized through prolonged guarding, given that males are to consort some time before females are ready for copulation and/or given that females admit several copulations distributed over an extended period.

(2) Retreats are used to which access can be controlled by the male. (This seems necessary (i) since oniscids lack the sensory equipment to be aware at a distance of the location of a conspecific, its movements and interactions with other individuals, and (ii) since guarding females by carrying them for a prolonged period, as is very common in aquatic isopods and amphipods (e.g. Ridley & Thompson, 1979; Birkhead & Clarkson, 1980), is unsuitable in the terrestrial environment).

(3) Encounters between males searching for receptive females are not exceptional but relatively frequent events.

(4) Males fight for receptive females if they meet in the presence of such a female.

(5) Winning or losing fights reflects phenotypic differences in the quality of the opponents which will be caused — to some extent — by genetic differences (at least in so far as males with low genetic quality are excluded; see discussion of these problems, e.g. in Thornhill, 1980).

Given these prerequisites females should not "oppose" the monopolizing attempts of males. But they should be selected to postpone the *decisive* copulations to some time after consorting with the first male. Only by choosing to delay copulation for a time sufficient to allow competition between males to take place can the female be sure of admitting the male with the best fighting ability in the area. This correct span of time should among many other things depend on the average frequency of encounters of competing males at the retreat, on the mean number of potentially available males and on the usual amount of relevant variability within this subset of males and of course on other requirements of females and males which set an upper limit on expendable time.

The main assumption in this still rather theoretical hypothesis is that transient pair formation (as the assumed precursor of monogamy) in oniscids originally started with males trying to monopolize females during their receptive phase and then, as a next step, females using this situation for optimal mate choice. As soon as one or both partners gain additional advantages as a result of this temporary pair formation new selection pressures will arise, eventually shifting the essential adaptive values so fundamentally that the old ones can hardly be recognized any more.

Pair formation, as we see it at present in the subsocial Canarian *Porcellio* sp., can be explained without contradictions in terms of the male monopolizing and female choosing behaviour discussed above. Numerous observations in the field and in the laboratory have demonstrated that it is body-size, as in *Hemilepistus* (cf. Linsenmair, in press) which is the most important parameter for success or failure in an aggressive encounter of two males. As a rule, it is the larger male who wins. Therefore it is not surprising to find that only large males build copulation burrows and stay for prolonged periods with females, whereas small males follow a very different strategy (see p.432). Females — especially the larger — resist the copulation attempts of small males, but they consort "voluntarily" with large males. As we see there is an active component and not only indirect choice by male–male interactions in *Porcellio*. Since body-size and age are — as in many crustaceans — closely correlated in *Porcellio* sp., large males are also old males — and to select old males in good physical condition is always a good choice so far as it is a means

of avoiding all those males which owing to genetic defects are unable to survive for a long time (Halliday, 1978; Shuster, 1981). Since females consorting with such a male allow copulations only after some time and then in the beginning as a rule interrupt matings before males can transfer large amounts of sperm (see above) they can "scrutinize" the male's quality during this period. Only a male which is not inferior to one of its competitors can keep its burrow and thus the female. The male, sometimes helped by the female, provides the conditions suitable for a prolonged bonding of the pair: he constructs a burrow of exceptional length and depth which microclimatically is highly favourable as a refuge and he collects large amounts of forage which he carries into the den.

Contrary to *Hemilepistus* the *Porcellio* sp. female — because of important differences in ecological conditions (see below) — neither is particularly endangered during parturial moult or during pregnancy, nor has great difficulties in raising its young. These females are iteroparous and apparently follow no seasonally fixed breeding scheme, but a rather irregular, opportunistic pattern (most probably strongly dependent on the irregular rainfalls). They are far less synchronized than the semelparous *Hemilepistus* females. Therefore *Porcellio* sp. males normally have chances of finding a new female for many months of the year. Consequently it is to be expected that males would leave females soon after these have definitely lost their readiness to copulate, and this is what one observes.

Before further comparing pair formation of *Hemilepistus* with that of *Porcellio* a very important difference in habitat choice has to be pointed out explicitly. In contrast to *Hemilepistus*, *Porcellio* sp. and the other related subsocial Canarian and North African *Porcellio* species live on and in sand-dunes or light sandy soil. Into this ground burrows can be easily and quickly dug. Under the relatively mild climatic conditions of the Canary Islands most burrows reach a depth of less than 10 cm and a length rarely exceeding 15–20 cm (with the above-mentioned exception of copulation and breeding burrows). Not only are these burrows built in a fraction of the time with a fraction of the energy required to construct the den of *Hemilepistus* (reaching 40–95 cm in depth and between 1 and 3 m in length) but, still more significantly, the burrows of the Canarian *Porcellio* can be excavated at any time of the year. Burrows therefore should be less valuable for *Porcellio* and apparently they are, since competition for them is far less intense and means other than direct physical defence play a part in securing them: breeding dens of *Porcellio* sp. are to some extent protected by secretions with a repellent effect on most potential competitors (Linsenmair, in prep.).

There is still another essential point to which attention has to be paid: the burrows of *Porcellio* have a shape considerably deviating from those

of *Hemilepistus* owing mainly to properties of the sand and less importantly to differences in the burrowing behaviour. While a *Hemilepistus* which fits its burrow entrance and which is in good physical condition is practically invincible to any intraspecific intruder, however superior in strength, this is not so in *Porcellio*. The relatively large width of the den and properties of the sand make it impossible for a *Porcellio* to defend its den successfully against a superior competitor. Consequently the probability of intruders evicting burrow owners is very different in the two species, and besides this in *Porcellio* a burrow is not yet definitely lost when an alien has entered it, whereas this is usually the case when an alien *Hemilepistus* has succeeded in achieving a position in the burrow below the original occupier.

In comparing *Hemilepistus* with *Porcellio* many similarities in the basic features of pair formation can be found, but — besides those already mentioned — further differences exist which can be seen as special secondary adaptations to different ecological conditions, derived from a preceding state of a temporary pair formation fully comparable to that of *Porcellio* sp. Contrary to *Porcellio* sp. living in the Canaries in climatic conditions characterized by little predictable seasonal change, *H. reaumuri* dwells in an environment with very pronounced seasonality of climate (profoundly affecting food and moisture). It has had to adapt to these changing conditions during the annual cycle by following a seasonally fixed pattern of reproduction with the consequence of females being rather well synchronized.

Females of *Hemilepistus*, in the course of their evolution, gave up the usual iteroparous behaviour of most oniscids (Warburg *et al.*, 1984). They are strictly semelparous without any chance of replacing reproductive losses (Linsenmair, 1979, in press). Only paired females with their males surviving for some weeks after birth of their progeny have good prospects of rearing a brood. Females can replace lost males only up to about two to three days before parturial moult, whereas males have a chance of replacing a female for a further four to six weeks (if their first pair formation took place early in the breeding season — see below). Since females have less chance than males to replace partners one would expect them to make the initial choice of mate very carefully. Females of *Hemilepistus* cannot select males by any direct criteria. Only males encountering each other outside a burrow fight on equal terms (see above). A female therefore has to employ methods differing from those of *Porcellio*. She will have the best choice if she starts digging a burrow and chooses by delayed admittance. She should start as early as possible, since the earlier she ''looks'' for males the fewer males are already paired and the more males are interested in consorting with the female and fighting with competitors. Besides this an early female is not in a hurry.

she waits longer until admitting a male than females later in the season, and additionally early breeding yields many further advantages (Linsenmair, in prep.). This most probably explains why — contrary to *Porcellio* — it is females which start digging dens.

The further advanced the season, (1) the less the possible choice, since most of the preferred males are then paired and (2) the more important the burrow, as sudden sandstorms with high air temperature and very low relative humidities endanger isopods without protective retreats. For females starting pair formation very late in the season, it then should be often more profitable to consort with a male which already owns a burrow. Most of these males have lost their females by accident and have already passed through the sieve of intrasexual competition. Therefore they should be good choices, often much better than males still searching around which will frequently be those defeated in previous fights. (Those males which were not admitted by a female but found an empty burrow, conquered one, or dug a burrow themselves probably also had to fight with competitors and they can in any case offer the female a den and help her save some time, risk and energy.)

These assumptions about how females should behave are supported by observations in the field. With advancing season females spend increasingly more time trying to get admittance to burrows owned by males (Linsenmair, in prep.) and preliminary data suggest that four weeks after the very first pair formation within a population about 20% — and within the last two weeks of this phase more than 50% — of the unpaired females join males owning burrows. (This explains why males only start to dig new burrows later in the reproductive season and never during the very beginning.)

The most important difference in male behaviour between *Porcellio* sp. and *Hemilepistus* is that the latter is strictly monogamous. Why do *Hemilepistus* males not try a simultaneous or successive polygamy to maximize their reproductive success? As already stressed the main advantage to the females of consorting with a male is most probably the readiness of the male to guard the vital burrow, not only against competitors of its own sex but, and this is decisive for the female, also against alien females. Why does a male deter potential sexual partners?

With rare exceptions adult females encountering each other at the entrance of or in a burrow are very aggressive towards each other. They will always fight until one is driven off from the den; probably partly because dispersed dwelling lessens the probability of overgrazing, and partly because the first female to release her young normally would risk them being cannibalized by the other female, since a female accepts alien newly released young only if she is releasing her own progeny within the next few hours (for details see p.444 and Table XI). This would

require a degree of reproductive synchronization between females which could hardly ever be achieved.

Admitting a second female, while the first is in the burrow, would cause combats which normally the first female would win. These aggressive encounters would often last a long time since inside the burrow the defender is at less of an advantage than at the entrance. The disturbance leads to time losses for the first female, which are disadvantageous for the male too. Admitting the second female while the first is foraging would normally lead to an exchange of females. Would this benefit a male on average? Under most conditions certainly not (cf. Linsenmair, 1979). There is a considerable time investment on the part of the male until the female is ready for those copulations in which large amounts of sperm are transferred. A female in search of a burrow and a male is normally still in the initial phase of its reproductive cycle, demanding from the male a full investment of time which he has already partly committed to his first female. Therefore an exchange of females would in most cases involve loss of time and offer no advantages at all. It could only benefit a male if the second female were more advanced in her reproductive cycle without offering at the same time only reduced reproductive prospects. A male would have to be able to recognize these criteria and to discriminate between females according to their reproductive stage and reproductive value, which he obviously cannot do (see below).

A female losing its partner after parturial moult has nothing to offer a new male. It is therefore always left to its own, normally insufficient, devices. But before parturial moult a female which succeeds in attracting a further male after loss of the first one should be greatly favoured even if this were unnecessary for fertilization of her eggs. This in fact females achieve: formerly paired females are, up to a few days before their parturial moult, as attractive to alien unpaired males as virgin females, which is not so in *Porcellio* females (Linsenmair, in prep.). The expectation that these females should then offer the same reproductive chances to males as virgins is not met. As the preliminary experiments with X-ray irradiated males show, the sperm of the new male are not preferentially used (see above).

This still tentative result raises two questions.

(1) Would it not pay males to leave their females shortly after the long copulations to try to find a further, still unpaired female? It would, of course, if they were able to more than compensate for the losses. To achieve this males would have to have thorough knowledge of (A) their female's reproductive condition and (b) their own chances of finding and recognizing a second female still offering good reproductive prospects. Leaving would only then benefit males if their females allowed

long copulations well before parturial moult and only in cases of early
pairing. Late females — within their own as well as within the population's
cycle — would only have a very limited probability of finding and securing
a second male. The same is true — *mutatis mutandis* — for males. There
are no indications that males possess any of these necessary abilities.
As females vary their copulation patterns (Linsenmair, 1979), that
described above being only the most common scheme, males without
the required sensory capacities would make many costly mistakes, leaving
too early or too late. Therewith they would incur high average losses
in terms of missed fertilizations: they often would leave more than 50%
of fertilizable eggs to their successor. These losses cannot be compensated
for by pairing with (an) additional female(s), since males have only about
a 10–50% chance to reach the same stage at which females allow long
copulations for a second time (K. E. Linsenmair, unpublished
observations; cf. Shachak, 1980, for survival probabilities within different
phenophases in the Negev population). Therefore we cannot expect
selection to favour a mate-deserting behaviour — and we have never found
any indication that it exists.

(2) The second question is: Why do males, when they still have the
choice, accept females which offer only a considerably reduced
reproductive success with the same readiness as they accept females with
better prospects? Most probably males are simply not able to distinguish
the latter from virgin females or those paired females which have not
yet allowed long copulations. But in order to decide whether or not this
is maladaptive behaviour of males, additional aspects have to be taken
into account (e.g. better survival probability of the late female due to
the shortened period until parturial moult; advantages of earlier birth
of the young of such a female; male's prospects, average time expenditure
and risks when continuing to search). As the data base is not yet solid
enough these points cannot be answered definitely.

A male leaving its female during parturial moult or early in pregnancy
would be even worse off from the point of view of leaving progeny. He
would incur nearly a 100% rate of loss, for two reasons. (a) Females
are greatly hampered by their brood pouches in carrying out burrow
defence and alone they are nearly always expelled (Linsenmair, in press).
(b) They show extremely high mortality even when protected against
competitors. This is true under laboratory conditions and most probably
in the field too. In a laboratory experiment 18 out of 20 females, left
in their burrow but isolated after parturial moult from their males, died
before release of their young or too early after birth for their progeny
to survive on their own. Their sisters, in the control experiment, survived
the same period in a proportion of 20 to 1. Given the near 100% risk

of the loss of all investment it can be predicted that a male should not leave its female during pregnancy, because these losses can never be compensated. All observations support this prediction. Males paired with their female not less than four days before parturial moult never left her "voluntarily" during this moult or during pregnancy. Could males desert their females after release of the young? If they were to leave during the first eight to 14 days after birth they would — on average — lose about 40% of their progeny (Linsenmair, 1979 and unpublished); waiting somewhat longer would further diminish losses. Then deserting the first female could be a profitable strategy, if the male still had a reasonable probability of finding a new female. But in that time within the reproductive phase even males of the very early pairs would have only a minimal chance of still finding an unpaired female offering any promising prospects for reproduction, owing to the synchronization of the females (see above). Therefore compensation of even slight losses would be too rare an exception to allow for a positive selection of such behaviour.

Overall, physiological and behavioural mechanisms of the females, originally probably developed for a transient pair formation in connection with mate choice on the one hand and ecological requirements of the extreme living conditions on the other, have made males of *Hemilepistus* strictly monogamous and rendered polygamy unprofitable.

CHEMICAL COMMUNICATION WITHIN FAMILIES OF *HEMILEPISTUS REAUMURI*

The Family Badge: Variability and Origin

Besides the individual recognition of pair partners in *H. reaumuri*, family members can distinguish between strangers and kin. Alien isopods are in some situations avoided, very often they are attacked and never are they allowed to enter the family burrow, whereas members of the family itself are completely unaggressive towards each other whenever and wherever they meet (Linsenmair, 1972; cf. Schneider, 1971 for *H. aphganicus*). To discern between kin and aliens chemical "discriminators" (Hölldobler & Michener, 1980) are used, identified by a pair of contact chemoreceptor organs, the "apical cones" on the tips of the second antennae (Krempien, 1983; Schneider, 1973; Seelinger, 1977; see Holdich, 1984, for other species).

There is such a high variability in the family-specific badges that even well over 50,000 tests have up to now failed to detect two families with completely identical discriminator-sets. The chemical badges which have

been studied intensively (Linsenmair, Schildknecht & Esswein, in prep.) owe their specificity to genetically determined secretions (Linsenmair, 1972, 1975, 1979, in press). Body odours originating from the environment are of negligible effect.

The Recognition of Offspring

A normal, i.e. not sex-linked, transmission of the genes responsible for these discriminator substances must engender problems: e.g. parents could hardly know the badge of their own young before birth. Small strange young are generally not only driven off from the vicinity of the burrow, but hunted and eaten. If one is prepared to eat neighbour's children, one must be sure of recognizing one's own.

If parents are isolated from their young immediately after release and put back 24–70 h later they always cannibalize them (Table VIII).

TABLE VIII

Reactions of parents, separated from their own progeny immediately after release, towards own and strange young of different age

Encounters with	Number of parents attacking	Number of parents not attacking[b]	Significance
Own young > 24–70 h old	13	0	
			$p < 0.001$ (FEt)
Strange young ≤ 6 h old	$(6)^a$	34	

Separations were performed at the latest one hour after release of own young; duration of separations 24–70 h.
[a] All six adults which were aggressive against these young (≥ 6 h old) attacked only lightly and only at first encounters.
[b] An adult was categorized as not attacking if no aggressiveness could be detected in at least 20 contacts with different young.

But, if one brings these parents into contact with alien newly released young not more than six hours old, the great majority show no aggression at all, irrespective of where they meet the young (Table VIII). These results are clear-cut: own progeny are neither recognized before birth nor are the young recognized site-specifically. What then protects the newly released young?

Normally alien badges induce aggression. Do the newly released young lack such badges? The discriminators *Hemilepistus* uses are easily transferred between individuals by direct body contact (Linsenmair, 1972). If members of different families exchange discriminators, their badges are changed and they become alien to their families.

If family-specific discriminators are absent in the newly released young, they should be unable to render older young alien, when forced into close contact, whereas they themselves should be alienated from their families. As it happens, just the contrary occurs (Table IX). The older young become completely unacceptable to their unaltered kin. The newly released young remain fully accepted and protected. Obviously newly released young already possess discriminators, but their aggression-releasing effects are somehow inhibited.

TABLE IX

Are newly released young H. reaumuri *devoid of family-specific badges?*

Age of young	Number of single attacks of (n) parents	Number of encounters without attacks of (n) parents	Significance
5–12 h	0	303 (n = 10)	
6–21 days	211 (n = 11)	23 (n = 2)	$p \ll 0.001$ $(\chi^2)^a$

The young of two families were put into small vials for 35–100 min and thus forced into very close body contact. Since the young at these ages differ considerably in length and colouration experimental marking was not necessary.
[a] Fisher's Exact test is not feasible with these numbers, therefore a chi-square test was used (and the 0 was replaced by a 4).

Which conspecifics are inhibited by these properties (presumably inhibiting substances)? No inhibition could be demonstrated in young *Hemilepistus* and in adults which are not already parents or about to become so. Those already parents—for a period not longer than four to six weeks—and those becoming parents in the near future are inhibited. It is no great surprise that paired males, owing to their lack of information concerning, e.g. time of birth of their young, are more tolerant than females. Males, in order not to cannibalize newly released strange young, have to have copulated and they must have lived at least 14 days together with a pregnant female. They then always accept young less than six hours old and very often those not older than 24 h (Table X). Females are much more critical (Table XI). They can certainly perceive whether their young are already hatched from the eggs and are close to leaving the brood pouch or not. A reliable 100% tolerance to newly hatched strange young in all females is confined to only the last 2–4 h before their own young are released.

The (assumed) aggression-suppressing substances show still further effects. Not only do those adults affected by their inhibiting properties become unaggressive towards the newly released young immediately after their first contact, but also—after spending 1–3 h with newly released

TABLE X

Reactions of paired males[a] encountering alien young of different ages

Age of young	Number of males attacking	Number of males not attacking[b]
	(n) = number of single encounters	
≤ 6 h	0	26 ($n = 693$)
6–24 h	9 ($n = 105$)	18 ($n = 417$)
> 1–6 days	21 ($n = 283$)	1 ($n = 23$)

[a] Males used in this experiment lived for at least 14 days together with their respective females after these had terminated parturial moult.

[b] Only males showing not a single attack in all (at least 20) encounters appear in this category.

TABLE XI

Reactions of pregnant females (i.e. carrying eggs or mancas in marsupium) in encounters with alien young of different ages

Females: days before releasing own young (from marsupium)	Age of strange young	Number of females attacking	Number of females not attacking	Significance
		(n) = number of single encounters		
(a)	6 h	23 ($n = 164$)	8 ($n = 311$)	
(b) ≥ 1	6–24 h	21 ($n = 150$)	2 ($n = 68$)	
(c)	24 h– 6 days	12 ($n = 131$)	0	a:d $p < 0.05$ (χ^2)
(d) < 1	6 h	3 ($n = 15$)	7 ($n = 222$)	

Aggressive females, due to release their young 6–12 h later, could in all cases be detected, because they showed — mostly during their first contacts with the alien newborn — obvious signs of inhibition of aggressiveness. Females which released their young more than 24 h later also showed signs of inhibition and 26% of females in (a) were not aggressive at all (six of them giving birth to their own young 48–80 h later).

TABLE XII

Reactions of parents towards alien young 2–10 days old in relation to the age of their own young

Age of own young	Age of strange young	Number of parents attacking	Number of parents not attacking	Significance
		$(n$ = number of single encounters)		
(a)* < 6 h	2–10 days	6 ($n = 141$)	16 ($n = 396$)	$p < 0.001$ (FEt)
(b) > 2–6 days	2–10 days	26 ($n = 274$)	0	

*In this experiment parents were kept together with their young for 1.5–3 h.

young—they become unaggressive towards older alien young (≤ 10 days of age) which they otherwise always attack and kill (Table XII). The inhibiting substances also seem to interfere with learning. In spite of touching the young very frequently, these can be exchanged with aliens of the same age for 18 and often even up to 48 h after birth (Table XIII) without recognizable reactions of the parents. Does *Hemilepistus* need such a long time, involving many hundreds of single contacts, to learn a badge? This is most unlikely, since in adoption experiments (Linsenmair, 1972) and during pair formation they can learn much faster with fewer contacts.

TABLE XIII
Reactions of parents towards alien young of the same age as their own progeny

Age of own and alien young	Number of parents attacking	Number of parents not attacking
	(n) = number of single encounters	
> 6–18 h	2(n = 30)	15 (n = 306)
> 18–48 h	10 (n = 111)	10 (n = 309)

It therefore seems that this retardation of learning is a special adaptation, its probable value being as follows. The badge substances are distributed all over the body (Linsenmair, 1972) including the brood pouches. In the latter the young after hatching get contaminated with substances produced by their mother. Since adding substances to a badge changes its character considerably, parents cannot learn the pure badge of their progeny before the loss of the maternal substances. Because of the extremely low volatility of the discriminators (Linsenmair, 1975 and unpublished), they can only be lost by moulting. As definite learning takes place in a period lasting from about 18–60 h after birth, in most cases not only a first but a second moult has taken place before learning can be demonstrated.

If inhibitors resemble discriminator substances in their volatility, their disappearance would indicate the moment after which the young bear a pure badge. This then could release learning in the parents.

Individual Variability in Badge Production and Intrafamilial Communication

Since badges (both family- and individual-specific) are always mixtures of different chemical compounds, a multi-locus system (with at least a few alleles per locus) is to be assumed (Linsenmair, in press). In *Hemilepistus* special behavioural mechanisms guarantee outbreeding

(Linsenmair, in prep.). Under natural conditions male and female originate — with very few exceptions — from different families. Given outbreeding, high genetic variability and normal autosomal inheritance of the relevant genes within progeny, variability in the production of badge substances must be expected. How then is the common badge of a family achieved? It obviously exists, as is shown by, for example, adoption experiments: parents forced to adopt alien progeny need only to get acquainted with a portion of the young in order to accept — after a while — the remainder (Linsenmair, 1972). If *Hemilepistus* were able to alter the pattern of produced badge substances to conform with the chemical environment that it perceives via its chemoreceptors, there could be a secondary "agreement" on a common badge within a family community, e.g. by every member confining its production to the smallest common denominator. Then (a) an elimination of the relevant chemoreceptors should have an effect on the badge production and (b) the most clearcut and more predictable results should be expected by forcibly integrating single isopods into alien families* with differing family badges.

After being forced to live for weeks in alien families, these isopods were removed — shortly before a moult — and kept in isolation until moulted. Then they were tested both in their genetic and in their foster-family. The results are summarized in Table XIV.

If the "agreement hypothesis" were right, the integrated individuals should have changed their production, adjusting it to the new chemical environment. Therefore — after moulting — they should be acceptable to their foster rather than to their original genetic family. Just the opposite happens, pointing very clearly to a fixed production pattern, which is not influenced by a changed "discriminator environment". In control experiments with young newly released from brood pouches identical results were obtained.

If inter-individual differences exist, a common badge within a family-community could be achieved by mutually exchanging and mixing all individual substances. This in fact was demonstrated (Linsenmair, 1972, 1975, in press, in prep.).

Because of the very low vapour pressure of the badges it is only by direct contact that these substances can be exchanged. This should cause communication problems: every isopod will, by moulting, lose all those compounds it does not produce itself. This changes its badge and leads, as in experiments like those summarized in Table XIV, to strong alienation. How are isopods which deviate from the norm in their badge production treated if moulting within their foster family?

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*Under certain experimental conditions, especially by forcing the isopods into very close direct contacts, integration of aliens is possible without releasing aggression which threatens survival.

TABLE XIV
Is the production of discriminators influenced by the "badge environment"?

Moulted	Where tested	Attacks		No attacks	Significance
Not yet moulted; (a) test immediately after removal from the foster family	In its original original family	192^a	$(n = 11)^b$	3	a:b $p \ll 0.001$ (χ^2)
(b) Moulted	In its original family	164	$(n = 22)$	879	b:c $p \ll 0.001$ (χ^2)
(c) Moulted	In foster family	522	$(n = 17)$	92	

Reactions of kin members of the foster family towards individuals which had been integrated for 4–8 weeks into foster families. Integrated individuals were removed from their foster families about 24 h prior to the beginning of ecdysis. During moulting they were completely isolated in containers without any contamination by conspecifics. Test 36–60 h after ecdysis completed. (For explanation of the result, see text.)

[a] Number of observed reactions.

[b] Number of tested isopods.

The experiments summarized in Table XIV give valuable hints. Isopods which had been integrated into alien families for a period of about eight days or more could perform moults without being attacked. Isolating them before a moult and replacing them 36–60 h after completion led in most cases to severe attacks. In repeating this experiment with members of pure families, i.e. those without integrated aliens, the following result was obtained: 80% ($n = 99$) were accepted after replacement without any aggression, 20% ($n = 27$) released attacks. Conditions during the isolation experiments were identical for all individuals. In a few cases two sibs of the same pure family were isolated jointly in the same container. One became alien, the other remained familiar, showing especially clearly that the alienations were not caused by exogenous influences but by differences in discriminator production.

What protects those individuals which would—after a moult in isolation—be treated like alien individuals from being attacked if they stay during moult within their group? The experiments aimed at answering this question used either strange young, integrated into foster families at least eight days before moult, or parents which normally differ considerably in their badges from the common badge of their young (details will be described elsewhere). If these individuals were taken out of their community a few hours prior to the beginning of the moult and replaced not later than 6–16 h after complete ecdysis, most of them were accepted without aggression. The majority of isopods left in isolation for a longer period after their moult released attacks.

TABLE XV
Reactions towards alien newly moulted conspecifics

Time between stripping off one hemiexuvium and test	Number of tested newly moulted individuals	Attacks[a]	No attacks[a]	Significance
(a) 1–14 min	20	124	397	
(b) 14–30 min	23	171	419	a + b:c + d
(c) 30–60 min	23	249	331	$p \ll 0.001$ (χ^2)
(d) 1–3 h	9	149	40	

[a] Number of observed single reactions released in the control animals after touching the newly moulted body half of the test isopods.

In their production of badge substances deviating individuals obviously enjoy a temporary protection. Is this a common property of all newly moulted *Hemilepistus*? It is easily shown that this assumption is false (Table XV). But these tests yielded valuable indications as to the nature of the transient protection. Very often, after touching a newly moulted part of the strange test animal, controls showed clear signs of inhibition: e.g. quickly withdrawing the antennae, retreating some steps, suddenly stopping an already started attack. Nevertheless, the inhibition dwindled within the first minutes of contact and aggressiveness quickly increased. Test animals not removed were then cannibalized.

Obviously not only the newly released young but also the newly moulted *Hemilepistus* have inhibiting properties. But in the newly moulted these show their inhibiting effect reliably only in connection with a certain badge. Only if the individual has already lived before its moult for a period of at least some days in the community is it acceptable. It is obviously essential that every family member has had sufficient opportunity for direct contact with the individual concerned. In spite of the extensive mixing of badge substances individual traits of deviating community members remain detectable. These individual traits have to be learned. Neither this learning nor the inhibiting substances alone guarantee a newly moulted individual, deviating far from the norm of the community, absolute protection. Learning and inhibition must act in unison. A complete glossing over a badge of a deviating animal within a family or a mixed group of the size of a family is impossible (Linsenmair, in press).

Discussion: Why are Family Communities so Strictly Closed?

The basic problem is easy to recognize and the fundamental answer to the question is in the light of our present sociobiological knowledge trivial.

All the benefits the social unit offers to its members are of course costly. In order to be selected they have to have a corresponding pay-off. This pay-off is to be found in an enhancement of the direct or indirect component of the inclusive fitness of the performer (Hamilton, 1964a,b). Brood-caring activities and similar social acts executed to the direct advantage of a recipient have to be confined to kin (or to individuals which reciprocate (cf. Trivers, 1971)). The family community has to protect itself against being parasitized by genetically alien conspecifics. If the young of *Hemilepistus* were — during the whole period of brood-care — "altricial", dispersing from their parental burrow on their first excursion and being thereafter no longer dependent on brood care by their parents and sibs as is the case in one of the Canarian *Porcellio* species (Linsenmair, in prep.) it would be sufficient for parents to be able simply to recognize their own burrow and to deter every conspecific coming to the entrance except their partner. Since the young, when starting to seek nourishment for themselves, are still dependent for weeks on the food gathered and protection offered by their parents and since they co-operate intensively later on, the family community must have a better means of discriminating between its members and aliens trying to enter the burrow.

Many social insects have solved the same problem by using body odours which to a great extent originate from the environment (see summaries in Wilson, 1971; Hölldobler & Michener, 1980). Considering (a) the high population density — up to 14 families with progeny have been counted in especially densely populated areas on a single square metre — and (b) the more or less complete overlap in the foraging areas of neighbouring families, one can easily see that *Hemilepistus* has had to find another solution. The genetically determined persistent and highly variable badges *Hemilepistus* produces are an excellent answer to this need. The problems they bring about through their variability and genetic fixation are reliably solved through the use of inhibitors which produce their effects only under special circumstances.

Attributes of the badges on the one hand and a highly evolved learning ability and a good memory on the other hand allow for an intrafamilial communication of great efficiency. These attributes of the badges not only enable *Hemilepistus* to form strictly closed units but, beyond that, they compel the community to remain completely exclusive. Body contact with an alien leads to mutual exchange of badges resulting in a changed badge which is acceptable to neither family. Admitting only a single strange isopod into a family would therefore lead to alienation of a number of family members without rendering the stranger familiar. Since these altered family members are not distinguishable from strangers, either control of access has to be completely abandoned or family

members have to be thrown out. This most probably is the reason why family communities remain absolutely closed when ecological and sociobiological conditions would not prohibit the admission of single aliens.

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