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Zoologia. — *Relations between social status and activity toward the sea anemone* Calliactis parasitica *in the hermit crab* Dardanus arrosor(*). Nota(**) di DANILO MAINARDI(***) e ALESSANDRO C. ROSSI(***), presentata dal Corrisp. S. RANZI.

RIASSUNTO. — Viene dimostrato, nel *Dardanus arrosor*, un rapporto fra la competizione per lo stato sociale ed il possesso delle attinie *Calliactis parasitica*. L'esperimento, su 52 paguri, ha avuto due fasi: 1) osservazione dello stabilirsi delle gerarchie in gruppi di due individui; 2) osservazione della distribuzione delle attinie assegnate loro fra il predominante ed il sottomesso di ciascuno dei gruppi di due paguri. Dalla prima fase è risultato che si stabilisce spesso una gerarchia anche in assenza di attinie e che si manifesta un atteggiamento di sottomissione tale da esercitare una inibizione incompleta della aggressività del predominante. La seconda fase ha messo in evidenza che il possesso delle attinie assegnate è prerogativa solo del predominante che impedisce la attività del sottomesso nei gruppi di due paguri. Una volta che però il predominante sia allontanato dall'acquario, anche il sottomesso si appropria delle attinie.

One of the best known cases of symbiosis between two animals surely is the association of hermit crabs with sea-anemones. Considering the interest of these associations and their widespread occurrence, it is surprising how many aspects of the lives of the partners are still obscure. Nevertheless since the times of Gosse [1] the binding together of these animals has been investigated by a number of workers and they have become standard examples of commensalism [2, 3, 4]. More recent works remind that these are not simple two-way partnerships in which only crabs and sea-anemones are involved. There is a third factor in the association, the shell, which seems to provide the basic element in the behaviour patterns that bind these animals together [5, 6].

The classic interpretation of the relation between the hermit crab and the sea-anemone is based on the mutualism and the commensalism, which are bilaterally advantageous symbiotic associations. The crab in fact should be defended by its actinian in two ways: directly, owing to the presence of cnidocysts and exploiting the mimicry through a kind of warning coloration. On the other hand the actinians are actively transported (phoresy), with considerable increase of their food resourches. Old data [7] lately confirmed [8], testify that *Pagurus prideauxi* feeds its *Adamsia palliata* placing food in the anemone's mouth with its claws. It is yet to be noted, in the interpretation

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of these symbiotic associations as mutualistic and commensalistic, that the very different behavioural patterns underlying this kind of relations have seldom been considered. On the contrary it is interesting to notice the range of the behavioural patterns of the various crabs and anemones in establishing the relation. *Pagurus prideauxi* is quite active toward its anemone *Adamsia palliata* and is able to transport it from shell to shell. Only some individuals of *Dardanus arrosor*, the so called "performers" [6], seem to be active toward *Calliactis parasitica*. In most cases the crustaceans, i.e. *Pagurus bernhardus*, passively accept the activity of the coelenterates, without interest for them [9].

The behavioural mechanisms underlying the activities of *Dardanus* in seeking out, releasing and resettling the anemones on the shell were observed by Cotte [10]. Faurot [11] later stressed that *Calliactis* does more than simply lend itself passively to the manoeuvres of the crab. After describing how the crab stimulates the anemone's column and base, he noted that the anemone's tentacles adhered to the shell and that after detaching, it somersaulted on the shell.

In the fig. 1 is shown the series of postures assumed by an active *Dardanus* during the transferring of a sea-anemone *Calliactis parasitica* from an empty gastropod shell to its one. Now, if a crab is so interested and active toward

a *b* *c*

Fig. 1. – Three phases of the transferring of *Calliactis parasitica* by *Dardanus arrosor*.

actinians, it seems reasonable to think that it must obtain at least some advantages from owning them. On the other hand the relations in which the crab species are indifferent to actinians do not provide the same kind of inferences on the existence of advantages for these crustaceans. The same reasoning may be transferred from the species level to the population one, that is, in other words, if the crabs show a specific activity directed to owning actinians (in this case intraspecific competition), this may be considered as an indication of the existence of an advantage, for the crabs, in owning them. So, we have sought a possible link between social status (in an at least partially active species: *D. arrosor*) and possession of sea-anemones (*C. parasitica*). For this purpose our experiment consisted of: 1) observing the establishment of hierarchies in groups of two hermit crabs; 2) giving sea-anemones to the hermit crabs and observing their distribution between the dominant crab and the submitted one.

The experiments were performed in glass tanks (cm 40 × 16 × 21), with filtering apparatus, divided in two sections by a movable plastic screen (fig. 2), on 52 *D. arrosor* trawled in the Tigullio gulf, in front of Santa Margherita Ligure. In each compartment a crab was placed deprived of its sea-anemones. The crabs' choice and destination were made at random and we obtained the following assortments: 8 pairs female/female, 5 pairs male/male and 13 pairs male/female. When both the crabs gained confidence in their area, the screen was removed.

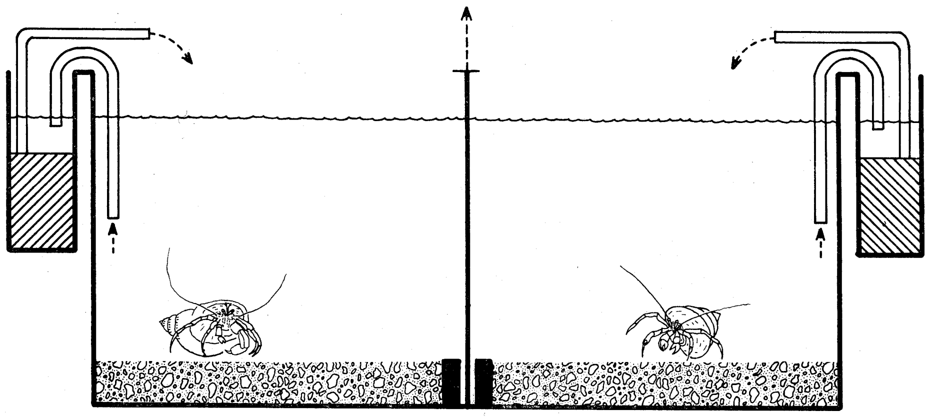

Fig. 2. – Experimental set for testing the dominance relationships. (for details see the text).

In 15 pairs the hierarchy was clearly established, through fights, before placing actinians in the aquaria, whereas in other 9 pairs the competition for the first actinian was the cause of the fights, which too ended in well fixed hierarchies. In the 2 remaining cases (both male/female pairs of nearly equal size) a stable hierarchy was never established, and one of the crabs alternatively acted as dominant (in the Table I; the attachment times of the actinians for

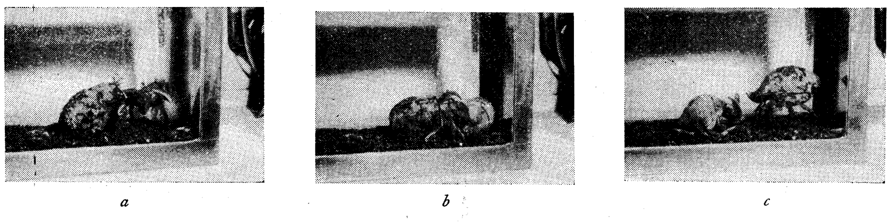

Fig. 3. – *a*) Initial fighting of one pair of *Dardanus arrosor*. *b*) Forced submissive posture assumed by the submitted crab (right). *c*) Spontaneous submissive posture assumed by the submitted crab (left).

these two cases were not computed in the statistic analysis). In the Table I are reported the species of the shells inhabited, the sex and the size of each crab and the final settlement of the social order in every pair. In most cases the competitions ended with the dominance of the larger crab. During the initial fighting which established the dominance relationship between the two crabs, the submissive posture did not occur (fig. 3*a*). The defeated crabs

TABLE I.

Dominance relationships and activity toward the sea anemone Calliactis parasitica *in the hermit crab Dardanus arrosor.*

DARDANUS ARROSOR ●			DARDANUS ARROSOR ○			DOMINANT CRAB	ATTACHMENT OF THE ACTINIANS BY THE CRABS							
							By the dominant in each pair						By the submitted alone	
Sex	cm (*)	Inhabited Shell	Sex	cm (*)	Inhabited Shell		I t	II t	III t	IV t	V t	VI t	I t	II t
♀	8.5	Murex brandaris . . .	♀	7.4	Cassidaria echinophora .	● (1)	● 55	● 12	● 30	● 8	● 17		○ 9	○ 14
♂	6.9	Cassidaria echinophora .	♂	6.2	Murex trunculus	● (2)	● 20	● 7	● 9	● 13	● 24		○ 5	○ 8
♀	7.0	Cassidaria echinophora .	♂	6.5	Cassidaria echinophora .	○ (1)	○ 6	○ 8	○ 6	○ 15	○ 29		● 12	● 10
♀	7.8	Cassidaria echinophora .	♀	8.2	Cassidaria echinophora .	○ (2)	○ 32	○ 14	○ 21	○ 40			● 9	● 13
♂	8.0	Cassidaria echinophora .	♀	7.8	Cassidaria echinophora .	● (1)	● 10	● 9	● 10	● 23	● 31		○ 5	○ 6
♀	8.1	Cassidaria echinophora .	♀	8.2	Cassidaria echinophora .	○ (2)	○ 5	○ 16	○ 13	○ 20	○ 26		○ 13	● 10
♂	6.7	Cassidaria echinophora .	♂	6.3	Murex brandaris . . .	● (2)	● 8	● 10	● 6	● 38			○ 21	○ 8
♀	9.5	Cassidaria echinophora .	♂	7.0	Cassidaria echinophora .	● (1)	● 8	● 21	● 18	● 12	● 16	● 32	○ 7	○ 9
♂	6.8	Cassis saburon	♀	6.5	Cassidaria echinophora .	● (1)	● 19	● 12	● 26				○ 12	○ 23
♀	8.8	Cassidaria echinophora .	♀	9.3	Cassidaria echinophora .	○ (2)	○ 12	○ 7	○ 11	○ 24	○ 20		● 5	● 10
♂	7.9	Murex brandaris	♀	7.2	Murex trunculus	● (1)	● 25	● 29	● 33	● 41			○ 13	○ 15
♂	8.9	Cassidaria echinophora .	♂	8.7	Murex trunculus	● (2)	● 7	● 15	● 19	● 26	● 23	● 31	○ 6	○ 11
♀	7.4	Cassidaria echinophora .	♀	7.6	Cassidaria echinophora .	○ (2)	○ 10	○ 8	○ 16	○ 13	○ 19		● 15	● 9
♂	6.9	Murex brandaris	♀	6.9	Murex brandaris	● (1)	● 14	● 13	● 17	● 17			○ 26	○ 17
♀	8.3	Cassidaria echinophora .	♂	7.2	Murex brandaris	● (1)	● 17	● 6	● 21	● 28	● 14		○ 8	○ 13
♀	8.6	Cassidaria echinophora .	♀	7.4	Cassidaria echinophora .	● (1)	● 11	● 10	● 14	● 10	● 10		○ 19	○ 10
♂	9.1	Cassidaria echinophora .	♂	8.3	Cassidaria echinophora .	● (1)	● 8	● 5	● 7	● 9	● 6	● 7	○ 6	○ 11
♂	7.2	Cassidaria echinophora .	♀	6.2	Murex trunculus	● (1)	● 30	● 22	● 32	● 46			○ 12	○ 17
♂	7.7	Cassidaria echinophora .	♂	7.9	Cassidaria echinophora .	○ (2)	○ 10	○ 18	○ 20	○ 16	○ 18		● 28	● 18
♀	9.0	Cassis saburon	♀	8.3	Cassidaria echinophora .	● (1)	● 12	● 9	● 22	● 13	● 9		○ 12	○ 16
♀	6.9	Murex trunculus	♂	8.5	Cassidaria echinophora .	○ (1)	○ 6	○ 11	○ 13	○ 21	○ 10	○ 8	● 5	● 5
♀	9.5	Cassis saburon	♀	9.0	Cassis saburon	● (2)	● 14	● 8	● 10	● 17	● 21		○ 10	○ 14
♀	8.7	Cassis saburon	♀	7.5	Cassidaria echinophora .	● (1)	● 5	● 12	● 17	● 14	● 16		○ 17	○ 4
♂	6.9	Cassidaria echinophora .	♀	7.8	Cassidaria echinophora .	○ (1)	○ 7	○ 20	○ 28	○ 23	○ 20		● 6	● 11
♀	8.0	Murex brandaris	♂	7.9	Murex brandaris	●/○ (**)	● 9	○ 17	● 10	● 14	○ 18	○ 23	—	—
♀	8.9	Cassidaria echinophora .	♂	8.0	Cassidaria echinophora .	○/● (**)	● 9	○ 25	○ 19	● 6	○ 15		—	—

(*) Acron/telson length.
(**) For these two cases, see the text.
t = time in minutes.

(1) Dominance relationship established before placing the Actinians in the aquarium.
(2) Dominance relationship established in presence of Actinians.

later avoided further contact by retreating from and almost never approaching the dominant crabs, which displayed ritualized aggressive postures when the submitted ones tried an approach: ambulatory raise, cheliped presentation, cheliped extension (12). When the submitted crabs were cornered or attacked by the dominant ones, they spontaneously assumed a submissive posture consisting of rolling over on their back or side and making no effort to defend themselves from the attacking crabs (fig. 3 *b*, *c*). This posture exerted only an incomplete inhibition of the dominants' aggressiveness.

Successively we put in the presence of every pair some *C. parasitica*, one by one. They were always taken by the dominant crab (mean time $\bar{m} \pm s = 16.8' \pm 8.9'$). Also when the dominant's shell was already overloaded of sea-anemones, the submitted crab was never allowed to take a free actinian lying on the bottom of the tank. Only when the dominant crab was removed from the tank, the submitted one immediately took possession (mean time $\bar{m} \pm s = 11.7' \pm 5.5'$) of the two *C. parasitica* we had put on the bottom, one by one. There was a highly significant difference between the mean times of attachment of the sea anemones by the group of the dominant crabs and by the group of the submitted ones (t of Student $= 3.43$ with 163 degrees of freedom). The times of attachment of each sea anemone by the crabs are reported in the Table I.

During their studies on the association between *D. arrosor* and *C. parasitica* carrying out matched tests with marked animals in groups, Ross and Sutton [6] found that their experimental crabs could be classed as "performers" or "non-performers". The performers, comprising about half the crabs, actively participated in transferring the *Calliactis* to their shells. The non-performers seemed to be incapable of this behaviour and in this case *Calliactis* transferred to the shells unaided. Cotte [10] also reported that some *Dardanus* are indifferent to *C. parasitica* and that others are active to excess, detaching anemones from other crabs even when their shells are already overloaded. However he observed that in his aquarium one crab that had been inactive for some time suddenly appeared with several anemones on its shell. In our experiments dominant crabs were always "performers", submitted ones were never "performers", but they turned into "performers" as soon as the dominant crabs were removed.

So, in conclusion, in the species *D. arrosor* among the privileges of owning a high social status there is the possession of actinians. In fact in our experimental conditions submitted crabs, in the presence of dominant ones, were not capable of actively transferring *Calliactis* to their shells.

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