Egg-species recognition in cannibalistic hatchlings of the land snails *Arianta arbustorum* and *Helix pomatia*

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Summary. Laboratory experiments were conducted to determine whether cannibalistic hatchlings of the land snails *Arianta arbustorum* and *Helix pomatia* discriminate between eggs of the two species. Hatchlings from both species showed a significant choice for conspecific eggs and consumed on average 1 egg in 4 days. Eggs from the other species were only occasionally eaten.
Key words. Food choice; recognition; cannibalism; predation; gastropods; pulmonates.

Quantitative information on different facets of interspecific interactions is necessary for increasing our understanding of the structure and dynamics of ecological communities. In land snails, egg and juvenile survival are crucial factors in determining population trends[1]. However, the specific mechanisms influencing mortality of eggs and juveniles are not well known[1]. Abiotic factors, such as drought and high temperature, are regarded as harmful to these two stages[2-4]. In addition to anurans and various arthropods, several land snail species are predators of snail eggs[5-7]. Furthermore, egg cannibalism by hatchlings has been recorded for a few snail species under natural conditions[8-10]. It is not known, however, whether these species consume eggs of other species as well. The present study examines whether cannibalistic hatchlings of *Arianta arbustorum* and *Helix pomatia* discriminate between eggs of their own and other species.

Materials and methods. 23 egg batches of *A. arbustorum* and 18 of *H. pomatia* were collected in the forest Stadsskogen near Uppsala, central Sweden (59°50'N, 17°40'E). Eggs of *H. pomatia* are oval, with their larger diameter averaging 6.4 mm (range: 5.8–7.5 mm, N = 36); those of *A. arbustorum* are nearly spherical with a mean diameter of 3.2 mm (range: 2.7–3.5 mm, N = 45). For each batch, half of the eggs were allowed to hatch and half were used as food in choice tests. Hatchlings of *H. pomatia* averaged 6.1 mm in shell breadth (N = 11), those of *A. arbustorum* 2.9 mm (N = 29). In both species, emerging young consume their empty egg shells (which provide nutrients and calcium), as well as the shells of conspecific unhatched eggs[8,9]. This type of egg predation is restricted to the hatchling stage[11], and no discrimination is exhibited between sib and non-sib eggs[10]. To test for interspecific discrimination by egg-predating hatchlings, 3 eggs of each of the two species were offered to each animal tested. Single snails were placed in the center of a 65-mm diameter petri dish lined with 5 mm moist soil; the eggs were arrranged uniformly in a circle 2 cm from the snail. Each dish was checked once per day for wholly or partially eaten eggs. Tests were terminated as soon as snails started to eat their first egg and lasted no more than 4 days. Three newly hatched snails were tested from each batch, and each hatchling was tested only once.

To evaluate rates of egg consumption, hatchlings of each species were placed in petri dishes lined with moist soil and were presented with either 8 eggs of *A. arbustorum* or 3 eggs of *H. pomatia*. Experiments were run for 4 days, after which the number of eggs consumed was recorded.

Results and discussion. A total of 69 hatchlings of *A. arbustorum* and 39 of *H. pomatia* was tested. Of these, 29 *A. arbustorum* (42.0%) and 2 *H. pomatia* (5.1%) consumed no eggs; egg predation was thus more frequent in *H. pomatia* than in *A. arbustorum* ($\chi^2 = 16.58$, df = 1, $p < 0.001$). Snails showing no egg consumption were excluded from further data analysis.

In egg-choice tests, hatchlings of both species demonstrated a significant preference for conspecific eggs (table 1); they only occasionally consumed eggs from the other species. Thus, egg consumption by *A. arbustorum* and *H. pomatia* did not occur in response to chance encounters, but rather resulted from active food choice. Indeed, gastropods are known to use chemical cues in locating food and to discriminate between food types on the basis of taste and smell[12]. In the present experiments, the hatchlings of both species seldom ate the egg they first encountered. The length of time up to initiation of egg consumption did not differ between hatchling species or egg species (Kruskal-Wallis test, $p = 0.62$). *A. arbustorum* started to eat conspecific eggs after 1.9 ± 0.9 days (mean $\pm$ SD, N = 37) and eggs of *H. pomatia* after 2.0 ± 1.0 days (N = 3). Corresponding figures for *H. pomatia* were 1.8 ± 1.0 days (N = 36) for conspecific eggs and 1 day (N = 1) for those of *A. arbustorum*.

In experiments with only conspecific eggs, hatchlings of both species consumed approximately 1 egg within 4 days (table 2). In contrast, when offered only eggs of the other species, most snails refused to eat (table 2).

Snail species differ in terms of the histochemical properties of their egg shell[13]. Similarly, the hatchlings' behavior of eating their own egg shells and, therefore, the occurrence of egg cannibalism are characteristics of species. As a consequence of eating their own egg shells, hatchlings of *A. arbustorum* and *H. pomatia* may be conditioned to the taste of conspecific eggs.

Snail eggs are rich in energy and nutrients (mucopolysaccharides, calcium)[14,15]. Newly hatched *A. arbustorum* doubled their weight within 6 days when fed exclusively on conspecific eggs, whereas siblings given vegetarian food increased their weight by only 18%[16]. In the light of such benefits, egg cannibalism may well be adaptive even among siblings[10]. In the field, the probability of encountering an

Table 1. Results of egg-choice experiments in which cannibalistic hatchlings of *A. arbustorum* (Aa) and *H. pomatia* (Hp) were offered conspecific and heterospecific eggs

Hatchling species	No. of tests[a]	Egg species chosen Aa	Hp	p[b]
Aa	40	37	3	< 0.001
Hp	37	1	36	< 0.001

[a] Tests with no observed egg-predation excluded; [b] two-tailed binomial test.

Table 2. Summary of egg consumption experiments in cannibalistic hatchlings of *A. arbustorum* (Aa) and *H. pomatia* (Hp)

Hatchling species	Egg species offered	No. of snails tested	No. (percentage) of snails consuming eggs	No. of eggs consumed per snail and day
Aa	Aa	33	32 (97.0%)	0.27
Aa	Hp	24	2 (8.3%)	0.02
Hp	Hp	25	24 (96.0%)	0.23
Hp	Aa	26	4 (15.4%)	0.06

egg batch of *H. pomatia* may be very small for *A. arbustorum*, since *H. pomatia* lays its eggs in a hole about 6 cm deep[8,17]. In contrast, batches of *A. arbustorum* eggs are often laid in grass tufts or in moss, i.e., at sites where hatchlings of *H. pomatia* often forage[5]. In spite of this, the rarity of either of these two species encountering other eatable eggs (egg shells of sympatric *Cepaea nemoralis, C. hortensis* and *Perforatella incarnata* are not eatable[9]), as well as the restriction of egg cannibalism to a short period of life (viz. the hatchling stage[11]), may prevent the evolution of interspecific egg predation of cannibalistic hatchlings.

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A semi-automatic computerized analysis of tracks of ciliates

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Summary. The behavior of Protozoa can be studied by using the ethogram as a conceptual tool capable of giving an almost complete picture of the motor biology of these microorganisms. A new semi-automatic, computerized method for drawing ethograms is described here: it allows a time-saving of about 70%, in comparison with the similar manual procedure. Microorganism movements are photographed by a Pentax LX camera from the screen of a TV monitor, connected to the stereomicroscope by a TV camera, and resolved into single images using a stroboscopic apparatus. The pictorial data are introduced into the computer by means of a digitizing tablet, and the track analysis is performed semi-automatically. The measurements recorded are then processed using a commercial statistics package in order to obtain a general view of the quantitative parameters of each ethogram.
Key words. Computer analysis; ethogram; ethology; Protozoa.

After Jennings' masterpiece[1], the behavior of Protozoa has been long disregarded, and investigated rather as cell motility than as true behavior, so that quantitative descriptions of the actual movements of protozoan organisms are today almost nonexistent, as has been clearly stated by different authors[2-4]. The first ethogram as defined by Eibl-Eibesfeldt[5], for a protozoon was drawn by Ricci[6,7], using both the dark field time exposure technique[8] and TV recording, for *Oxytricha bifaria,* Ciliata, Hypotrichida, according to Corliss[9]; its behavior was described by means of 9 basic elements. A far more complete standard ethogram (45 quantitative and qualitative elements) is now used; it makes it possible to gain more insight into the adaptative strategies of the ciliates, to monitor the effects of experimental treatment and to analyze, in terms of both qualitative and quantitative alterations of the standard ethogram, the effects of experimental treatment on several cellular targets (ciliary engines, membrane potential, cell shape, cell adhesion, etc.). So far, however, the extreme complexity of the process of drawing a single ethogram (4–5 weeks, for an expert operator) has discouraged the frequent use of this tool and strongly reduced the opportunity of testing its potentialities. On the other hand, it has already been shown[10] that microorganism tracks can be analyzed by means of fully automatic procedures. If the speed of the microorganism is low, the analysis is performed in real time; in this case the hardware system consists of a TV camera mounted on a microscope and connected to an image-digitizer plugged into a computer bus. If the speed of the microorganism is high, the analysis is performed off-line; for this purpose a videorecorder is inserted between the TV camera and the image-digitizer; the computer controls the feed of the videorecorder and thus the speed of the analysis. By means of this technique, the microscopical images are analyzed and the cell bodies are recognized and followed in time and space by the computer; in the semi-automatic technique, on the contrary, the positions of the microorganisms are introduced by the operator by means of an input device such as a digitizing tablet. A fully automatic analysis of the tracks requires very expensive equipment: therefore, we adopted a semi-automatic procedure that requires a hardware set-up which is within the reach of every laboratory.

Materials and methods. The microorganisms creep and swim freely in a droplet of physiological medium between a slide and a coverslip, kept at a distance of 3 mm from each other. A Hitachi TV camera is mounted on a microscope Wild M 420 and is connected to a Sony monitor. The microorganism's movements are photographed either by means of a Wild MPS 51 camera directly mounted on the dark-field equipped Stereomicroscope (the camera shutter is kept open for 4 s of 6 s) or from the screen of the TV monitor, by a Pentax LX camera; in this case, the tracks previously recorded under dark field conditions by a tape recorder Sony Betamax, are resolved into a series of single images by a strobo-