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A CHAMELEON AS PREDATOR OF BUTTERFLIES AND ITS AVOIDANCE OF KNOWN APOSEMATIC SPECIES

TORBEN B. LARSEN

Jacobys alle 2, DK-1806 Frederiksberg C, Denmark

ABSTRACT.– The African chameleon, *Chameleo dilepis* Leach, was observed attacking various butterflies in Botswana. Experiments to determine the unpalatability of various butterfly species are reported on.

KEY WORDS: *Acraea*, African, *Axiocerses*, *Azanus*, *Belenois*, Botswana, *Byblia*, *Catopsilia*, Coleoptera, Danainae, *Danaus*, Ethiopian, *Hypolimnas*, *Junonia*, Meloidae, Nymphalidae, Orthoptera, *Papilio*, Papilionidae, Pieridae, predation, Pyrgomorphidae, Reptilia, Satyrinae, Tenebrionidae, *Zygaena*, Zygaenidae.

On 13 January 1991, I brought back to our house in Gaborone, Botswana, a female flap-necked chameleon (*Chameleo dilepis* Leach), measuring just under 30 cm, indicating that it was a mature adult. She was actively hunting among the branches of an acacia bush (*Acacia fleckii* Schinz) which at that time of the year is one of the most favoured nectar sources of Lepidoptera, Hymenoptera, and Coleoptera of all kinds. Among the butterflies most frequently seen on the tree were: *Belenois aurota* Fabricius, *Catopsilia florella* Fabricius, *Axiocerses tjoane* Wallengren, *Azanus jesous* Guérin-Ménéville, *Danaus chrysippus* Linnaeus, and *Junonia hierta* Fabricius. Among the Coleoptera, a common blister beetle, *Mylabris* sp. (Meloidae), was most evident.

I decided to do some experiments on food palatability with the chameleon, and was encouraged to do so also by the record of Hargreaves (1979) that two different chameleons in Malawi (*C. dilepis* and *C. melleri* Gray) had consistently refused to eat *Acraea zetes* Linnaeus, a butterfly which is generally considered to be aposematic, and which—with other large members of the genus—forms models in mimicry and co-mimicry complexes. The latter chameleon is large and robust, eating even birds (e.g. waxbills).

Chameleons are known to use Lepidoptera for food, and for 18 months in Lebanon I once had a tame common chameleon (*Chameleo chameleon* Linnaeus) which sustained itself for more than a year in a curtain in a bay window, mainly on moths that had been attracted to light and on crippled butterflies that hatched in the house and were offered to it.

Ever since seeing a species of skink eating large numbers of aposematic zygaenid months in Lebanon (*Zygaena carniolica* Scopoli), I have wondered whether lizards and chameleons reacted or not to the same visual and chemical stimuli that have so extensively and rigorously been tested in birds. Praying mantids and crab-spiders certainly do not avoid proven aposematic butterflies; I have seen many eating both *D. chrysippus* and *Acraea* species in Africa and India.

Fig. 1. The chameleon eating a live *Papilio demodocus* Esper.
Fig. 2. The chameleon grasping an unpalatable *Phymaeus* grasshopper; it was later released in damaged condition.

Table 1. Summary of hand-held feeding experiments

Species	Offer	Refuse	Accept	Percent accepted	Decision time/sec.
*P. demodocus**	3	1	2	67%	3.5
Pierids	155	18	137	87%	2.7
D. chrysippus	30	30	0	0%	-
Acraea	62	62	0	0%	-
H. misippus ♂	26	25	1	4%	9.0
H. misippus ♀	26	26	0	0%	-
B. ilithyia	14	14	0	0%	-
Nymph/Satyr**	36	15	21	58%	6.5
Lyc/Hesp	42	***9	33	79%	3.6
TOTAL	396	200	196	49%	-

Notes: * Many other *P. demodocus* were taken in demonstrations and photo-sessions (Table 2).
** Mainly *J. hierta* – decision time for those taken was 6 seconds, whereas decision time for pierids was less than 3 seconds.
*** Five of the refusals were *A. tjoane* whose colour is towards *D. chrysippus*; decision time longer than for pierids.

FEEDING EXPERIMENTS

The chameleon was initially installed in our garden in a large cage (2.0m x 1.5m x 1.5m) made from an old packing case, much too big to be convenient for feeding experiments. Nonetheless, the chameleon usually found freshly introduced, live butterflies within fifteen minutes or so. It was, therefore, transferred to a finely masked, plastic laundry basket, about 120 cm tall and averaging 40cm in diameter. All subsequent experiments took place in this basket.

Initially, live insects were introduced into the basket, but it soon became clear that the chameleon (christened Margrethe) was quite willing to accept freshly killed insects offered by hand. From the outset it was evident that the chameleon had strong likes and dislikes. Thus, blister beetles (Coleoptera, Meloidae, *Mylabris* sp.) remained untouched in the cage for days on end; blister beetles are known to contain large concentration of cantharadin, which is highly toxic, causes blisters, and damages kidneys, resulting in death in large doses (Skaife 1979). The famous toktok beetles (Coleoptera, Tenebrionidae, *Psammodes* sp.) were never touched. A large carabid beetle, with a strong 'nauseous vanilla' smell was always avoided; this smell also gave our two kittens a shock when they ambushed one. Three cetoniid beetles, oozing a putrid-smelling fluid, were also ignored. A very large Pyrgomorphic grasshopper (Pyrgomorphidae; *Phymaeus* sp.), feeding on Asclepiads, was seized, released after some time, and never touched again although it remained in the cage with some life left. These grasshoppers are so toxic that a child in South Africa died after eating one (*P. leprosus*) (Skaife 1979). There was a smell like nauseous ammonia, but no foaming at the tegulae. Small, brilliant green or purple chrysomelid beetles feeding on Asclepiads proved acceptable, much to my surprise. Finally, large centipedes were ignored after one had been sampled. Most other insects, including slow moving caterpillars, were acceptable food items, grasshoppers and walking sticks being the favourites.

During the first week we placed a wide variety of living insects in the cage to observe behaviour and to habituate the chameleon to us. She soon became quite tame and structured feeding experiments with butterflies began. Every morning the chameleon was offered about twenty dead butterflies, held by the antennae in such a way the she could see either the upper or the underside. The offer was held for ten seconds and then withdrawn if it was not accepted. As far as possible, a random sequence of offers were made, and as far as possible, butterflies of different sizes and colours were included in each controlled feeding session. The totals are given in the appendix, while a summary is given in Table 1.

When recognizing an acceptable food item with one eye, the chameleon would immediately swivel the other eye into focus, the tongue would be slightly extruded, and then the target struck. The preparatory procedure would generally take two seconds or so, which represents the fastest possible reaction time.

The results were very conclusive. Pierids were the most acceptable prey, and nearly 90% of all offers were accepted immediately, the average reaction time being 2.7 seconds. Similarly, 80% of all Lycaenids and Hesperiids were accepted, the average reaction time being 3.5 seconds. A variety of Nymphalids and Satyrids suffered a high rate of rejection, only 60% being accepted, with an average reaction time of 6.5 seconds. It was quite clear that the chameleon only took these items after due consideration. She gave the impression of going through a mental check-list that was not necessary with the Pierids. The overall refusal rates would have been lower, had not the chameleon sometimes been distracted by the passing of one of our kittens and other extraneous events.

From the outset *Danaus chrysippus* and *Acraea* species were sight-rejected. Of 92 offers over a period of three weeks not a single specimen was accepted in the hand-feeding experiments. Five species of *Acraea* were offered, three of which the chameleon could not have encountered in nature, since they were brought down from the north. These butterflies are known to be

Table 2. The fate of other butterflies placed with the chameleon (live or dead) for periods ranging from 3 to 36 hours

Species	Eaten	Uneaten	Species	Eaten	Uneaten
P. demodocus	13	1	*H. misippus* ♂	3	2
C. florella	2	0	*H. misippus* ♀	2	6
P. eriphia	2	0	*B. ilithyia*	0	3
C. vesta	1	0	*J. oenone*	3	0
C. ione	6	0	*J. hierta*	7	0
C. danae	11	1	*P. phalantha*	2	0
C. auxo	3	0	*A. natalica*	2	4
C. evenina	1	0	*A. anemosa*	4	7
B. aurota	101	3	*A. eponina*	0	1
B. creona	4	0	TOTAL	173	50
A. tjoane	1	0			
C. leroma	1	0	Aposematic	9	34
A. amarah	1	0	Suspect *	5	11
D. chrysippus	3	22	Palatable	159	5

NOTE: Most aposematic species that were eaten disappeared overnight after spending most of the day in the cage.
* *Hypolimnas misippus* and *Byblia ilithyia*.

aposematic. All offers of female *Hypolimnas misippus*, a near perfect mimic of *D. chrysippus*, were also rejected. Much to my chagrin, all offers but one of the very different male of *H. misippus* were also rejected; it would have been most interesting if the non-mimetic male had been acceptable and the mimetic female not. Finally, *Byblia ilithyia* was always rejected. This species may be aposematic (the larval food plants are Euphorbiaceae), but its general pattern elements include all the characteristics of *D. chrysippus* and the *Acraea*, though they are ordered somewhat differently. Interestingly, the chameleon always rejected these species without any consideration; a quick look with only one eye was sufficient for rejection (we had the impression of a weary 'oh no, you cannot be serious!' look at us as well).

The rejection rates are not correlated with size. *Papilio demodocus* proved very acceptable (see also Table 2), and the rejected *B. ilithyia* and some *Acraea* are no larger than the palatable Pierids.

The evidence for discrimination is supported by a number of other feeding experiments with live and dead butterflies. Three dozen tests were made where a plate containing six or seven mixed butterflies were placed in the bottom of the cage for several hours. Almost without exception, the palatable species were picked out, the others left untouched. However, inside the cage some mistakes were made, and occasionally a *D. chrysippus* or an *Acraea* would be eaten, though many survived for days inside the cage, while other live butterflies were immediately snapped up. The mistakes were chiefly made when the light was bad, and when the chameleon was watching the butterfly on the bottom of the cage from its perch. From this angle the chameleon can see movement but not the colour of the wings. In a few cases it was possible to see that an *A. natalensis* had been captured by the chameleon and then released.

Two larvae of *D. chrysippus*, which have an apparently aposematic pattern, were untouched for more than 24 hours; the fresh pupa lacked an aposematic pattern, and one was eaten while wriggling as it attached its cremaster to the silken pad.

TERMINATION OF THE EXPERIMENTS

One morning, I left four freshly hatched *A. natalensis* in the cage. They were still present at 22.00, but early the next morning two had been eaten. Instead of being its usual light green, the chameleon was grey with darker blotches, looking decidedly unhappy. In order to cheer it up, its usual favourite Pierids were offered; they were consistently refused, something that had never happened before.

Two days later the chameleon was back to green, and the experiments were restarted. All species of butterflies, including pierids, were consistently rejected. Grasshopper controls (mainly *Truxalis* sp.) were avidly eaten, as were some moth caterpillars. Till I left on a long field trip a week later, no hand-offered butterflies were accepted, while all grasshoppers immediately were. Live Pierids inside the cage were eventually taken, but usually only after several hours. The chameleon appeared gradually to be regaining confidence in pierids.

The chameleon was placed for three months with a colleague who was asked not to feed it butterflies. The chameleon unfortunately died during this period, apparently from sheer over-exertion after laying 37 eggs. I had hoped to continue the experiments with models.

DISCUSSION

It is obviously dangerous to generalize from six weeks' experience with a single chameleon, but some interesting points do emerge. The wild-caught chameleon had a strong distaste for the main aposematic butterflies in the country, as well as for other toxic insects. Given the wide geographical range of the flap-necked chameleon, these reactions are almost certainly learnt and not innate, since there is much geographical and seasonal variation in the prey spectrum.

It is also clear that the chameleon was giving due consideration before catching a prey item. Easily recognizable prey items such as Pierids were taken immediately, while more ambiguously coloured prey items needed longer consideration, and were more often refused within the ten second period.

The chameleon was also able to generalize the *Acraea* pattern, avoiding on sight all the species of that genus, even those not seen before. Admittedly, the colour pattern of *Acraea* species is fairly similar, though far from identical. This means that both Batesian and Mullerian mimicry-rings might be wider than is sometimes assumed. The avoidance of *B. ilithyia* is of special interest, since its usual flight behaviour is not typical of an aposematic insect. The data are certainly indicative that even slight mimetic resemblance may have significant survival value —for a butterfly the difference between being attacked after 2.7 seconds or 6.5 seconds when visiting a flower may easily spell the difference between life and death.

The ability to generalize was also shown by the chameleon abandoning all butterflies as food items after eating two fresh *Acraea*, while maintaining its appetite for other usual prey items.

Finally, the survival of at least two *Acraea* after an attack shows that the exceptionally tough and flexible exoskeleton, characteristic of many aposematic butterflies, does provide some protection against the accidents that will happen.

I am at a loss as to why male *H. misippus* were not eaten. Half the 25 offers were of the underside, which has slight resemblence to *D. chrysippus*; half were of the upperside which does not. There have been occasional suggestions that *Hypolimnas* might be somewhat aposematic, but I doubt if the chameleon would ever have come into sufficient contact with them in the field.

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APPENDIX: Total hand-feeding experiments

Species	Offer	Refuse	Accept	Average delay (seconds)
P. demodocus	3	1	2	3.5
C. florella	3	-	3	3.3
E. brigitta	2	-	2	3.5
P. eriphia	4	1	3	2.3
C. vesta	1	-	1	2.0
C. danae	21	4	17	2.7
C. auxo	12	3	10	3.1
C. evagore/pallene	6	2	4	2.7
C. agoye	1	-	1	3.0
C. subfasciatus	1	-	1	3.0
B. aurota	102	8	94	2.6
B. creona	1	-	1	2.0
M. agathina	1	-	1	3.0
S. natalensis/ella	2	-	2	5.5
A. tjoane	12	6	6	4.6
A. taikosama	5	-	5	3.8
C. leroma	1	-	1	2.0
L. gorgias	3	-	3	2.3
A. amarah	5	-	5	2.8
L. pirithous	5	1	4	3.5
A. jesous	5	1	4	2.3
D. chrysippus	30	30	0	-
M. leda	3	3	0	-
B. ilithyia	14	14	0	-
H. misippus ♂	26	25	1	9.0
H. misippus ♀	26	26	0	-
J. oenone	7	2	5	6.2
J. hierta	25	10	15	6.3
V. cardui	1	-	1	9.0
A. eponina	9	9	0	-
A. axina	2	2	0	-
A. natalica	12	12	0	-
A. anemosa	32	32	0	-
A. neobule	7	7	0	-
C. forestan	1	1	0	-
S. phidyle	1	-	1	7.0
K. callicles	2	-	2	2.5
TOTAL	396	200	196	-

NOTE: The authorities of all the butterflies may be found in Larsen (1991).

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