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Research Article

Maternal care in *Omaspides bistriata* Boheman (Coleoptera: Chrysomelidae: Cassidinae: Mesomphaliini)

Cuidado maternal en *Omaspides bistriata* Boheman (Coleoptera: Chrysomelidae: Cassidinae: Mesomphaliini)

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Abstract. Maternal care (subsociality): characterization of the different stages of maternal care and its efficiency as a strategy. Maternal care and larval development of *Omaspides bistriata* Boheman, 1862 (Coleoptera: Chrysomelidae: Cassidinae: Mesomphaliini) are described; including characteristics and manner in which maternal care is given across the different stages of development of the specie (eggs, larvae, pupae and teneral adults). We report the oviposition of eggs, the duration to hatch the eggs, and the duration of larval period, pupal stage, and emergence. A life table and survival curve is presented covering all life stages. Changes in the behavior and feeding habits are also noted for the immatures and the attending mother.

Key words: Beetle, behavior, hostplants, parental care.

Resumen. Cuidado maternal (subsocialidad): caracterización de las diferentes etapas del cuidado materno y su eficiencia como estrategia. Se describen el cuidado maternal y el desarrollo larvario de *Omaspides bistriata* Boheman, 1862 (Coleoptera: Chrysomelidae: Cassidinae: Mesomphaliini); incluyendo características y forma en que se brinda el cuidado materno en las diferentes etapas de desarrollo de la especie (huevos, larvas, pupas y adultos tenerales). Informamos la oviposición de los huevos, la duración de la eclosión de los huevos y la duración del periodo larvario, estado de pupa y emergencia. Se presenta una tabla de vida y una curva de supervivencia que cubre todas las etapas de la vida. También se notan cambios en el comportamiento y en los hábitos alimentarios de los inmaduros y de la madre que los atiende.

Palabras clave: Comportamiento, cuidado maternal, escarabajo, planta hospedera.

Introduction

Subsociality (i.e. extended parental care) is the most widespread social behavior among insects (Royle *et al.* 2012). It is known to occur in 167 families of 19 insect orders (Machado & Trumbo 2018). Subsocial behavior encompasses care for offspring by protection against natural enemies, guiding towards or provisioning of food resources during most or all

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immature stages (Clutton-Brock 1991; Royle *et al.* 2012). Within Coleoptera, subsociality is a rare phenomenon and the behavior has been recorded in 12-17 out of 176 beetle families (Chaboo *et al*. 2014; Leocádio *et al.* 2020). Chrysomelidae Latreille, 1802 is one of the beetle families in which this behavior has evolved indepentently in two subfamilies of 15: Cassidinae Gyllenhal, 1813 and Chrysomelinae Gyllenhal, 1802 (Windsor & Choe 1994; Chaboo *et al.* 2014; Leocádio *et al.* 2020).

It is noteworthy that many Chrysomelidae larvae feed on the external tissues of plants (exophytic) (White 1983; Jolivet 1997), being more exposed to predation or parasitism than larvae of most Coleoptera, which live and hide in logs or underground (Wilson 1971; White 1983; Costa 2006). Many exophytic insects developed parental care, probably in a response to their feeding behavior (Cornell & Hawkins 1995).

Cassidinae *sensu lato* is the second largest subfamily of leaf beetles with 6,300 species, distributed worldwide (Borowiec & Świętojańska 2018). Within Cassidinae, parental care has evolved independently in two closely related lineages that feed on distinct host plants families: Asteraceae and Convolvulaceae (Leocádio *et al.* 2020). Until now, parental has been recorded in 24 species belonging to five genera (Chaboo *et al.* 2014; Flinte *et al.* 2015; Macedo *et al.* 2015). The genus *Omaspides* Chevrolat, 1836 (Mesomphaliini) belongs to the Convolvulaceae feeding clade (along with *Acromis* Chevrolat, 1836 and *Paraselenis* Spaeth, 1913) and parental care has been recorded in 11 out of its 40 recognized species (Gomes *et al.* 2012; Chaboo *et al*. 2014).

Parental care and number of eggs per clutcth were briefly described for *Omaspides* (*Omaspides*) *bistriata* Boheman in Panama (Windsor & Choe 1994). This genus has three subgenera with 40 recognized species. Here we present a detailed life history description for *O.* (*O.*) *bistriata* in Costa Rica, including development time of all imature stages and number of individuals per clutch with survival rates for each stage.

Materials and Methods

Study area

The Veragua Rainforest Park is located at the foothills of Fila Matama sector, in La Amistad Caribe International Park (Costa Rica-Panamá), Limón, Costa Rica within the very humid tropical forest life zone (bmh-T) (Holdridge 1967). The monitoring and specimen collection were carried out within an area composed mainly of secondary forest at an average elevation of 430 m (N 9°55'35.7'' - W 83°11'27.9''). With a minimum average annual temperature of 19.6 °C and a maximum of 27.1 °C. The vegetation surrounding the Veragua Rainforest reserve was monitored between December (2008) and February (2011), observing the behavior and development of individuals of the species *O.* (*O.*) *bistriata*.

In the monitored area, there are high altitude trees distant from each other, so the canopy is not complete, and this enables the entrance of light and the formation of clearings which are, in turn, favorable for the proliferation of herbaceous, shrubs and vines, among which is the morning-glory *Ipomoea purpurea* (L.) Roth (Convolvulaceae), the host plant of *O.* (*O.*) *bistriata*.

Biological studies

Three couples in copula were spotted on three distinct occasions on February 4, 2009; December 27, 2009 and January 16, 2011. In order to monitor their reproductive behavior, the sites were marked and visited daily for at least 6 hours a day.

Besides the three caring females and offspring, we found four eggs clutches without parental attendence and they were also monitored. An additional female caring for pupal offspring was monitored. The females remain feeding and sleeping in the plants where the copulation occurs. After three to four days it was observed that the volume of the females' abdomen increased gradually, until the time of eggs laying.

The oviposition of the first monitored female was performed on February 27, 2009 and was composed of 32 eggs, while the second female was oviposited on January 16, 2010 with 34 eggs and the third on January 30, 2011 with 29 eggs. All egg layings were monitored during their development and care process, up to adulthood individuals. In addition, four eggs clusters were found (January 2009 with 28 eggs, March 2009 with 35 eggs, April 2010 with 30 eggs and January 2011 with 31 eggs) with no adult individuals present and in January 2011 we found a mother caring for seven pupae.

Data analyss

Based on the analysis and on the data of the three eggs layings and their complete development cycles, a life table was created with their respective survival curve, the percentage of viable adults, completing development the average number of ovioposítions, survival to larval and pupal period, hatching of juvenile individuals and sexual adults at the end of the cycle observed under natural conditions.

To determine the values of the life table an average of the data between the three ovipositions was taken and classified of the following form:

- X = Age in days, starting from eggs laying
- nx = Average number of living individuals at age X in days
- lx = Proportion of surviving individuals at the beginning of the age range X
- dx = Number of individuals killed during the age range X to X +1
- qx = Per capita mortality rate during the interval X to X +1 Where:
- lx = nx / n0 nX+1 = nx – dx qx = dx / nx

To plot the exponential survival curve data were used:

- Axis X = Age in days, from oviposition (X)
- Axis Y = Average number of living individuals at age X

Specimen Voucher

All samples were deposited at Veragua Rain Forest biological collection. Host plant was determinated by Fabian Araya (Universidad Nacional) and beetles were deteminated by Rolando Ramírez (Universidad Estatal a Distancia).

Results

Live cycle

The complete life cycle lasts 44-50 days as can be seen in Table 1.

Eggs. Oviposition occurred 19 days after copulation. The eggs measured 1-1.5 mm long, and they hatched after 5-6 days of incubation. The eggs were light orange in color, and in clutches of 29 to 34 eggs on abaxial surface of host plant leaves (Figs. 1A, 1B).

Larvae. Larval stages develop in 34 days average, with a length from 1.5-2 mm on the first instar to 9-10 mm on the last one, highlighting the formation of the circular exuvial-fecal shield (cycloalexy), with the head inwards in the group of larvae during their early stages. In the first stages, the larvae fed mainly on mature leaves, while in the later stages they ate tender, mature leaves and even the stem. When the larvae move through the plant, the mother travels the entire area in which they are found, and at night they regroup again. (Figs. 1C, 1D).

Pupae. Between days 38 and 42. The pupae began to form (Figs. 1E, 1F), presenting a size between 8-10 mm, they were attached in both the bundle and the underside of the leaves, mostly individually, however, some were observed in groups of two to four pupae.

The pupae emergence occured at 44-50 days, the new adults were 10 to 11 mm in size, with the soft body and the slightly hardened pronotum, of the black color. The elytra were very fragile and of a slightly transparent yellowish hue, some that had not hatched properly began to dry, leaving their elytra wrinkled, which damaged both elytra and hind wings incapacitating them for flight and dying within a few hours or being easily depredated.

Finally, on 54th day, they took the definitive color of the mature adult, dispersing mainly terrestrially, moving between neighboring vegetation to the host plant and raising immediate flight when they were disturbed. They also moved short distances.

Table 1. Life table for offspring of *O. bistriata* up to the adult's phase.

(X)	(nx)	(lx)	(dx)	(qx)
0	33 eggs	1.0	5	0.15
6	28 larvae	0.848	11	0.40
40	10 pupae	0.909	3	0.30
47	7 eclosions	0.7	1	0.14
54	6 adults	0.857	-	-

Maternal care behavior

The adult did not change its behavior with respect to the stage of development (egg or larva), but instead moved towards each of the small groups of 1-4 larvae while they feed on different parts of the plant, from the young leaves even on the stem, so that it is maintained with each group periodically, taking care of them in the same way as when they were still eggs (Figs. 1A, 1D).

At the pupal stage, the adult remained close by periodically reviewing them. We even observed the female relocating some pupae that had not adhered correctly, those that were in very visible places or with the anterior dorsal part of the pupa in contact against the surface of the leaf (Figs. 1G, 1H). In the latter case, the female changed the position of the pupae by turning them until it was the ventral part that was in contact with the surface of the leaf. For this, using the jaws and the front legs, the female raises the pupa to detach it from the substrate and then dragged it with the front legs until it reached te desired position.

Then, the pupae hatched into a group of adults in perfect condition. Teneral adults were held together and the mother continued to direct their movements and attending to them care. Between 51-56 days, all surviving adults (Fig. 2) had well-formed and hardened elytra. Although they were not as brightly colored as their mother, so it was easy to recognize the mother within the grouped. These continued to be fed during the day under the care of the mother, who grouped them on the underside of a single leaf to sleep at night. The mother, for the three cases observed, died within 2 to 3 days after this, having cared for her young for approximately two months.

Predators observed

Among the pupae of each ovoposition that failed to hatch (3 of the first, 3 of the second and 2 of the third), at the time when hatching occurred, a fly larva (Tachinidae) emerged. The same happened for three of the seven pupae found that were not monitored since the beginning of the cycle. Other predators such as praying mantises and wasps had been observed around the larvae during all instars.

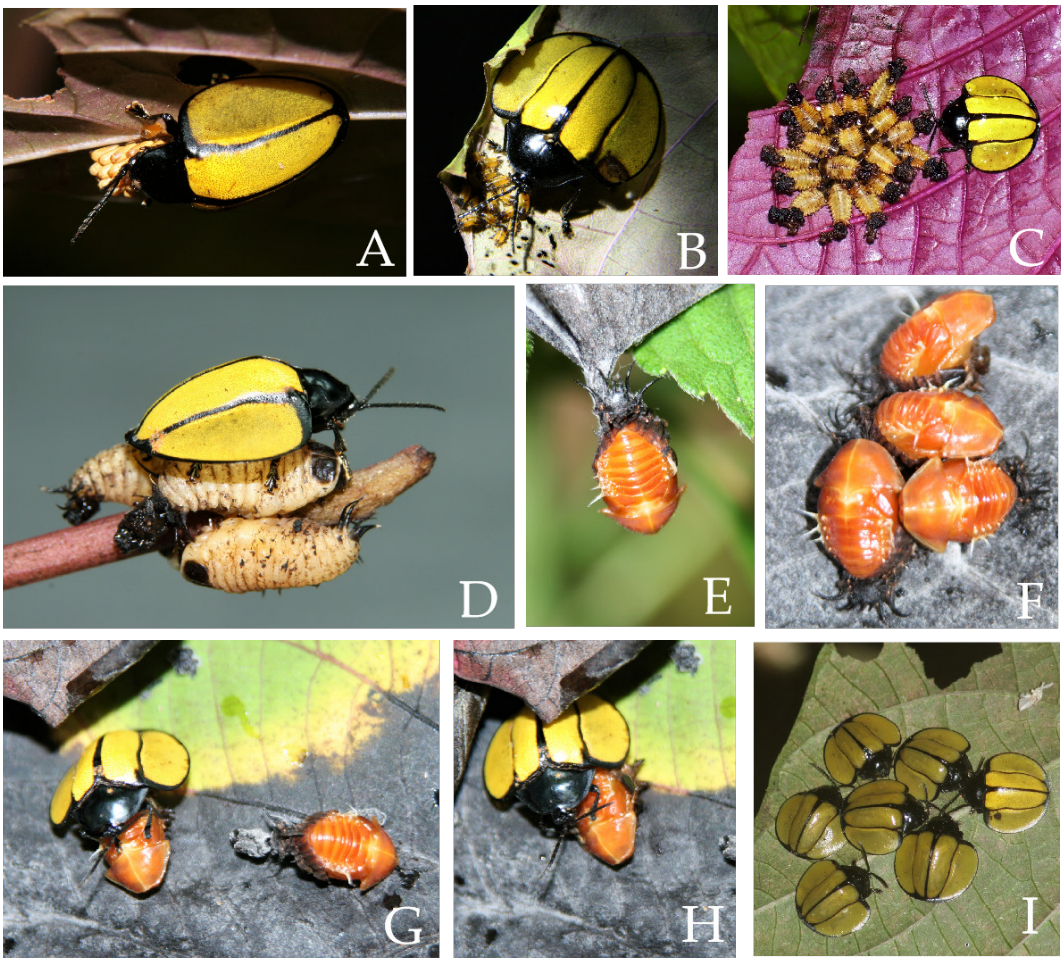

Figure 1. Life cycle of *Omaspides bistriatra* Boheman on host plant (*Ipomea purpurea*) in Costa Rica. A) Female with eggs mass, B) Female on first instar, C) Female with group of second instar, D) Female on third instar, E) Pupae, F) Group of pupae. G- H) Female manipulating pupae, I) Female with their group of newly adult offspring.

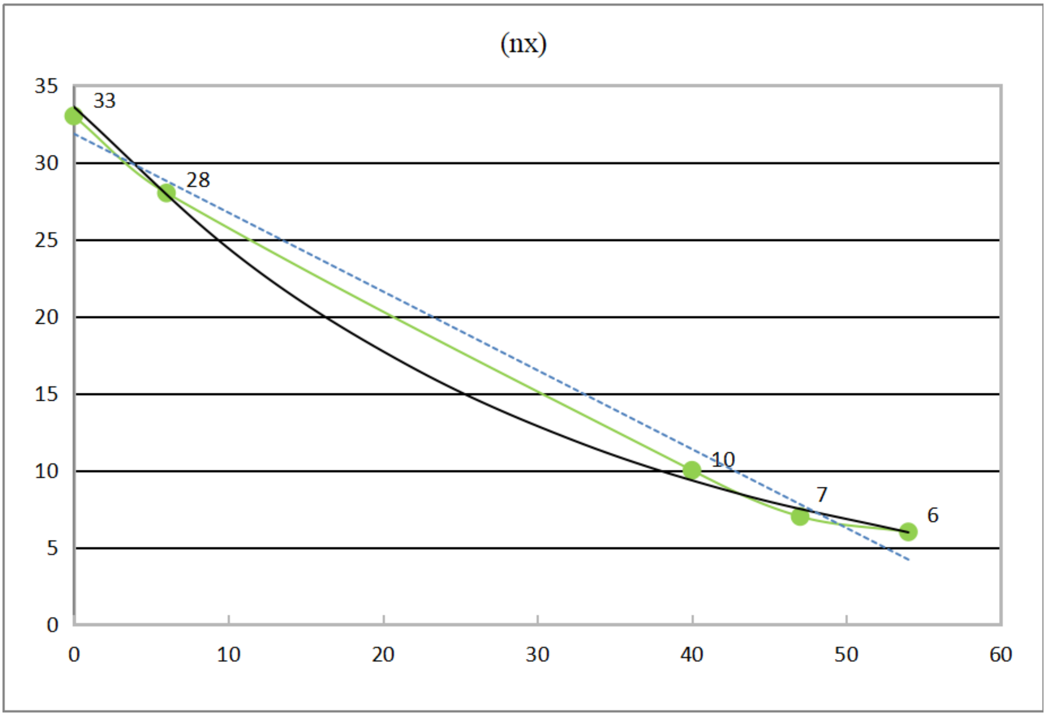

Figure 2. Exponential survival curve (y = 32,694e-0,032x; R2 = 0,9849) of the developmental stages of *O. bistriatta* (X axis) and curves of survival of the stages of the development cycle from *O. bistriatta* (Y axis). 6 adults from 32 eggs, 8 of 34 and 4 of 29.

Discussion

During the study period *O. bistriata* was found using only the plant *Ipomoea purpurea* (Convolvulaceae) as host (Rodriguez 1994; Cedeño-Loja & Chaboo 2020), even despite the presence of other plants designated as potential hosts, such as the genera *Calathea* G. Mey. (Marantaceae), *Cordia* L. (Boraginaceae) and *Tabebuia* Gomes Ex DC. (Bignoniaceae) (Jolivet 1988; Flowers & Janzen 1997). In addition, we observed that adult individuals are much more frequent between the months of December and May, with the period from January to April when they have been found from eggs to juveniles, which presumes a limited reproductive period. The sightings for the rest of the year are sporadic adult specimens.

The meticulous care process performed by the mother during the development of the young shows the protection against frequent parasitoids and predators during the egg stage and larval stages, characteristic in several species of Chrysomelidae (Windsor 1987; Choe 1988; Windsor *et al.* 1992; Rodriguez 1994; Kudo & Ishibashi 1995; Chaboo 2002; Gomes *et al.* 2012; Dury *et al.* 2014; Cuozzo *et al.* 2017; Leocádio *et al.* 2020). Intensive care is also evidenced during the pupal stage in which the individuals are totally defenseless, which involves handling and cleaning them (Costa 2006).

According to the information provided by the life table (Table 1; based on small sample of only three ovopositions), the fertility of ovopositions is high, with the percentage of unborn eggs being 15%. The highest mortality (qx) during the development cycle occurs is during the first larval instars, with the first instar larvae presenting a 40% mortality and the second instar larvae 35%.

This changes radically at the last three instars where practically 99% of the larvae achieve the formation of the pupae. However, with respect to the pupal stage, a decline in survival is registered since only 70% of the pupae managed to hatch. One of the causes of this decline were pupae parasites by Tachinidae, for the case of the three samples monitored.

Finally, for hatchling mortality is 14% is also present, which corresponds to individuals who do not become healthy adults because they do not hatch properly or arise with physical damage. We infer that for this species, even with meticulous maternal care, only about 20% of the eggs placed by the mother would become healthy mature adults.

This pattern is reflected in the survival curve of *O. bistriata*, which can be classified as a trend line, denoting that the mortality rate is relatively constant throughout the development cycle, but presenting two slopes due to a high mortality rate in the first larval intars. It should be mentioned that the first instar is the longest life stage, which is graphically observed as a gradual decrease.

During last the phases of larval instar and pupate the curve is much more linear; with a further increase in mortality, with respect to hatching, this time in a short time, which shows a more abrupt decline, corresponding to the number of pupae without hatching.

At the end of the developmental cycle, one can see a process of “maternal attachment” on the part of the mother towards the new adults, who remain with her for a few more days, after hatching and being fully formed. The parent continues to manipulate the group of pups as during the larval phase, even though she no longer has protective functions physically speaking and is even noticeably weakened.

Comparison with other species

The complete life cycle observed in *O.* (*O.*) *bistriata* was about 44-50 days (average of 47 days) which starts with the laying clusters of eggs which were composed of 28, 29, 30, 31, 32, 34, 35 (three monitored and four found open that were only counted) for an average of 31.3 eggs per mass. The periods in which life cycles were observed were between the months of December to January, January to February, February to March and March to April. The incubation period of the eggs masses was on average 6 days, the larval stage had an average duration of 34 days and the time of the pupation phase was on average 7 days, all these measurements from n = 3 pups monitored.

For the species *Omaspides* (*Omaspides*) *pallidipennis* Boheman, 1854 the complete life cycle of approximately 54.4 days, broken down as follows: Average eggs masses of 55.7 ± 15.5 (October to December) and 61.6 ± 14.2 (February to April), combined average 58 days, with a mass range of 12 to 80 eggs; incubation period 19.2 ± 1.4 (n = 31) (October to December) and 16.7 ± 1.4 (n = 71) (February to April), combined average of 17.9. Its larval stage 26.0 ± 1.5 days (n = 19 hatchlings) (October to December) and 27.0 ± 2.4 days (n = 35) (February to April), total average of 26.5 and pupation phase time 8 , 7 ± 0.8 days (n = 20 pups) (October to December) and 10.2 ± 1.5 days (n = 30) (February to April), total average of 9.4 days (Gomes *et al*. 2012).

In the species *Metriona elatior* Klug, 1829, the effect of temperature in the cycles and survival, determined an average complete life cycle of 35.5 days (at 25 °C) and 55 days (at 20 °C), with a total average of 45.3 days; the eggs masses used in the experiment had an average of 8.5 eggs, the incubation periods were between 5 to 6 days (at 30 °C temperature at which they did not reach adulthood), 6 to 7 days (at 25 °C) and 10 to 12 days (at 20 °C) for a total average of 8 days; the larval stage at 25 °C lasted between 17 and 28 days while at 20 °C it was from 23 to 43 °C for a total average of 27.8 days, while the pupation phase time was from 5 to 8 days at 25 °C and 10 to 12 days at 20 °C, a total average of 8.8 days (Medal 2008).

For other subsocial species of Cassidinae there are key data of some stages of their life cycle, for example, for the species *Acromis sparsa* Boheman, 1854, their total cycle is estimated at approximately 40 days, determining a pupation phase of between 10 and 17 days, total average of 13.5 and eggs masses composed of an average of 40 in ranges that go from 13 to 49 eggs per mass with n = 126 (Windsor 1997). Other subsocial species mentioned by Gomes *et al.* (2012) are *Omaspides* (*Omaspides*) *tricolorata* Boheman, 1854 with average eggs masses 55.1 and *Omaspides* (*Omaspides*) *convexicollis* Spaeth, 1909 with average 48.8 eggs (Gomes *et al.* 2012).

Next, the values obtained for *Omaspides (O.) bitriata* are compared with data from the average point life cycle of the subsocial species mentioned above within the Cassidinae subfamily (Table 2).

Table 2. Comparison in days of life cycle of four subsocial species of Cassidinae.

Stage	*Omaspides* (*O.*) *bistriata*	*Omaspides* (*O.*) *pallidipennis*	*Metriona elatior*	*Acromis sparsa*
Eggs incubation	6	17.9	8	-
Larval	34	26.5	27.8	-
Pupal	7	9.4	8.8	13.5
Life cycle	47	58	5.3	40

Conclusions

The period in which the greatest number of adults were observed was between December and May, only sporadically found the rest of the year, which indicates a reproductive period between January and April.

Eggs clusters number about 30 eggs, with most eggs hatching. However, during the first larval instars, there is a significant mortality of more than 70% between the two instars, similar to that reported for other groups insects at this stage (Hinton 1981). This indicates the need for maternal care in this type of organisms whose larva is so exposed to parasitoids, adverse climatic factors, and habitat alterations, among others.

For the last stages of growth, the larvae have a very high survival, as well as the formation of the pupae. However, there is a significant decline in the number of these that hatch in good condition and become healthy adults. About 70% of the pupae reach adulthood through the sensitivity of the care process, especially since the threat of parasitoids is constant.

Finally, after a meticulous work of caring for their offspring throughout the entire development process, the mother concludes the rearing with what seems to be a brief stage of training, where obedience behavior is observed by her now adult offspring already adult, showing traits of a social organization in this group of beetles (Wilson 1971; Costa 2006).

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Literature Cited

Borowiec, L. and Świętojańska, J. (2018) *World Catalog of Cassidinae*, Wrocław, Poland. Consulted 30 May 2020. Available at: http://www.cassidae. uni.wroc.pl/katalog%20 internetowy/index.htm

Cedeño-Loja, P. and Chaboo, C.S. (2020) Natural history notes on *Cyrtonota sericinus* (Erichson, 1847) in Ecuador (Coleoptera: Chrysomelidae: Cassidinae: Mesomphaliini). *Revista Peruana de Biología*, *27(2)*: 127-130.

Costa, T. (2006) The other insect societies. The Belknap Press of Harvard University Press. Massachusetts, United States of America. 767 pp.

Chaboo, C. (2002) First report of immatures, genitalia and maternal care in *Eugenysa columbiana* (Boheman) (Coleoptera: Chrysomelidae: Cassidinae: Eugenysini). *The Coleopterists Bulletin*, *56*(1): 50-67.

Chaboo, C.S., Frieiro-Costa, F., Gómez-Zuritac, J. and Westerduijnd, R. (2014) Origins and diversification of subsociality in leaf beetles (Coleoptera: Chrysomelidae: Cassidinae: Chrysomelinae). *Journal of Natural History*, *48*(37-38): 2325-2367.

Choe, J. (1988) Maternal Care in *Labidomera suturela* Chevrolat (Coleoptera: Chrysomelidae: Chrysomelinae) From Costa Rica. *Psyche A Journal of Entomology*, *96:* 63-66.

Clutton-Brock, T. (1991) *The Evolution of Parental Care*. Princeton University Press. New Jersey, United States of America. 368 pp.

Cornell, H. and Hawkins, B. (1995) Survival patterns and mortality sources of herbivorous insects: some demographic trends. *The American Naturalist*, *145*: 563-593.

Cuozzo, M., Frieiro-Costa, F. and Souza, B. (2017) Life history of *Paraselenis spaethiechoma dichroa* Germar 1824 Coleoptera Chrysomelidae Cassidinae in natural conditions of Atlantic Forest from Brazil. *Journal of Natural History*, *51*(9-10): 531-543.

Dury, G., Bede, J. and Windsor, D. (2014) Preemptive circular defence of immature insects: definition and occurrences of cycloalexy revisited. *Psyche A Journal of Entomology*, *2014*(9-10): 1-13.

Flinte, V., Hentz, E., Morgado, B., Lima, A., Khattar, G., Monteiro, F. and Macedo, M. (2015) Biology and phenology of three leaf beetle species (Chrysomelidae) in a montane forest in southeast Brazil. *In*: Jolivet, P., Santiago-Blay, J., Schmitt, M. (Eds) Research on Chrysomelidae 5. *ZooKeys*, *547*: 119-132.

Flowers, R. and Janzen, D. (1997) Feeding records of Costa Rica leaf beetles (Coleoptera: Chrysomelidae). *Florida Entomologist*, *80*(3): 334-366.

Gomes, P., Prezoto, F. and Frieiro-Costa, F. (2012) Biology of *Omaspides pallidipennis* Boheman, 1854 (Coleoptera: Chrysomelidae: Cassidinae). *Psyche A Journal of Entomology*, *2012*: 1-8.

Hinton, H. (1981) *Biology of Insect Eggs, Vol. 1*. Pergamon Press, Elmsford. United States of America, New York. 473 pp.

Holdridge, L. (1967) *Life Zone Ecology*. Tropical Science Center. San José, Costa Rica. 206 pp.

Jolivet, P. (1988) Sélection trophique chez les Cassidinae (Coleoptera Chrysomelidae). *Publications de la Société Linnéenne de Lyon*, *57*(9): 301-320.

Jolivet, P. (1997) *Biologie des coléoptères chrysomélides*. Société novelles des édition boubée, Paris, 279 pp.

Kudo, S. and Ishibashi, E. (1995) Notes on maternal care in the ovoviviparous leaf beetle *Gonioctena japonica* (Coleoptera: Chrysomelidae). *Canadian Entomologist*, *127*: 275-276.

Leocádio, M., Simões, M., Sekerka, L., Schrago, C., Mermudes, J. and Windsor, D. (2020) Molecular systematics reveals the origins of subsociality in tortoise beetles (Coleoptera, Chrysomelidae, Cassidinae): Evolution of subsociality in Cassidinae. *Systematic Entomology*, *2020:* 1-17.

Macedo, M., Flinte, V., Abejanella, A. and Chaboo, C.S. (2015) Three new reports of subsocial tortoise beetles from South America (Chrysomelidae: Cassidinae). *Annals of the Entomological Society of America*, *108*(6): 1088-1092.

Machado, G. and Trumbo, S. (2018) Parental care. pp. 203-218. *In*: Córdoba-Aguilar, A., González-Tokman, D. and González-Santoyo, I. (eds.) *Insect Behavior: From Mechanisms to Ecological and Evolutionary Conse-quences*. Oxford University Press. Oxford, United Kingdom.

Medal, J.C. (2008) Efects of temperature on the development and survival of *Metriona elatior* (Coleoptera: Chrysomelidae) Immatures. *Florida Entomologist*, *91*(3): 491-493.

Rodriguez, V. (1994) Sexual behavior in *Omaspides convexicollis* Spaeth and *O. bistriata* Boheman (Coleoptera: Chrysomelidae: Cassidinae), with notes on maternal care of eggs and young. *The Coleopterists Bulletin*, *48*(2): 140-144.

Royle, N., Smiseth, P. and Kölliker, M. (2012) *The Evolution of Parental Care.* Oxford University Press. Oxford, United Kingdom. 376 pp.

White, R. (1983) *Beetles of North America*. Edt. Peterson Field Guides. New York, United States of America. 368 pp.

Wilson, E. (1971) *The Insect Societies*. Harvard University Press. Cambridge, United Kingdom. 548 pp.

Windsor, D. (1987) Natural history of a subsocial tortoise beetle, *Acromis sparsa* Boheman (Chrysomelidae, Cassidinae) in Panama. *Psyche A Journal of Entomology*, *94*: 127-150.

Windsor, D. and Choe, J. (1994) Origins of parental care in Chrysomelid beetles. *In*: Jolivet, P. Cox, M. and Petitpierre, E. (eds). Novel aspects of the biology of Chrysomelidae. Kluver Academic Publishers, Netherlands. p. 111-117.

Windsor, D., Riley, E. and Stockwell, H. (1992) An introduction to the biology and systematics of Panamanian tortoise beetles (Coleoptera: Chrysomelidae: Cassidinae). pp. 372-391. *In*: Quintero, D. and Aiello, A. (eds.) *Insects of Panama and Mesoamerica*. Oxford University Press. Oxford, United Kingdom. 692 pp.