Host plant specificity and feeding preferences of *Morpho epistrophus argentinus* (Lepidoptera: Nymphalidae) larvae in coastal woodlands of Argentina

Especificidad de la planta hospedadora y preferencia alimentaria de larvas de *Morpho epistrophus argentinus* (Lepidoptera: Nymphalidae) en bosques costeros de Argentina

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ABSTRACT

The selection of suitable host plants for larval development is critical for most herbivorous insects. In this study, we examined host plant preferences of larvae from Epistrophus white morpho butterfly, *Morpho epistrophus argentinus* (H. Fruhstorfer), a specialized butterfly that oviposits on a few plant species. In many species, the selection of host plant for larvae development is under the control of ovipositing females and the role of larvae in host selection is minimal. At field, we characterized larval host plant use in coastal woodland patches of its southernmost distribution range (36º 25' S, 56º 57' W; Argentina). All sampled *M.e. argentinus* larvae groups (n = 40) were found on *Scutia buxifolia* trees, although the number of larval groups did not correlate with cover of this plant at patch scale. Translocation experiments showed that *M.e. argentinus* larvae translocated to unsuitable host plants had a shorter residence time than those translocated to suitable (i.e. control) hosts. Choice assays

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made also indicated strong feeding preferences of wild larvae for *S. buxifolia* leaves. The results highlight the high degree of host specificity of *M.e. argentinus* by *S. buxifolia*, and reveal that growing larvae preference for host plant matches that of ovipositing females.

Palabras clave — Butterfly, host plant selection, larval behavior, larval preferences.

RESUMEN

La selección de plantas hospedadoras adecuadas para el desarrollo larvario es crítica para la mayoría de los insectos herbívoros. En este estudio, examinamos las preferencias de la planta hospedadora de larvas de la mariposa Bandera Argentina, *Morpho epistrophus argentinus* (H. Fruhstorfer), una mariposa especializada que ovipone en pocas especies de plantas. En muchas especies, la selección de plantas hospedadoras para el desarrollo de las larvas está bajo el control de las hembras y el papel de las larvas en la selección de hospedadores es mínimo. En el campo, caracterizamos el uso de la planta hospedadora por parte de las larvas en parcelas de bosques costeros de su área de distribución más meridional (36º 25' S, 56º 57' W; Argentina). Todos los grupos de larvas de *M.e. argentinus* muestreados (n = 40) fueron encontrados en árboles de la especie *Scutia buxifolia*, aunque el número de grupos de larvas no se correlacionó con la cobertura de esta planta a escala de parche. Experimentos de translocación demostraron que las larvas de *M.e. argentinus* translocadas a plantas hospedadoras inadecuadas tuvieron un tiempo de residencia más corto que las translocadas a hospedadores adecuados (*i.e.* controles). Ensayos de elección realizados también indicaron fuertes preferencias de alimentación de las larvas por hojas de *S. buxifolia*. Los resultados resaltan el alto grado de especificidad de *M.e. argentinus* por el hospedador *S. buxifolia* y revelan que la preferencia de las larvas por la planta hospedadora coincide con la de las hembras cuando oviponen.

Keywords — Mariposa, selección de planta hospedadora, comportamiento de las larvas, preferencias de la larva.

INTRODUCTION

In plant feeding insects, the selection of suitable plants for neonate larvae development is critical as it affects their growth rates and ultimately, their fitness. It has been proposed that females of these species should choose hosts where larval performance is optimal («mother knows best» principle; Thompson, 1988). Accordingly, in many species, the selection of host plant species for larvae development is under the control of ovipositing females (Wiklund, 1975; Futuyma, 1990; Thompson and Pellmyr, 1991; Nylin and Janz, 1993; Price, 2003; Gripenberg *et al*., 2010). In such species, the role of larvae in host selection is minimal and usually constrained by the difficulty of larvae to move across plants (Prager *et al*., 2014). In the other extreme, ovipositing females of some species play a minor role in host plant selection, and larvae must be able to find suitable hosts for their development (Chew, 1977; Bernays and Chapman, 1994; Berdegué *et al*., 1998, Crespo and Castelo, 2008).

Many butterfly species have a wider range of suitable host plants for larval development than that they actually use for oviposition (Thompson and Pellmyr, 1991). This reflects mother's preferences and it would be the result of females maximizing their own performance rather than seeking to improve offspring development and survival with their choices (Mayhew, 1997; Prager *et al.,* 2014). In this scenario, larvae may be restricted in host plant use by its mother's preference, and their performance will depend on selection of high-quality hosts by its mother. However, larvae may not be entirely dependent on female's decisions. In some butterfly species, oviposition is not selective with respect to host plant, and larvae must to locate the suitable host (Wiklund, 1984). Then, larval host selection can act as a reinforcing (or correcting) mechanism of maternal host choice, through which immature offspring can circumvent eventual female's oviposition errors (Gamberalle-Stille *et al*., 2014). In fact, it has been found in the comma butterfly (*Polygonia c-album* Linnaeus) that larvae can show similar host preference than ovipositing females (Nylin and Janz, 1996; Nylin, Bergström and Janz, 2000; Gamberalle-Stille *et al.*, 2014). Therefore, host-plant choice is not necessarily restricted to female or larvae decisions, and can imply hierarchical mechanisms where both female and larvae decisions are involved.

In this study, we examined preferences of the butterfly larvae *Morpho epistrophus argentinus* (H. Fruhstorfer) for host plant, in coastal woodlands of central-east Argentina. This conspicuous and specialized *Morpho* butterfly oviposits on a few plant species (Ackery, 1988; Canals, 2000; Beccaloni *et al.,* 2008). The larvae feed on plant where they hatch, but Orlandi (2016) found that larvae of *Morpho epistrophus* can be feed with other plant species than those where they were collected. At our study site in the southernmost distribution range of *M.e. argentinus*, females laid eggs on only one tree species, *Scutia buxifolia* (Rosales:Rhamnaceae). However, female choice of this perennial tree species may be restricted because the offspring that overwinter in the stage, need protection and shelter, and therefore, may not reflect the larval preferences. In that sense, *S. buxifolia* is the most abundant perennial native species in the southernmost distribution of the butterfly. However, in the last decades, native woodlands at this range have been severely reduced which threaten the biota that depend on this habitat type (Goya *et al*., 1992; Arturi and Goya, 2004). Therefore, considering that *M.e. argentinus* is at risk due to habitat loss, determine the ability of larvae to use alternative host-plant species is important for conservation purposes. Then, our objectives were to characterize plant use by larvae and to assess their host plant preferences using both a translocation experiment and feeding choice assays. We expected that if larvae preferences match those of ovipositing females, they must to prefer to stay on *S. buxifolia* trees and feed on their leaves avoiding unusual host plants as substrate and food.

MATERIALS AND METHODS

Species studied

Morpho epistrophus argentinus is a big and conspicuous nymphalid butterfly (wingspan: 90–110 mm) that inhabits riparian and xerophytic forests along North and East Argentina. The conservation status of this species has not been evaluated yet, but at their southernmost distribution range it is considered as threatened due to the degradation and loss of suitable habitat (Nuñez-Bustos, 2009). At this range, adults are seen flying between late January and March (Gallardo, 1908; Nosswitz, 1927). The females lay small eggs (~2 mm diameter) under the leaves of specific plant species such as *S. buxifolia*, *Lonchocarpus nitidus* (Fabales: Fabaceae) and *Inga vera* (Fabales: Fabaceae) (Gallardo, 1907; Canals, 2000; Nuñez Bustos, 2009). At the southernmost distribution range of *M. e. argentinus*, only *S. buxifolia* is present. Larvae emerge after about two weeks, remaining on the host plant (Bourquín, 1944). They do not eat and stay on diapauses gregariously over winter months (Gallardo, 1908; Otero and Marigo, 1990). During September, they resume feeding activity. After first molt, the larvae exhibit an intense reddish color that presumably makes them highly aposematic (García *et al.*, 2014). They rest gregariously during daylight hours, forming clusters of up to 30 individuals. Feeding occurs mostly during night when the cluster breaks up (Turner, 1936). Larvae reach a size of 55-70 mm at the final instars (Bourquín, 1944). Early in summer (December-January), the larvae migrate from their host plants and pupate.

Field methods

From October to early December 2015 (austral spring), we searched for larvae clusters at woodland patches at General Lavalle (36º 25'S, 56º 57' W), Buenos Aires province, Argentina. The site comprises patches of deciduous woodland of *Celtis ehrenbergiana* and *S. buxifolia*, with a mean vegetation height < 5m, surrounded by pastures (Lacoretz, 2018).

We quantified host-plant specificity through field observations and censuses. We searched for larvae clusters at 10 randomly selected woodland patches in which the preferred host plant (*S. buxifolia*) of *M.e. argentinus* larvae was absent and at other 10 patches where the host plant was present. We surveyed the patches using a 4 x 40 m strip transect, walking through them and carefully searching for *M.e. argentinus* larvae. Once localized, we identified the host plant species and counted the number of larvae in the cluster. For each larvae cluster, we measured the body length (nearest 2 mm) from four arbitrarily selected larvae. Body length was used to estimate the instar to which each group belonged following Orlandin (2016).

We also estimated species cover in each of the 20 woodland patches using eight randomly located sampling points within a 20m radius area from the starting point of the strip transect. At each point, a sampling rod (7 m height) marked off in 1m intervals was held vertically on the ground and the plant species contacting the rod were recorded. Cover for each plant species was estimated as the percentage of sampling points at each woodland patch where the species was present (*i.e.* contacted the rod).

In one woodland patch, we also searched for *M.e. argentinus* larvae within a plot of 50 x 50 m, and when localized, we marked the location of the cluster with a colored and numbered tape for cluster identification. These larval groups (n = 12) were revisited after 30 days to note the permanence in the site where they were first found.

Host plant specificity experiments

To determine host specificity of *M.e. argentinus* under field conditions, we performed experimental translocations in groups of larvae during late November. Twenty larvae groups were removed from host plants where they were found, and moved to trees located more than 30 m apart. Ten randomly selected of these groups were placed on branches of *S. buxifolia* (its natural host plant), and the other 10 groups on branches of *C. ehrenbergiana*. The latter is the dominant deciduous tree in the woodlands and thus broadly available for consumption by larvae. Larval size of these groups ranged from 35 to 45 mm (presumably corresponding to 3rd–4thinstars) and group size was 8–19 individuals. We monitored these groups every 3–4 days up to 17 days after the beginning of the experiment. On each visit, we recorded the number of larvae present at each group and inspected neighbor trees to detect missing individuals or groups.

Feeding preferences

We also tested the feeding preferences of *M.e. argentinus* larvae using a choice assay at our field station. We collected 20 individuals (40–52 mm in length; presumably 4th instar) from 5 larvae clusters (4 individuals/group) at evening hours (18:00–20:00 h) during November. Each larva was placed individually on a plastic box (approximately 15 x 25 x 10 cm) with the bottom covered with a filter paper slightly moistened with a few drops of water. Boxes were closed with perforated lids and kept in the shade under natural photoperiods and environmental temperatures. After collection, caterpillars were deprived of food for about 12 h. Then we offered leaves of the two most common tree species at our study area to individual larva. Five 1x1 cm pieces of fresh *S. buxifolia* leaves and 5 of *C. ehrenbergiana* leaves were arranged alternately along the edges of the boxes. Trials started at 8:00 hs. After 12 h, we collected the remaining leaf pieces from each box and estimated the individual consumption of each species as the number of quarters of eaten leaf pieces. Then, the assay was replicated to estimate nocturnal consumption. After the 24 h trial, 10 of these larvae were returned to their original clusters in the field and the remaining 10 individuals were subjected to a second experiment. At this, the larvae were kept in boxes and were induced to feed only on green leaves of *C. ehrenbergiana* during 3 consecutive days. After this period, a choice experiment as described above was conducted during night hours. After testing, the larvae were returned to their original field locations. No larval mortality was recorded during the experiments.

Data analyses

We used descriptive statistics to quantify host plant specificity and the characteristics of plant hosts. The occurrence of *M.e. argentinus* larvae in woodland patches where *S. buxifolia* plants was present and absent was compared using a Fisher's exact test. Relationship between the number and size of larvae and the size of group were assessed using Spearman rank correlations. We used a Cox proportional hazard mixed regression model to analyze the results of the translocation experiment. The model included the residence time, defined as the number of visits in which larvae were seen at the translocation site, as the response variable, host plant treatment as a fixed factor and larvae group identity as a random variable. Analysis was performed using the COXME package, v2.7.1 (Therneau, 2015) in the R environment (v3.3.0, R Core Team, 2016). Feeding preferences of *M.e. argentinus* larvae were tested using generalized linear mixed models (GLMM) with a Poisson structure and a log-link function. We performed these analyses using the lme4 package, v1.1-17 (Bates *et al.*, 2015) for R. First, we tested for differences in leaf consumption of each tree species by individuals recently collected from the field. For this model, the response variable was the number of leaf quarters consumed, and time of day (day or night), plant species and the interaction term as predictors. Individual identity was included as a random variable. In a second analysis, we compared the feeding preferences of individuals before and after being induced to feed on *C. ehrenbergiana*. The model included sampling time (before or after induction) and plant species as predictors, and larvae identity as a random factor. The interaction was not assessed because no larval feeding was detected on *C. ehrenbergiana* before the induction treatment. For all these models, we used residual and normal probability plots to check model assumptions. We assessed the global contribution of predictors to the response variables by comparing the deviance of nested models (i.e., with and without the factor) using likelihood-ratio tests.

We report means with ± SE for all data (unless otherwise specified). All tests are two-tailed, and differences were considered significant at $P < 0.05$.

RESULTS

The occurrence of *M.e. argentinus* larvae was strongly related to the presence of *S. buxifolia* plants in the woodland patches (Fisher's exact test, $P < 0.01$). *Morpho epistrophus argentinus* larvae were recorded in seven out of 10 woodland patches with *S. buxifolia*, but in none of 10 patches where *S. buxifolia* was absent. Sampled woodland patches were mostly dominated by *C. ehrenbergiana* (mean cover percentage: 58.7 %; SD: 30.1 %). In woodland patches with presence of *S. buxifolia*, its mean

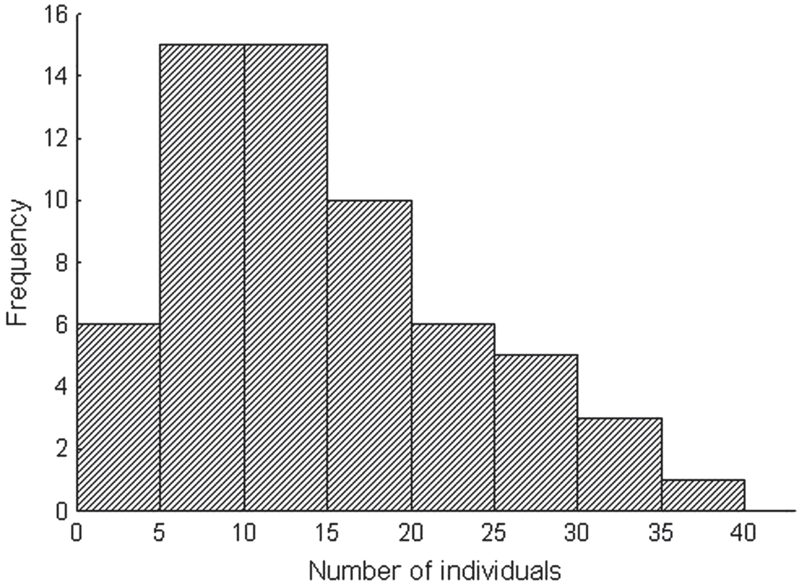

Figure 1 Frequency of group sizes of *M. e. argentinus* larvae (n = 40). Larval body size varied from 15 to 35 mm in length (1st –3rd instars).

cover was 56.7 % (SD: 22.1 %) and was co-dominant with *C. ehrenbergiana* (mean cover percentage of this last species: 42.5 %; SD: 27.8). Other tree species (e.g., *Schinus longifolius*, *Jodina rhombifolia*) had a vegetation cover of less than 5 % at the studied patches.

We found a total of 40 larvae groups, all located on branches of *S. buxifolia*. Larval size of groups recorded varied between 15 and 34 mm, corresponding to 1st-3rd instars. Larvae size was not related to group size (Spearman rank correlation, $R = 0.07$, $P = 0.79$), and the number of larval groups was not related to *S. buxifolia* cover at patch scale (Spearman rank correlation, $R = 0.19$, $P = 0.59$). Furthermore, surveyed larvae groups at the 50 x 50 m plot (n= 12) remained in the same branches where first observed after 30 days.

Host plant specificity experiments

From the 10 larvae groups translocated to *C. ehrenbergiana*, only one remained on this host plant after 17 days. Three other larvae groups migrated to neighbor *S. buxifolia* trees and the remaining six were missing. The *C. ehrenbergiana* plant which the larvae group remained showed slight signs of herbivory on its leaves. In contrast, nine of the larvae groups translocated to *S. buxifolia* branches remained in their new location. Only one group was missing and it was not observed in the neighboring trees. As expected, residence time was significantly lower for individuals translocated to *C. ehrenbergiana* than to *S. buxifolia* trees (Cox regression model: $\chi^2_1 = 16.77$, $P < 0.01$; Fig. 2).

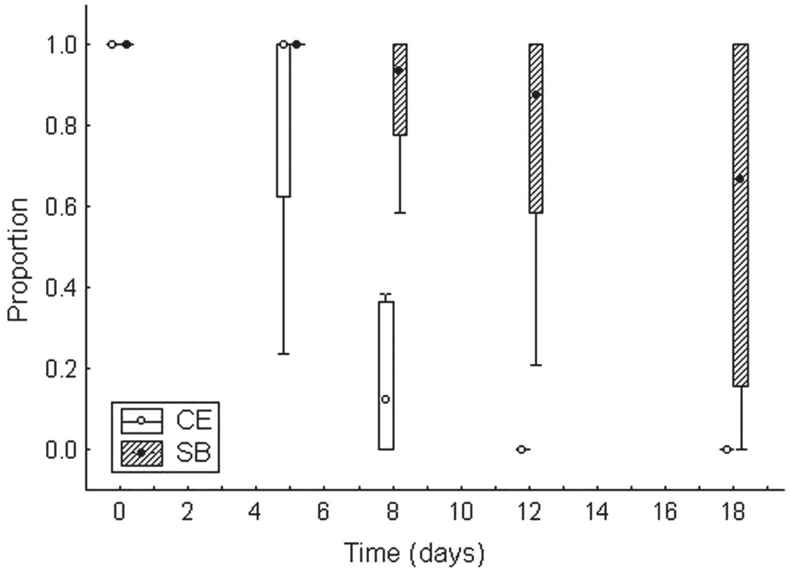

Figure 2 Proportion of *M.e. argentinus* larvae that remained in clusters translocated to *C. ehrenbergiana* (CE; n = 10; white boxes) and *S. buxifolia* trees (SB; n = 10; sptriped boxes) along the experiment. Median (dots), interquartil range (boxes) and minimum and maximum values (whiskers) values are shown.

Feeding preferences

The choice experiment showed a marked preference of *M.e. argentinus* for feeding upon *S. buxifolia* leaves ($\chi^2_1 = 305.47, P < 0.01$; Fig. 3a). Larval feeding activity was highest during the night ($\chi^2_1 = 19.20, P < 0.01$; Fig. 3a), but preferences did not change with the time of day (interaction term: $\chi^2_1 = 0.17, P = 0.68$). Although the larvae increased slightly the consumption of *C. ehrenbergiana* leaves after being induced to feed on this host plant (Fig. 3b), they fed preferentially on *S. buxifolia* leaves both before and after that treatment (plant species: $\chi^2_1 = 208.31, P < 0.01$, sampling time: $\chi^2_1 = 0.28, P = 0.59$; Fig. 3b).

DISCUSSION

It is widely accepted that herbivorous insects should prefer host plant species that will maximize their fitness. This concept can be expanded to include the selection of oviposition sites, as females should choose those host plants that are optimal for the development of their offspring (Thompson, 1988; Valladares and Lawton, 1991; Scheirs *et al.*, 2000; Gripenberg *et al.*, 2010). *Morpho epistrophus argentinus* oviposits on a few plant species (Ackery, 1988; Canals, 2000; Beccaloni *et al.*, 2008) and, in its southernmost distribution range, it uses exclusively *S. buxifolia* for oviposition. Consistent with this, all larvae groups in this study were found attached to branches of *S. buxifolia*, in woodland patches that had this tree as a co-dominant species. Conversely, we could not find *M. e. argentinus* larvae in patches were *S. buxifolia* was absent. These observations suggest a high degree of specializa-

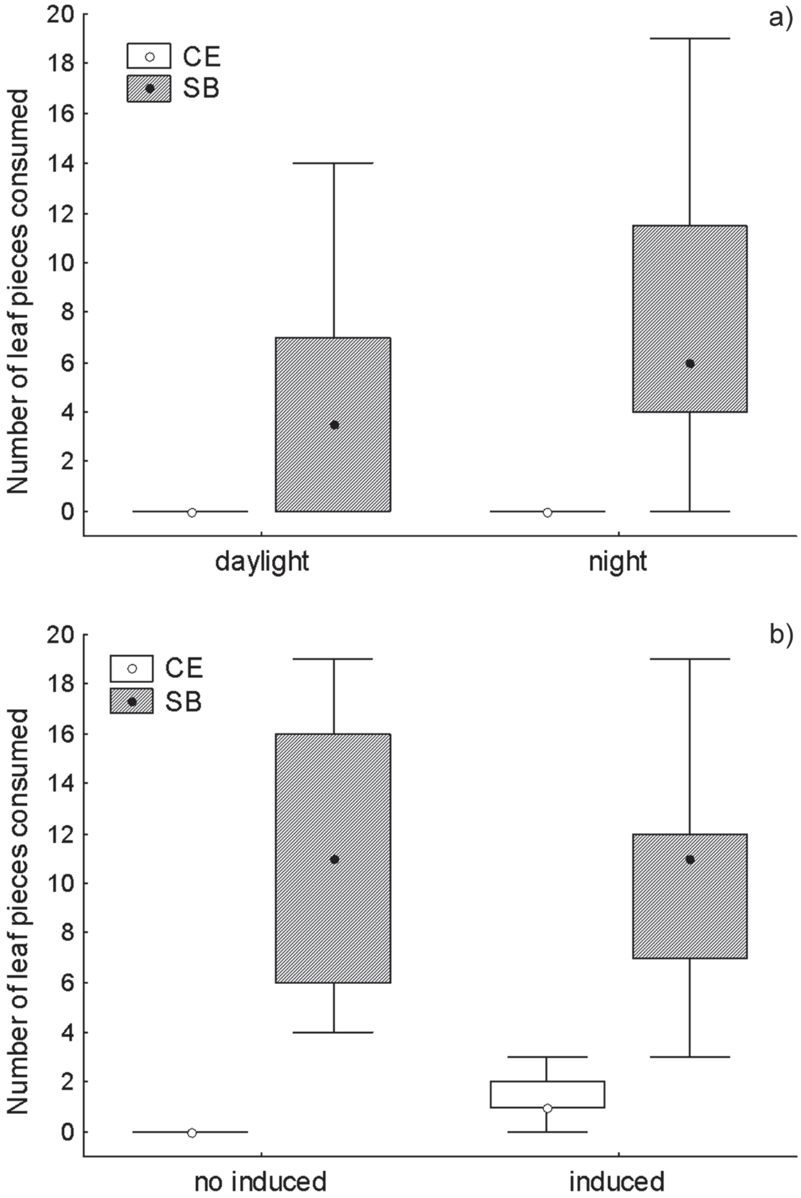

Figure 3 Consumption of *C. ehrenbergiana* (CE; white boxes) and *S. buxifolia* (SB; grey boxes) leaves by wild *M.e. argentinus* larvae in choice assays. a) Leaf consumption of each plant species during daytime and night time (n = 20 larvae). b) Leaf consumption of each plant species of individual larvae before and after being induced to feed on *C. ehrenbergiana* leaves for three days (n = 20). Medians (dots), interquartile ranges (boxes) and minimum and maximum values (whiskers) are shown.

tion in host plant use, although the causes of such specificity are not known yet. It is possible that *S. buxifolia* provides larvae with crucial nutrient components or secondary compounds that maximize their growth and survival. Alternatively, this plant species could provide better habitat quality for offspring that begin to emerge at the end of the summer and overwinter as larvae. *S. buxifolia* is the main evergreen species present at our study area, and therefore, it can provide refuge and food for *M.e. argentinus* throughout the larval stage.

Our experiments also demonstrate that larvae of *M.e. argentinus* have a strong preference for settling and feeding on *S. buxifolia.* Most of the caterpillar's groups translocated to *C. ehrenbergiana* abandoned this host plant within a week. We observed that three of these larvae moved to nearby *S. buxifolia* trees, indicating that larvae are able to switch among host plants, at least after achieving a certain degree of development. This host-switching ability of mobile larvae might allow them to reduce fitness costs associated to adverse development conditions.

Feeding experiments further confirm this apparent larval preference for *S. buxifolia*. Wild caterpillars showed strong preferences for *S. buxifolia* leaves in choice assays, even after being induced for 48 h to feed upon an alternative host plant. It is possible that such induction period was insufficient to change larval preferences, but it has been observed that feeding preferences can change even after shorter periods (Jermy *et al.*, 1968). The results suggest that host-plant preferences of *M.e. argentinus* larvae could be innate or acquired through imprinting in early life stages (Jermy *et al.*, 1968; Yamamoto, 1974; Jermy, 1987; Bernays and Weiss, 1996; Silva, Gonçalves and Moreira, 2014; Rosenwald *et al.*, 2017). The observed preferences could reflect larval constraints in host selection if larvae are influenced by mother choice at early stages rather than active host choice. The mechanisms underlying host selection in this species deserves further investigation. For example, additional cross-fostering experiments of newly hatched larvae could help to understand how host plant preferences develop in *M.e. argentinus*.

In sum, our results show that larval preferences for host plants were highly species-specific and match those of ovipositing females in *M.e. argentinus*. From a conservationist perspective, such host-plant species specificity implies that actions to secure the status of this butterfly must rely on local ecological information and should be focused on habitat and host-plant preservation. Therefore, considering that native woodlands have suffered a strong reduction at the southernmost distribution range, the persistence of *M.e. argentinus* in this region will depend on the efforts made for the conservation of the remaining native woodland areas.

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ETHICAL STATEMENT

No larva died or was physically damaged as a consequence of our experimental procedures. During manipulations, we handled the individuals carefully to remove them from the field and to return them to their original locations after the experiments.

PARTICIPATION

MEC, MVL, MCDM and GJF planed and designed the study; MVL and MCDM performed field censuses; GJF performed translocation experiments and field observations; MEC executed feeding preferences experiments; MEC and GJF performed all data analyses; MEC, MCDM and GJF wrote the manuscript.

CONFLICTS OF INTEREST

The authors declare that there is no conflict of interest.

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