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Battus polydamas (Lepidoptera: Papilionidae) uses the open-field *Aristolochia sessilifolia* (Piperales: Aristolochiaceae) as its host plant in Uruguayan savanna areas

Nicolás Oliveira Mega[1,], Vanessa Willems Scalco[2], Guilherme Wagner Gutierrez Atencio[2], Ana Beatriz Barros De Morais[3], and Helena Piccoli Romanowski[1]*

Abstract

Butterfly species with broad geographical ranges are expected to be tolerant of ecological/ environmental constraints and to shifts in host plant use. This seems to be the case of the butterfly *Battus polydamas* (Linnaeus, 1758) (Lepidoptera: Papilionidae), which in the absence of better host plants may lay eggs on low-quality *Aristolochia* (Piperales: Aristolochiaceae) plants, increasing the developmental time and mortality rate of immatures. *Battus polydamas* populations from the Uruguayan savanna were investigated to verify whether *A. sessilifolia* (Klotzsch) Duch. was being used as a host plant in grassland areas where no other *Aristolochia* species are available. Species distribution models (SDM) for both species were built to verify whether ecological conditions could cause overlapping distributions between them. Extensive field surveys were performed to investigate whether *B. polydamas* actually uses *A. sessilifolia* as larval food source in the field. The performance of larvae on such host plant was also tested under controlled conditions in a laboratory environment. The SDM analysis showed a large overlap between the distributions of *B. polydamas* and *A. sessilifolia*. Field surveys revealed the occurrence of an interaction between the butterfly and the potential host plant, and laboratory experiments corroborated that *B. polydamas* larvae can successfully use *A. sessilifolia* as a host plant. The wide distribution of *B. polydamas* suggests that this butterfly species evolved the ability to develop in unfavorable environments (e.g., poor host plants, adverse climate), allowing it to use virtually all *Aristolochia* species of the Neotropics as host plants. Thus, adult females appear to have developed the capacity to identify any *Aristolochia* spp. as a suitable host plant, enabling the exploitation of various landscapes and ecoregions.

Key Words: ecological plasticity; grassland areas; larval performance; Neotropical Region; species distribution model; swallowtail butterflies

Resumen

Se espera que las especies de mariposas con rangos geográficos amplios sean tolerantes a las limitaciones ecológicas / ambientales y cambios en el uso de la planta hospedante. Y este parece ser el caso de la mariposa *Battus polydamas* (Linnaeus, 1758) (Lepidoptera: Papilionidae), que en ausencia de mejores plantas hospedadoras pueden poner huevos en *Aristolochia* (Aristolochiaceae) de baja calidad, aumentando el tiempo de desarrollo y la tasa de mortalidad de los estados inmaduros. Es así como poblaciones de *B. polydamas* de la sabana Uruguaya fueron investigadas a objeto de verificar si *A. sessilifolia* (Klotzsch) Duch. estaría siendo utilizada como planta hospedera en zonas de pastizales, donde no se encuentra ninguna otra especie de *Aristolochia*. A este respecto, se construyeron modelos de distribución de especies (SDM) para ambas especies, con el objetivo de verificar si las condiciones ecológicas podrían permitir la sobreposición de distribución geográfica entre ellas. Se realizaron encuestas de campo extensivas para investigar si *B. polydamas* realmente utiliza *A. sessilifolia* como fuente de alimento larval en condiciones naturales. El rendimiento de las larvas en esta planta hospedera también se puso a prueba bajo condiciones controladas en laboratorio. El análisis de SDM mostró un gran solapamiento entre las distribuciones de *B. polydamas* y *A. sessilifolia*. Los estudios de campo revelaron la ocurrencia de interacción entre la mariposa y la potencial planta hospedera, y los experimentos de laboratorio corroboraron que las larvas de *B. polydamas* pueden utilizar con éxito *A. sessilifolia* como planta hospedera. La amplia distribución de *B. polydamas* sugiere que esta especie de mariposa ha tenido la capacidad de desarrollarse en ambientes desfavorables (*e.g.* pobres en plantas hospedadoras, clima adverso) durante su evolución, lo que le ha permitido utilizar prácticamente todas las especies de *Aristolochia* del Neotrópico como hospedera. Por lo tanto, las hembras adultas podrían haber desarrollado la capacidad de identificar cualquiera *Aristolochia* como hospedera adecuada, permitiendo la explotación de diferentes paisajes y ecorregiones.

Palabras Clave: desarrollo larval; modelo de distribución de especies; papilionidos; pastizales; plasticidad ecológica; región Neotropical

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Among the several variables affecting the distribution of herbivorous insects, the richness and abundance of host plants in different habitats are some of the most important ecological constraints to survival (Dennis et al. 2000). Herbivore species with the ability to explore a wide range of host plants are expected to have larger distributions when compared with those restricted to just a few hosts (Gaston et al. 1997). Generally, butterfly species with broad geographical ranges are expected to be more tolerant to ecological environmental constraints and to shifts of host plant use than species with smaller distributions. Therefore, with the increase in ecological specialization of the herbivores towards certain groups of plants, it is expected that the presence of an insect species in some areas would be much more influenced by the availability of food sources to immatures than by environmental constraints affecting the survival of adult forms (Dennis et al. 2005).

From the host plant selection standpoint, the choice to lay eggs on suitable food sources is one of the most important factors affecting the chances of a caterpillar developing into a viable butterfly (Chew 1977). The chemical and physical properties of different host plants, such as the concentration of nutrients and leaf toughness, may vary within and between species, producing changes in life histories (Scriber & Slansky 1981; Bernays & Chapman 1994). Another effect of nutritional quality variation of host plants is the decrease in survival caused by the extension of larval development time, which increases the exposure of larvae to predators and other natural enemies (Loader & Damman 1991). Therefore, changes in the type and quality of food may significantly alter larval performance and the priorities of resource allocation on highly monophagous species, whereas it would be less of a concern to polyphagous species (Dennis et al. 2005).

The butterfly *Battus polydamas* (Linnaeus, 1758) (Papilionidae: Troidini) is a broad-range species, occurring from central Argentina to southern USA. The adults are common in dry and disturbed habitats, while rare in humid forests (Tyler et al. 1994). Females lay egg clutches on about 24 *Aristolochia* species (Beccaloni et al. 2008), having a general preference for host plants that optimize the development of their larvae (Fagua et al. 1998). Under adverse conditions, or in the absence of better food sources to immatures, *B. polydamas* may lay eggs on low-quality host plants (Tyler et al. 1994), at the cost of an increase in the development time and mortality rate of immature forms (Fagua et al. 1998).

The generalist characteristic of *B. polydamas*, evident due to the large number of host plant species chosen by females during oviposition, suggests that many species of *Aristolochia* might be suitable as food sources for its larvae. Some authors have suggested that *B. polydamas* can, as a matter of fact, use all Neotropical *Aristolochia* spp. as host plants (Tyler et al. 1994), even though the suitability of various of these species has not been tested. According to Fagua et al. (1998), host plant shifts do not seem to significantly affect the survival rate of *B. polydamas* immatures, in spite of females showing a preference for more abundant species within their residential areas. On the other hand, the encounter-frequency theory (Southwood 1961) predicts that the use of more host plants would provide access to more biotopes, which would allow access to more resources for immatures of *B. polydamas*. Thus, polyphagous butterfly species could more easily adopt novel hosts and biotopes during range expansions when compared with monophagous species (Thomas et al. 2001). Therefore, it is expected that the great plasticity of *B. polydamas* would allow wider distributions by enhanced contact with a varied range of *Aristolochia* resources.

Aristolochia sessilifolia (Klotzsch) Duch. (Piperales: Aristolochiaceae) is a plant commonly found in natural grasslands from southern South America (Barros & Araújo 2013), especially in areas of the Uruguayan savanna, Espinal, and Southern Cone Mesopotamian savanna ecoregions (Olson et al. 2001). This plant species has a prostrate habit, growing in sunny open areas of dry shallow soils (Hoehne 1942). Individuals are often found in small patches from spring to autumn, suffering defoliation during winter due to frost. During the coldest months of the year the plants survive adverse conditions thanks to the perennial rhizome that promotes re-growth in the early spring. Its use as host plant by Troidini butterflies has already been observed for *Euryades* species (Beccaloni et al. 2008) but has never been recorded for other Troidini butterfly species.

The close association between the Troidini butterflies and the plants of the genus *Aristolochia* is a well-known example of coevolution between herbivores and host plants (Ehrlich & Raven 1964; Silva-Brandão & Solferini 2007; Fordyce 2010). It has been suggested that *Aristolochia* plants might have evolved toxic secondary compounds to avoid herbivorous attacks from insects (Ehrlich & Raven 1964; Bernays & Graham 1988; Brown et al. 1991; Nishida & Fukami 1989). On the other hand, the ecological specialization of the herbivores could have promoted the ability to neutralize the toxicity of herbivore deterrents, followed by an evolutionary step towards the sequestration of toxins to use them as chemical defense against predators (Futuyma & Keese 1992; Opitz & Müller 2009; Janz 2011; Morais et al. 2013).

Considering the generalist behavior and the broad range of *B. polydamas*, the populations from the Uruguayan savanna were investigated to discover whether they could be successfully using *A. sessilifolia* as a host plant in grassland areas, where few or no forest *Aristolochia* species are available. First, species distribution models (SDM) for *B. polydamas* and *A. sessilifolia* were built to verify whether ecological conditions would allow overlapping distributions between the herbivore and the host plant. Based on those SDMs, field surveys in areas where models suggested high probability of sympatry between the 2 species were performed, investigating whether *B. polydamas* was actually using *A. sessilifolia* as a larval food source in nature. Second, the performance of *B. polydamas* larvae on *A. sessilifolia* under controlled conditions was tested to assess survival and developmental constraints during the use of this host plant.

Materials and Methods

SPECIES DISTRIBUTION MODELLING

To determine whether there was overlap between the occurrence of *B. polydamas* and *A. sessilifolia*, SDMs were built for both species. The occurrence records used to build the SDMs were obtained from entomological collections, herbaria, scientific publications, and personal field observations. The environmental data used in the modeling were obtained from the bioclimatic database Worldclim (Hijmans et al. 2005) and the soil collection data sets available at ORNL-DAAC (Batjes 2000; Dunne & Willmott 2000; Global Soil Data Task Group 2000; Webb et al. 2000; Fischer et al. 2008). The environmental information for each occurrence point was obtained and subjected to a principal component analysis (PCA) to select the most significant variables for both species distributions. The most relevant PCA axis for each species distribution was selected by the inflection point observed in the Scree Plot (Gotelli & Ellison 2004). After PCA selection, the original environment variables showing the highest loading values at each axis were chosen for SDM generation. The SDMs were built applying the following algorithms: Bioclimatic Envelope (Bioclim) (Busby 1991), Malahanobis Distance (MD) (Farber & Kadmon 2003), Maximum Entropy (MaxEnt)

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(Phillips et al. 2006), Genetic Algorithm for Rule-set Production (GARP) (Stockwell & Noble 1992), and Support Vector Machine (SVM) (Cortes & Vapnik 1995) using the software Open Modeller v.1.3.0 (Muñoz et al. 2009) and Maxent (Phillips et al. 2006). Each model generated was validated by an internal test, selecting 70% of the records as training data and 30% as test data, and by an external test, using the area under the receiver operating characteristic (ROC) curve (AUC). The SDMs generated with different algorithms were corrected by the minimum training presence logistic threshold and joined in a consensus model for each species using DIVA-GIS v.7.5 (Hijmans et al. 2001). The locations of occurrences predicted by the SDMs for *B. polydamas* and *A. sessilifolia* were classified according to the biogeographical regions and provinces proposed by Morrone (2006) and to the South American ecoregions from Olson et al. (2001).

The niche breadth and overlapping of butterfly and host plant distributions were analyzed in the software ENM Tools v.1.4.3 (Warren et al. 2010) using the data from the SDMs. Levin's standardized niche breadth ($\dot{B}_A$) (Levins 1968) was estimated from consensus SDMs by measuring the uniformity of the environmental suitability throughout the distribution of each species. Thus, $\dot{B}_A$ is Zero when all the individuals occur in only one resource state (maximum specialization, minimum niche breadth) and One when individuals occur in all resource states (minimum specialization, maximum niche breadth). Three statistics were calculated to estimate niche SDM overlapping: Schoener's *D* (Schoener 1968), the *I*-statistic (Warren et al. 2008), and Relative Rank, *RR* (Warren & Seifert 2011). Schoener's *D* relies on the assumption that the probabilities are proportional to local species densities or any other measure of relative use. On the other hand, the *I*-statistic is a modification of Hellinger's distance and was used to compare community composition (Legendre & Gallagher 2001). The *D* and *I* statistics were calculated by taking the difference between the species suitability score at each grid cell, after the suitabilities have been standardized so that they sum to one over the geographic space being measured. The *RR* is an estimate of the probability that the relative ranking of any 2 patches of habitat is the same for the 2 models.

FIELD SURVEYS

Based on the SDMs generated, field surveys in areas with expected sympatry between the 2 species were performed to investigate if *B. polydamas* was, in fact, using *A. sessilifolia* as a host plant in the Uruguayan savanna areas. Field surveys were conducted in natural steppe areas and grasslands with livestock reared under extensive management (no forage added by sowing). Several localities of the Uruguayan savanna from latitude S 28° to latitude S 34° were selected, and transects of 500 m at each place were exhaustively surveyed. When an *A. sessilifolia* plant was found, the plant was inspected for eggs and immature forms of *B. polydamas*. If the plant harbored an immature form of *B. polydamas,* it was considered that the butterfly species was using it as a host plant in the inspected area. The presence of *B. polydamas* adults foraging in the surveyed areas was also recorded.

LABORATORY PERFORMANCE TRIALS

To analyze the performance and survivorship of *B. polydamas* on *A. sessilifolia*, laboratory trials under controlled conditions were performed. Eggs of *B. polydamas* were collected in the field, at Morro Santana, Porto Alegre, Rio Grande do Sul State (30°04'00.6"S, 051°07'20.3"W), placed in cylindrical plastic vials (200 mL) and brought to the laboratory to be reared at constant temperature (25 ± 2 °C) and photoperiod (16:8 h L:D) in a Biochemical Oxygen Demand incubator (BOD). After hatching, larvae were placed individually in other cylindrical plastic containers with screw caps (200 mL) and fed *ad libitum* with cuttings of *A. sessilifolia* previously disinfected with 0.01% sodium hypochlorite solution. Larval development was monitored daily and vial cleaning performed during each monitoring event. Immatures of *B. polydamas* were also reared on *Arislolochia triangularis* Cham., a well-known host plant broadly used with success by *B. polydamas* immatures, which is present only at forest edges, using the same methodology.

In order to analyze larval performance on *A. sessilifolia*, the differential immature survivorship at each instar and stage, the total develop-

Table 1. Statistics obtained for each algorithm and consensus model during the internal and external tests carried out with the several species distribution models, i.e., (**A)** *Battus polydamas,* and **(B)** *Aristolochia sessilifolia.*

A. Test type	Statistics	Bioclim	SVM	Maxent	GARP	Environmental distance	Consensus SDM
Internal	Accuracy	1.0000	0.9830	0.7642	0.9830	1.0000	0.9460
	AUC	0.9067	0.9481	0.7764	0.9012	0.9998	0.9064
	Sensitivity	1.0000	0.9830	0.7642	0.9830	1.0000	0.9460
	Omission	0.0000	0.0170	0.2358	0.0170	0.0000	0.0540
External	Accuracy	0.9868	0.9868	0.7632	0.9868	0.9868	0.9421
	AUC	0.8980	0.9510	0.7764	0.8999	0.9606	0.8972
	Sensitivity	0.9868	0.9868	0.7632	0.9868	0.9868	0.9421
	Omission	0.0132	0.0132	0.2368	0.0132	0.0132	0.0579

B. Test type	Statistics	Bioclim	SVM	Maxent	GARP	Environmental distance	Consensus SDM
Internal	Accuracy	1.0000	0.9355	0.3226	0.8710	1.0000	0.8258
	AUC	0.9863	0.9740	0.6136	0.9096	0.9977	0.8962
	Sensitivity	1.0000	0.9355	0.3226	0.8710	1.0000	0.8258
	Omission	0.0000	0.0645	0.6774	0.1290	0.0000	0.1742
External	Accuracy	0.8571	0.8571	0.5714	1.0000	0.7143	0.8000
	AUC	0.9136	0.9783	0.6939	0.9770	0.9046	0.8935
	Sensitivity	0.8571	0.8571	0.5714	1.0000	0.7143	0.8000
	Omission	0.1429	0.1429	0.4286	0.0000	0.2857	0.2000

AUC is area under the curve, i.e., the area under the receiver operating characteristic (ROC) curve.

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ment time, as well as the weight of the pupae and adult size (forewing length) were measured and compared with the data obtained on *A. triangularis* (control data). The differential immature survivorship was calculated using a life table built for mortality observed at each instar or stage change. The development time was calculated as the number of days spent from hatching to adult emergence, and all pupae were weighed with an analytical scale at the second day after pupation. The adult size was measured with a digital caliper (0.01 mm precision) using the thorax insertion of the forewing and the R4 vein terminus as anatomical landmarks. The differential survivorship between instars and stages was compared through a χ^2-test of independence. To analyze the larval development time, adult size, and pupal weight, only data from individuals that completed the whole development from egg to adult were used. Data were tested for normality (Kolmogorov-Smirnoff test) and further analyzed with *t*-tests.

All immatures reared during the laboratory assays that reached the adult stage were deposited as voucher specimens in the Lepidoptera Collection of the Department of Zoology (CLDZ), at the Federal University of Rio Grande do Sul, Brazil.

Results

SPECIES DISTRIBUTION MODELLING

The statistics for all algorithms and for the consensus models are shown in Table 1. All SDMs showed high values of accuracy and sensitivity, with low values of omission error. The consensus SDMs for both the butterfly and the host plant had high statistical significance and moderate omission errors. The consensus SDMs obtained for *B. polydamas* and *A. sessilifolia* are shown in Fig. 1. As expected, *B. polydamas* showed a wide range of distribution from southern South America to southern North America ($\dot{B}_{\text{A B. polydamas}}$ = 0.8319), occurring in several ecoregions of the Neotropics, which reflects the generalist trait of the species. On the other hand, *A. sessilifolia* had a less extensive distribution when compared with *B. polydamas* ($\dot{B}_{\text{A A.sessifolia}}$ = 0.6355), being restricted to savanna, altitudinal grasslands and Espinal formations located east of the Paraná River and south of the Paraguay River. The analysis of range overlapping between *B. polydamas* and *A. sessilifolia* SDMs indicated that the latter species is completely included in the potential distribution of the butterfly species (range overlap = 1.000). However, environmental suitability was not identical for both species, producing variations in the niche overlapping indexes when the whole distribution was considered (*D* = 0.7119, *I* = 0.9362, *RR* = 0.5254), and when information only from the Uruguayan savanna areas were used, niche overlapping indexes increased substantially (*D* = 0.8643, *I* = 0.9866, *RR* = 0.5974).

FIELD SURVEYS

The results from field surveys for *A. sessilifolia* in the Uruguayan savanna areas are shown in Table 2. In most areas of sympatric occurrence for both species, interactions were found between immature forms of *B. polydamas* and the host plant *A. sessilifolia*. Most records from the field were of eggs, arranged in clutches from 3 to 7 units, with a few records of larvae from 1st to 4th instar. During the field surveying, adult females of *B. polydamas* were observed inspecting and laying eggs on *A. sessilifolia* plants in 4 examined localities.

LABORATORY PERFORMANCE TRIALS

During laboratory trials, *A. sessilifolia* proved to be a suitable food source for *B. polydamas* larvae. Cumulative mortality during performance trials was approximately 49%, with the lowest larval mortality rates observed for the egg stage and 3rd instar (Table 3). Mortality was not uniform among the immature stages (χ^2 = 94.477, *P* < 0.0001). *Aristolochia triangularis* also proved suitable as a food source for *B.*

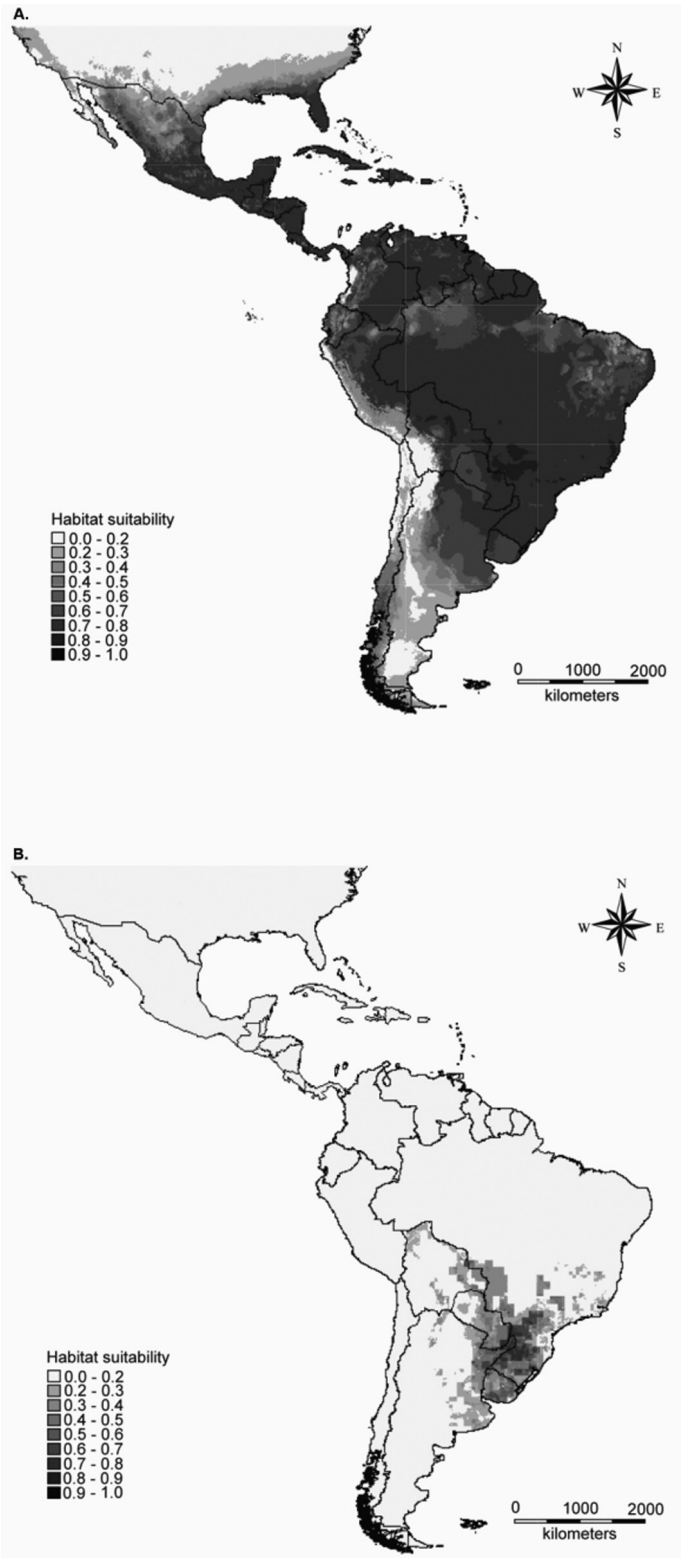


Fig. 1. Consensus species distributions obtained by an ensemble forecasting of models consisting of 5 algorithms (Bioclim, Malahanobis Distance, MaxEnt, GARP, and SVM) using environmental data from occurrence points of (A) *Battus polydamas* and (B) *Aristolochia sessilifolia*.

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Table 2. Localities, soil use, and geographical coordinates where field surveys were conducted to determine if *Battus polydamas* was using *Aristolochia sessilifolia* as a host plant in the Uruguayan savanna areas.

Location	Soil use	Geographical coordinate	*A. sessilifolia* plants	*B. polydamas* adults	Immature forms on plants
Brazil					
Alegrete	Livestock	30°05'36.6"S 55°41'08.9"W	+	+	+
Canoas	None	29°54'47.3"S 51°10'06.8"W	+	+	+
Barra do Quaraí	Livestock	30°11'02.9"S 57°30'04.5"W	—	+	—
Dom Pedrito	Livestock	30°57'15.2"S 54°22'43.6"W	—	—	—
Eldorado do Sul	None	30°05'58.2"S 51°41'40.9"W	+	+	+
Pelotas	Livestock	31°48'38.3"S 52°25'30.3"W	+	+	+
Porto Alegre	None	30°03'32.1"S 51°07'23.1"W	+	+	+
Santa Maria	None	29°43'38.3"S 53°51'01.9"W	+	+	+
Santa Vitória do Palmar	None	32°32'13.4"S 52°32'06.8"W	—	+	—
Santana do Livramento	None	30°51'36.7"S 55°31'14.1"W	+	+	+
São Gabriel	Livestock	30°08'09.0"S 54°37'09.0"W	+	+	+
Tupanciretã	Livestock	29°00'25.9"S 53°48'25.9"W	+	+	+
Uruguaiana	None	29°30'56.0"S 56°49'56.0"W	+	—	—
Viamão	None	30°05'35.5"S 50°50'57.4"W	+	+	+
Uruguay					
Artigas	Livestock	30°33'02.4"S 57°51'42.6"W	+	+	+
Colonia del Sacramento	None	34°26'25.6"S 57°43'34.4"W	—	+	—
Paysandú	None	32°22'06.2"S 58°03'08.6"W	+	+	+
Durazno	Livestock	33°22'05.7"S 56°32'28.7"W	+	+	+
Rivera	Livestock	30°58'48.7"S 55°26'29.7"W	+	+	+
Tacuarembó	Livestock	31°43'48.0"S 55°58'48.0"W	+	+	+
Treinta y Tres	None	32°54'31.7"S 54°26'46.3"W	—	—	—

polydamas larvae but produced significantly lower mortality rates (χ^2 = 4.352, $P < 0.037$). Cumulative mortality was approximately 29%, with the lowest larval mortality rates observed for the 2nd and 3rd instars (Table 3). However, mortality was not uniform through the immature stages (χ^2 =31.677, $P < 0.0001$).

Among those immatures that completed development entirely on *A. sessilifolia* (N = 27), the mean time spent from egg to adult was 31.95 d (Table 4), with no significant differences between the development time for each sex (t = 0.445, P = 0.661).The average adult size was 47.61 mm, and the mean pupal weight was 1.41 g (Table 4). Females and males showed significant differences in adult size (t = −2.381, P = 0.028) but not in pupal weight (t = −1.152, P = 0.264). The immatures that fully completed development on *A. triangularis* (N = 38), spent 31.37 d to go from egg to adult (Table 4), with no significant differences between the development time for each sex (t = 0.168, P = 0.868).The average adult size was 47.41 mm, and the mean pupal weight was 1.493 g (Table 4). Females and males showed significant differences in adult size (t = 3.079, P = 0.004) but not in pupal weight (t = 0.110, P = 0.913). No significant differences in performance were observed among the immatures that reached the adult stage from the egg stage between the 2 host plant species (development time: t = 0.416, P = 0.679; female adult size: t = 0.734, P = 0.471; male adult size: t = 0.620, P = 0.539; pupal weight: t = 0.227, P = 0.821).

Discussion

This study confirmed that *B. polydamas* can successfully use *A. sessilifolia* as host plant in the Uruguayan savanna ecoregion, even though higher mortality rates are produced when compared with the well-known and broadly abundant host plant *A. triangularis*. As far as we know, no other study has previously described this interaction, despite the abundant records of other *Aristolochia* spp. used by *B. polydamas* throughout the Neotropics. *Battus polydamas* is by far the Papilionidae

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Table 3. Mortality and survivorship levels of *Battus polydamas* immatures at different developmental stages and larval instars while using *Aristolochia sessilifolia* (*N* = 55) and *Aristolochia triangularis* (*N* = 59) as host plants under controlled laboratory conditions (25 ± 2 °C, 16:8 h L:D).

	Aristolochia sessilifolia			*Aristolochia triangularis*		
Stage/instar	Mortality	Cumulative mortality	Survival rate	Mortality	Cumulative mortality	Survival rate
Egg	0.036	0.036	0.967	0.017	0.000	0.983
I	0.075	0.111	0.924	0.017	0.017	0.983
II	0.082	0.193	0.918	0.000	0.034	1.000
III	0.023	0.215	0.978	0.000	0.034	1.000
IV	0.045	0.260	0.954	0.069	0.034	0.931
V	0.095	0.355	0.905	0.185	0.103	0.815
Pupa	0.132	0.487	0.868	0.136	0.288	0.864

species with the largest number of known host plant species in the Neotropical Region (Beccaloni et al. 2008), which reflects its great ecological plasticity and its high tolerance of environmental constraints. Organisms with such plasticity are considered to have broad-range geographical distributions mainly due to their ability to explore different biotopes. In the case of herbivorous insects with holometabolous development, such a capacity could have evolved with the ability to accept novel plants as hosts (Thomas et al. 2001). However, the reason why only a limited number of Papilionoidea species have the ability to complete their immature development by using many different plants species as food sources remains unclear.

According to the SDMs generated, *B. polydamas* could be found virtually in all ecoregions of the Neotropical zone, from the dry fields of the Chaco to the moist forests of the Amazon basin, whereas *A. sessilifolia* seems to be restricted to southern South American grasslands from the Uruguayan savanna, Humid Pampa, Espinal, Southern Cone Mesopotamian savanna, and Humid Chaco. Because the Neotropics encompass a broad range of variable environments, it is expected that *B. polydamas* populations from different ecoregions would have evolved local adaptations to use the *Aristolochia* species present nearby as host plants, or have, at least, developed the ability to deal with more phylogenetically related host plants in certain regions. To the present, there are no conclusive studies describing local host plant adaptations in any Troidini species. Nonetheless, as the SDMs obtained for *A. sessilifolia* indicate a completely overlapped distribution with *B. polydamas*, and considering the ecological plasticity of this butterfly species, the results corroborate the theoretical prediction that *A. sessilifolia* could be a suitable host plant to *B. polydamas* in the Uruguayan savanna areas where no better host plant species is available.

Regarding the interaction between the Troidini and the genus *Aristolochia*, derived Troidini species generally use fewer species of *Aristolochia* as host plants when compared with basal species in the phylogeny of the tribe (Silva-Brandão et al. 2005). Monophagous behavior is very rare among the Troidini, as most larvae can be induced to feed on more than one *Aristolochia* species, despite the preference and best performance of larvae being linked to some specific plants (see discussion in Tyler et al. 1994). Thus, the ecological specialization may simply reflect the geographical distribution of the butterfly species, instead of showing a trend in the direction of specialization in host plant use. If the species has considerable ecological plasticity, it is expected that oviposition may take place on the host plants more plentifully available in a specific area. Therefore, the use of suboptimal or less preferred host plants could be related to the lack of better resources at a specific place and time (Fox & Morrow 1981; Bernays & Graham 1988).

Especially for the Uruguayan savanna areas where forest *Aristolochia* spp. (e.g., *A. triangularis*) are restricted to riparian and hillside forests, the use of *A. sessilifolia*, an open-field plant with prostrate habit, may assure food sources for the development of immatures. As *B. polydamas* is considered a generalist species, with high ecological plasticity, the strategy of using *A. sessilifolia* could result in lower competition with other Troidini species. According to Tyler et al. (1994), the number of Troidini species with a predicted distribution in the Uruguayan savanna areas scores 10 taxa, with only 3 of them exhibiting open-field habits, namely *Euryades corethrus* (Boisduval, 1836), *Euryades duponchelii* (Lucas, 1839) and *B. polydamas.* The former 2 species are single-egg oviposition butterflies that use just a few open-field *Aristolochia* species as host plants, whereas *B. polydamas* lays eggs in clusters of 3 to 7 units and exploits more than 20 *Aristolochia* species (Beccaloni et al. 2008). Interestingly, the 2 *Euryades* species occur mainly in habitats in the biogeographical provinces of the Chaco and the Pampa (sensu Morrone 2006), which are characterized by very harsh environmental conditions, especially during summer, with very scarce food sources for both immature and adult forms. The existence under such severe circumstances would only be possible if some adaptations to the local climatic conditions had evolved, or in other words, if specialization had arisen in the resident populations subjected to the environmental constraints. *Battus polydamas* does not seem to have been the target of such selective forces. Its widespread distribution in all biogeographical subregions of the Neotropics suggests that, instead of specializing for a set of specific environment constraints, it evolved towards maintaining minimum developmental and adult physiological requirements under unfavorable environmental conditions. Despite the fact that just

Table 4. Life-history characteristics (± SE) of *Battus polydamas* that completed the whole life cycle when fed ad libitum with cuttings of *Aristolochia sessilifolia* (*N* = 27) and *Aristolochia triangularis* (*N* = 38). Rearing was done in a laboratory environment controlled at 25 ± 2 °C and 16:8 h L:D.

Host plant	Sex	Development time (days)	Pupal weight (g)	Forewing length (mm)
Aristolochia sessilifolia	Females	31.33 ± 1.120	1.503 ± 0.110	49.69 ± 1.453
	Males	32.63 ± 0.957	1.350 ± 0.078	46.04 ± 0.764
	Both sexes	31.95 ± 0.710	1.415 ± 0.065	47.61 ± 0.842
Aristolochia triangularis	Females	31.50 ± 2.000	1.496 ± 0.161	50.19 ± 1.552
	Males	31.33 ± 2.548	1.492 ± 0.165	46.32 ± 3.880
	Both sexes	31.37 ± 2.393	1.493 ± 0.134	47.41 ± 3.473

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a few *Aristolochia* species had been tested under controlled conditions for the suitability as host plant, there is plenty of empirical and field evidence supporting the assertion that *B. polydamas* has the ability to successfully use all *Aristolochia* species present in the Neotropics. Based on the presently available evidence, there is no doubt that *B. polydamas* stands as the most plastic Troidini species in the Neotropics.

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