

Article

Good Things Come in Larger Packages: Size Matters for Adult Fruit-Feeding Butterfly Dispersal and Larval Diet Breadth

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Abstract: Introduction: In animals, body size is correlated with many aspects of natural history, such as life span, abundance, dispersal capacity and diet breadth. However, contrasting trends have been reported for the relationship between body size and these ecological traits. Methods: Fruit-feeding butterflies were used to investigate whether body size is correlated with species abundance, dispersal, permanence, and larval diet breadth in a Neotropical savanna in Brazil (Cerrado). We used Blomberg's K and Phylogenetic Generalized Least Squares models (PGLS) to measure phylogenetic signal strength in species traits and to estimate size–dispersal–diet breadth associations, while also taking shared ancestry into account. Results: 539 individuals from 27 species were captured, and 190 individuals were recaptured, representing a 35% recapture rate. We found body size to be negatively associated with butterfly abundance, and positively associated with dispersal level, distance traveled, number of traps visited, individual permanence, and diet breadth. These results indicate that larger butterflies are more likely to disperse over longer distances. Moreover, larger butterflies have more generalized larval diets, based on the number of host plant families, genera, and phylogenetic diversity of the host plants they consume as larvae. Smaller butterflies rely on fewer resources, which is reflected in their higher survival in small patches and may explain their lower dispersal ability and higher diet specialization. Nevertheless, lower dispersal ability may, if not compensated by large population sizes, threaten small-bodied species inhabiting environments, such as the Cerrado, which have intense deforestation rates. Conclusions: Body size is positively associated with dispersal and diet breadth for the fruit-feeding butterflies collected in this study.

Keywords: body size; Cerrado; evolutionary history; Nymphalidae; phylogeny; species traits

1. Introduction

Dispersal is a key process for the survival and persistence of all organisms. It can help to reduce intraspecific competition and promote species coexistence [1]. This is especially true when there are environmental changes that require a population-level spatial response, such as a shifting climatic niche or the need to maintain connections among populations in increasingly fragmented landscapes [1], and it is clearly important to understand the conditions that modulate dispersal [2]. Identifying which life history traits co-vary with

dispersal-related traits should enable us to make predictions about species response in the face of environmental change [3,4]. This is particularly relevant for species inhabiting environments with high deforestation rates, such as the Neotropical Savannah in Brazil known as the Cerrado [2,5].

Body size is a morphological trait which is related to dispersal as well as many other aspects of a species' natural history, such as life span, abundance, and diet breadth [6–9]. Since body size is strongly associated with metabolism and resource use [6], its relationship with species abundance can also reveal how resources are partitioned in biotic communities [10,11]. In many cases, larger butterflies have greater life spans and dispersal ability, which can be an advantage for reaching and colonizing new habitat patches as compared to their smaller relatives [10,12,13]. However, in fruit-feeding butterflies (Nymphalidae), evidence suggests that larger butterflies are less abundant and have lower dispersal abilities, thus making them more vulnerable to habitat loss compared to their smaller relatives [12,14]. Although the interplay between body size, abundance, and dispersal is still not fully understood for papilionoids (butterflies), it suggests a trade-off between abundance and dispersal ability [2,14].

The relationship between body size and diet breadth has been studied over many decades, especially for insect herbivores [15,16]. From these studies, the common expectation is that “a jack of all trades is a master of none”, which in an ecological context refers to the idea that while generalists might be able to consume a wide range of resources, they will not be particularly well adapted to any of them [17]. Accordingly, most studies show that specialist species tend to be smaller [18,19], more abundant, and more spatially restricted than their larger relatives [19,20]. However, this pattern is not universal, and some studies report that such relationships do not exist for some insect clades [21,22]. Understanding how diet breadth mediates species trait relationships, such as body size, abundance, and dispersal ability can contribute to the identification of factors influencing community composition and may also inform conservation programs, especially in tropical regions [19,20].

As deforestation increases, the connectivity between forest patches decreases, which in turn can affect the ability of animal species to disperse and to colonize new habitats [4,7]. However, trait–environment relationships may not be exclusively explained by present-day ecological processes, and can also reflect the evolutionary history shared by different species in ecological communities [23,24]. Thus, phylogenetic information, especially when combined with both ecological and functional data, is essential for a more accurate understanding of community assembly [4,25]. The evaluation of phylogenetic signal strength for butterfly traits has been recently utilized to better understand the determinants of butterfly assemblages along spatial gradients in the Amazon forest [4,26]. Nevertheless, this approach remains underutilized in studies attempting to uncover the influence of body size on abundance, dispersal ability, and diet breadth for most insect populations, particularly in the Cerrado [7].

Using fruit-feeding butterflies (Nymphalidae), we estimated population size, dispersal ability, and diet breadth of different species in the Cerrado, and we addressed the two questions below for the assemblages we sampled:

(1) How is body size associated with the abundance, dispersal level, dispersal distance, permanence, and larval diet breadth of different fruit-feeding butterfly species? Due to strong associations between body size and metabolism, and the tradeoff between abundance and dispersal ability demonstrated for other taxa [2], we predicted that larger butterflies would be less abundant but would have greater dispersal capacity when compared with their smaller relatives [7,8]. Moreover, based on the “jack of all trades” paradigm, we also predicted that larger species would have wider larval diet breadth and disperse across longer distances compared to their smaller relatives.

(2) Does phylogeny partly account for the relationship between the body size, diet breadth, abundance, and dispersal of these butterflies? Body size is a highly conserved trait in the fruit-feeding butterfly guild [4,23]. Thus, we predicted at least an indirect

effect of phylogeny on dispersal ability and larval diet breadth, although not on species abundance, as this trait is generally defined by less predictable interactions with many different environmental factors [27–29].

2. Materials and Methods

2.1. Study Site and Sampling Design

An intensive butterfly survey was conducted over 35 consecutive days in 2013 (11 February to 17 March) in “Fazenda Água Limpa” (4500 ha). This period corresponds to the end of the rainy season, a period of high fruit ripening in the Cerrado [29]. The study site was inside a 10,000 ha protected area [29] near Brasília, Federal District, central Brazil (Figure 1). This period was chosen to optimize the sampling effort, and has been used as a baseline for previous reports for these butterflies in the Cerrado [29].

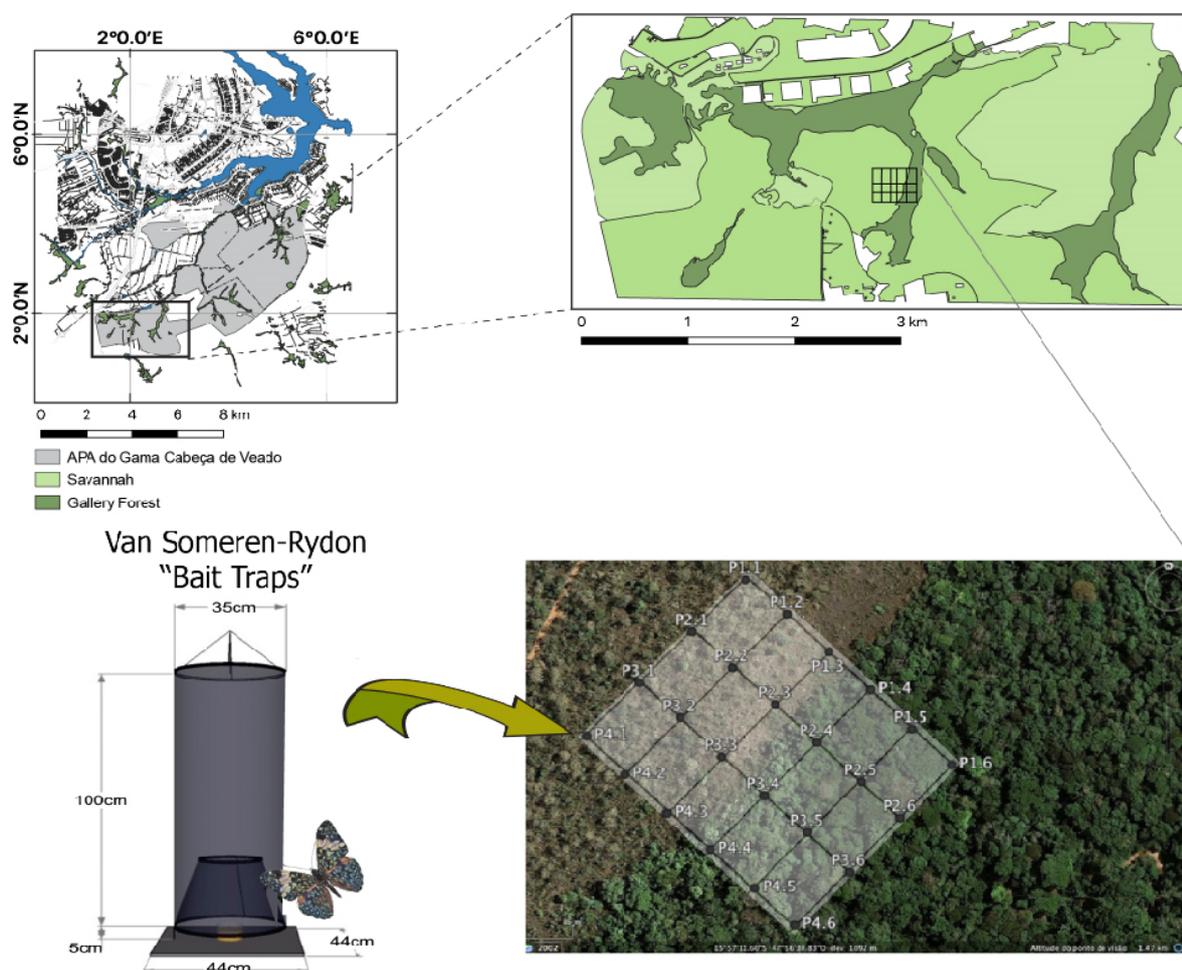


Figure 1. Experimental 1.8 ha (150 vs. 120 m) grid created at “Fazenda Água Limpa”, located at “APA do Gama Cabeça de Veado” a 10,000 ha conservation unity near Brasília, Distrito Federal, Central Brazil.

A grid of 1.8 ha (150×120 m) with four linear transects (P1–P4) was set up in the savannah-gallery forest ecotone. The transects in this grid were 40 m apart from each other. Six Van Someren–Rydon “bait-traps” (30 m apart) were equally distributed from savannah through gallery forest in each linear transect (Figure 1) for a total of 24 bait-traps. A mixture prepared with bananas and sugarcane (~50 mL) was fermented for 48 h and added to each bait-trap, following an established sampling protocol for these butterflies [12]. We marked all captured butterflies with an individual number at the ventral side of the forewing with a permanent ink pen. All marked butterflies were released at the same point of capture,

and subsequent recaptures were recorded. The traps were monitored once a day, and the baits were replaced every 48 h.

2.2. Fruit Feeding Butterflies

Fruit-feeding butterflies (Nymphalidae) include all those species that use rotting fruit as their major food source, and are easily sampled with a standardized trap protocol. Moreover, their life history traits and morphology are well studied. For these reasons, fruit-feeding butterflies are excellent model organisms for studies in ecology and evolution, including quantitative studies of dispersal [2,12,25,30–32].

2.3. Phylogenetic, Morphological and Ecological Traits

The phylogenetic relationships of fruit-feeding butterflies were estimated using the R package *phytools* [33]. We estimated the phylogenetic relationships between the species from our community based on the most recently published Nymphalidae phylogenetic hypothesis [34]. This phylogeny was inferred based on 10 genes and 250 morphological characters of 400 valid genera from Nymphalidae; for more details, see [34]. The branches of species from the original phylogeny that were absent from our community were pruned. To include the 19 species of our community that were absent from the published phylogeny, we consulted topologies from the specific taxonomic literature and specialists. The length of the new branches created by the insertion of these species was determined as half of the branch lengths from the same node on the original tree (Supplementary Materials).

We photographed ten specimens of each species to quantify forewing length (FWL) using ImageJ software [35]. We considered FWL a surrogate for body size, as the correlation between wingspan and body length is about 0.8 in fruit-feeding butterflies [13].

The following variables were collected for each species: (a) *abundance* (n), the number of individuals captured in each species; (b) *dispersal level* (%), the proportion of dispersing individuals for each species; (c) *dispersal distance* (m), the cumulative distance dispersed by each individual through the sampling period; (d) *visited traps* (v.t), the number of traps registered by each individual; (e) *permanence* (days), the period of time between the first and the last capture recorded for each individual in the study site; (f) *taxonomic and phylogenetic diet breadth*, the known number of host plant families, genera, and species used by larvae of each butterfly species [36]. In order to investigate phylogenetic diet breadth we used Faith's PD among host plant species, calculated with the R package *picante* and using the angiosperm phylogeny available via the *V.PhyloMaker* package [37].

2.4. Statistical Analysis

We calculated Blomberg's K in order to estimate a phylogenetic signal for all species traits (body size, abundance, dispersal distance and rates, number of visited traps, permanence, and larval diet breadth (hereafter "diet breadth") [38,39]). A value of Blomberg's K close to zero indicates phylogenetic independence, whereas values close to one indicate that the observed variation in the trait data is predicted by the structure of the phylogenetic tree [39]. We then used phylogenetic generalized least square models (PGLS) to estimate linear relationships between body size and the dispersal and diet breadth traits [40]. All analyses were performed using the R software packages *ape*, *picante*, and *phytools* [41].

3. Results

A total of 539 butterflies distributed across 27 species of 13 genera were captured (Figure 2a), with 190 individuals recaptured at least once (35% of recapture rate). The three most abundant species were *Pareuptychia ocirrhoe* (Fabricius, 1776) (N = 174), *Hamadryas feronia* (Linnaeus, 1758) (N = 70), and *Cissia phronius* (Godart, [1824]) (N = 47), while nine species were represented by less than five individuals each (Table A1). The tribe Satyrini (N = 374; 59%) and the subfamily Biblidinae (N = 179; 28%) were the most abundant clades, whereas the subfamilies Charaxinae (N = 13, 2%) and Nymphalinae (N = 14; 2%) had the lowest abundance.

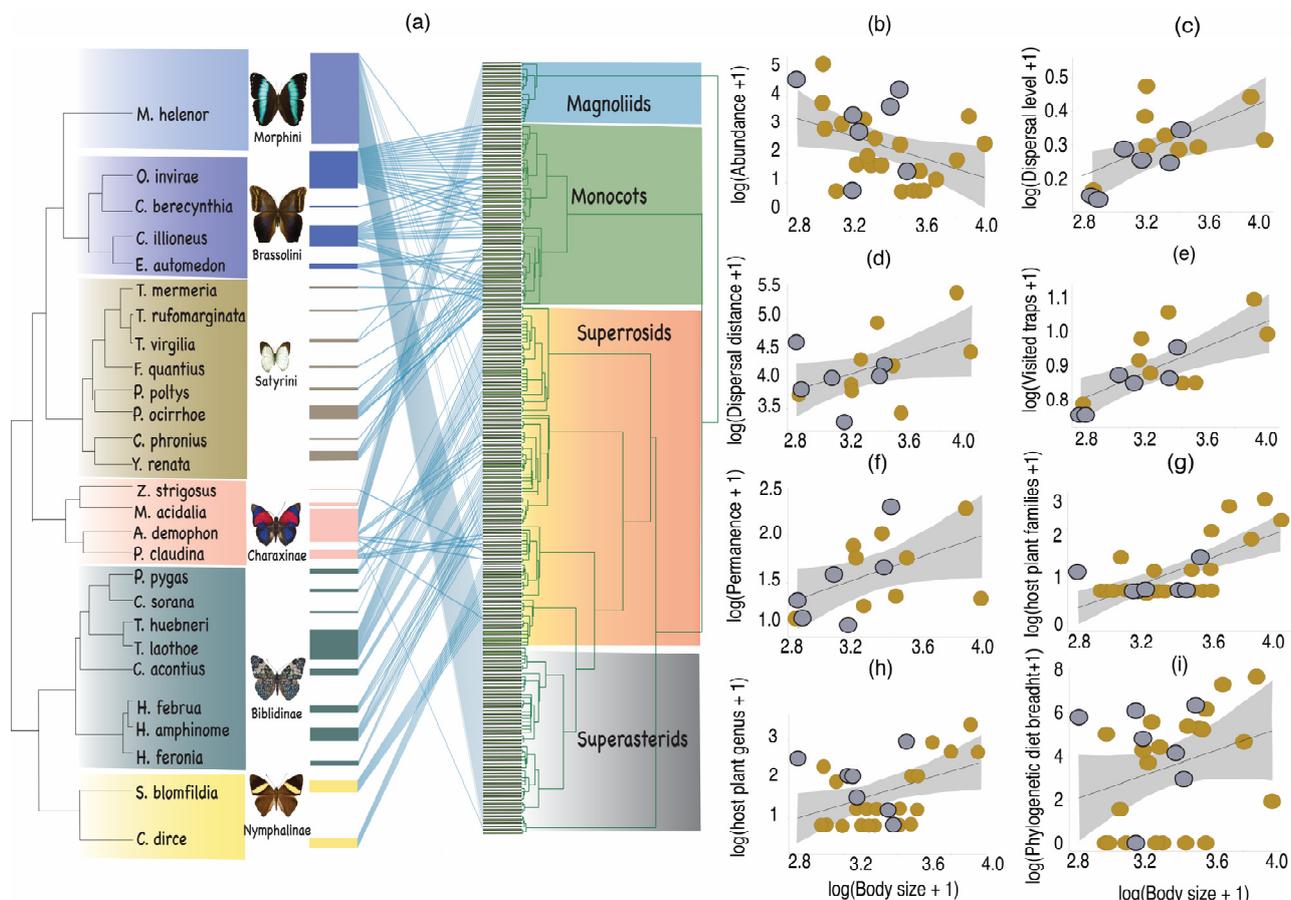


Figure 2. Nymphalidae Phylogeny of (a) the sampled butterflies species and the host plants their caterpillars eat; the Phylogenetic generalized least squares (PGLS) results for the associations between body size and (b) abundance; (c) dispersal level; (d) dispersal distance; (e) visited traps; (f) individual permanence; (g) host plant families; (h) host plant genus; and (i) phylogenetic diet breadth of fruit-feeding butterfly larvae captured in 35 days in the Cerrado of “Fazenda Água Limpa”, Brasília, Brazil. Yellow circles represent the forest specialist species, while savannah specialist species are represented by the gray circles (according to [41]). The overall raw effect size of body size on associated variables can be interpreted as a 1 cm increase in wing size yielding 0.19 decrease in abundance, 1.17 increase in levels of dispersal, 0.22 change in distance, 0.13 in traps visited, 0.13 in permanence, 3.8, 0.79, and 0.11 in diet breadth based on host plant families, genera, and phylogenetic relatedness, respectively.

Qualitatively, there was a phylogenetic signal for size; Satyrini presented smaller body sizes, while Brassolini and Morphini presented the largest body sizes (Appendix A). Considering all the measured traits, only body size and diet breadth were statistically associated with the evolutionary history shared by these species of butterflies (Table 1), indicating trait conservatism, whereby close lineages have similar body sizes and diet breadth. There was a negative relationship between body size and abundance ($\beta = -0.09$; $p = 0.01$, Figure 2b), while accounting for phylogenetic relatedness.

The PGLS analyses support the hypothesis that body size is positively associated with dispersal level (Figure 2c), dispersal distance (Figure 2d), number of visited traps (Figure 2e), individual permanence (Figure 2f), and diet breadth (Figure 2g–i for number of host plant families, genera, and phylogenetic diet breadth, respectively). These results altogether indicate that compared to smaller species, larger butterflies are less abundant and contain a greater proportion of individuals that disperse over longer distances. The larger species presented higher permanence when compared with their smaller relatives (Table 2). Moreover, larger species had broader diet breadths than smaller species, based on the number of families, genera, and host plant phylogenetic relatedness (Table 2).

Table 1. Phylogenetic signal values (Blomberg's K and *p*-value) of the species traits measured in fruit feeding butterflies captured in Fazenda Água Limpa, Brasília, Brazil.

Traits	Blomberg's K	<i>p</i> -Value	
Body size	1.1	0.001	***
Abundance	0.39	0.27	ns
Dispersal level	0.76	0.07	ns
Dispersal distance	0.53	0.53	ns
Visited traps	0.39	0.66	ns
Permanence (days)	0.39	0.78	ns
Diet breadth (Family of plants)	1.08	0.001	***
Diet breadth (Genera of plants)	0.84	0.002	**
Diet breadth (Species of plants)	0.79	0.01	**
Phylogenetic Diet breadth	0.48	0.06	ns

(***) Indicates $p \leq 0.001$; (**) $p \leq 0.01$; (ns) indicates non-significant.

Table 2. Phylogenetic generalized least squares (PGLS) between body size and other species traits in fruit-feeding butterflies captured in Fazenda Água Limpa, Brasília, Brazil.

Traits	F	Beta	<i>p</i> -Value	
Abundance	7.2	−0.09	0.01	**
Dispersal level	9.69	1.17	0.01	**
Dispersal distance	9.09	0.22	0.01	**
Visited traps	9.69	0.13	0.01	**
Permanence (days)	4.64	0.13	0.04	*
Diet Breadth (Family of plants)	16.23	3.8	0.001	***
Diet Breadth (Genera of plants)	4.64	0.79	0.04	*
Diet Breadth (Species of plants)	1.83	−0.03	0.81	ns
Phylogenetic Diet Breadth	4.83	0.11	0.001	***

(***) Indicates $p \leq 0.001$; (**) $p \leq 0.01$; (*) $p \leq 0.05$; (ns) indicates non-significant.

Dispersal levels were lowest for *Paryphthimoides poltys* (13% had dispersed), *Cissia phronius* and *Pareuptychia ocirrhoe* (16%), whereas *Zaretis strigosus* (66%), *Eryphanis automedon* (60%), and *Memphis acidalia* (50%) had the greatest proportion of individuals that had dispersed (Appendix A). For higher taxa, the subfamily Charaxinae (55%) and the tribe Brassolini (37%) had the greatest dispersal levels, while the tribe Satyrini (15%) had the lowest. Among the recaptured individuals, 88 (60%) dispersed a relatively short distance (0–70 m), 41 (27%) dispersed an intermediate distance (71–141 m), and 18 (13%) dispersed the longest distance (142–422 m). The shortest traveled distances were recorded for *Callicore sorana*, *Opsiphanes invirae*, and *Pareuptychia ocirrhoe*, while the longest distances were recorded for *Eryphanis automedon*, *Catonephele acontius* and *Cissia phronius* (Appendix A).

Individuals of *C. acontius*, *Hamadryas feronia*, and *Hamadryas februa* were collected for longer periods in the study site (6.3, 5.5, 5.5 days between the first and last capture, respectively), while *Yphthimoides renata*, *Zaretis strigosus*, and *Taygetis laches* were those with the shortest periods between the first and the last capture (2.1, 2.3, 2.5 days, respectively) (Appendix A).

Three species, *Morpho helenor*, *Caligo illioneus*, and *Eryphanes automedon* had the most generalized diets based on the number of known larval host plant families (13, 8 and 6, respectively) and genera (32, 12 and 12, respectively). *Morpho helenor*, *Archaeoprepona demophon*, and *Hamadryas amphinome* were the most generalized based on phylogenetic diet breadth (Figure 2a). Charaxinae, Morphini and Brassolini were the most generalized nymphalid clades among those included in our study (Appendix A). Overall, the Satyrini was the most specialized nymphalid clade examined here, with five out eight species using only one or two host plant families, genera, and species (Table A1).

4. Discussion

Trait-Dispersal Relationships

A clear phylogenetic signal was found for both body size and diet breadth, indicating trait conservatism where close lineages of fruit-feeding butterflies have similar body sizes [4,15] and similar host plant associations. This reiterates the importance of considering the evolutionary history of clades when examining their complex trait–environment relationships.

Among the larger species, charaxines have a large mass of flight muscles and are excellent flyers, inhabiting open areas such as savannahs and forest canopies [4,7,21]. These traits are likely to contribute to their high dispersal level (50%), as reported here. Moreover, larger butterflies are expected to demand more resources, which may force them to disperse in search of more suitable habitats [2]. On the other hand, smaller species may be better able to survive in small patches, reflecting their lower dispersal [2]. If true, the patchy distribution of small-bodied species, if not compensated by their larger population sizes, should constrain their persistence in environments with intense deforestation, such as the Cerrado. Thus, special efforts should be considered for the conservation of these small and more specialized butterflies.

The degree of dietary specialization may be an important part of the mechanisms that generate these patterns of dispersal. In this study, we demonstrated that larger and less abundant species have higher dispersal patterns and broader diet breadths compared to their smaller relatives. These associations corroborate the evidence found in a long-term study from Ecuador, in which generalist species were widespread and locally less abundant [18–20]. Further studies are required in order to confirm the causal mechanisms operating to generate the observed patterns as well as to test the correlations between fine-scale movements and large-scale dispersal.

5. Conclusions

Body size was a phylogenetically constrained trait in our study, corroborating the idea that phylogeny should be considered in studies on size–dispersal relationships. Clades comprised of large-bodied butterflies had a greater proportion of dispersing individuals, which dispersed over longer distances, were detected through longer periods, and fed on a higher number of host plant families and genera than their smaller relatives. In addition, the ability to disperse was higher in generalist butterflies compared to specialists, which suggests that specialists form isolated populations that are more susceptible to drift.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/d13120664/s1>.

Author Contributions: G.B.F.J., I.R.D. and O.J.M.-F. conceived, designed the experiment, and have edited the manuscript; T.S., J.P.D. and H.P.R. performed the experiments; G.B.F.J. analyzed the data; J.P.S. and A.V.L.F. contributed with phylogenetic analysis; G.B.F.J., C.C., H.O., A.M.S. and L.A.D. wrote the paper. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The data presented in this study are available in Table A1.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. Forewing length (FLW); abundance (N); dispersal level (%); dispersal distance (m); permanence (days); and diet breadth based on the number of family, genera, species, and phylogenetic relatedness of host plants (Fam/Gen/Spp-Phy, respectively) of fruit-feeding butterfly species captured in 35 consecutive days at Fazenda Água Limpa, Brasília, Brazil.

Subfamily-Tribe/Species	FWL—mm	N	Disp. Level (%)	Distance—m Max (Mean ± Sd)	Perm.—Days Max (Mean ± Sd)	Diet Breadth Fam/Gen/Spp-Phy
Biblidinae	30.5 ± 4.4	179	30	356.1 (50.7 ± 72.5)	26 (5.8 ± 7.1)	-
<i>Callicore sorana</i> (Godart, [1824])	26.9 ± 1.6	16	30	123.1 (24.6 ± 48.3)	6 (3.5 ± 3.6)	1/3/3-121
<i>Catagramma pygas</i> (Godart, [1824])	26.01 ± 1.4	4	-	-	-	1/2/4-21
<i>Catonephele acontius</i> (Hübner, [1823])	32.9 ± 2.6	24	30	356.1 (140.5 ± 56.7)	26 (6.3 ± 6.3)	1/1/4-416
<i>Hamadryas amphinome</i> (Linnaeus, 1767)	39.01 ± 2.1	1	-	-	-	1/1/13-718
<i>Hamadryas februa</i> (Hübner, [1823])	33.4 ± 1.2	38	20	341.1 (55.8 ± 54.8)	22 (5.5 ± 5.9)	1/2/8-335
<i>Hamadryas feronia</i> (Linnaeus, 1758)	34.7 ± 2.1	70	40	266.2 (69.0 ± 88.7)	11 (5.5 ± 6.3)	1/1/6-618
<i>Temenis laothoe</i> (Cramer, 1777)	24.7 ± 1.6	25	30	157.1 (54.7 ± 49.1)	20 (3.2 ± 4.3)	1/6/21-616
<i>Temenis huebneri</i> (Fruhstorfer, 1907)	24.7 ± 1.3	1	-	-	-	1/6/21-na
Charaxinae	28.1 ± 1.6	14	55	105.1 (47.8 ± 38.3)	17(5.1 ± 5.9)	-
<i>Archaeoprepona demophon</i> (Hübner, [1814])	46.3 ± 1.4	2	-	-	-	11/16/46-1480
<i>Memphis acidalia</i> (Hübner, [1819])	27.7 ± 1.4	6	50	105.1 (50.6 ± 47.3)	17 (4.2 ± 4.5)	2/2/3-na
<i>Prepona claudina</i> (Godart, [1824])	41.01 ± 1.4	1	-	-	-	6/ /6/7-471
<i>Zaretis strigosus</i> (Gmelin, 1790)	28.6 ± 1.6	5	60	69.1 (43.5 ± 33.5)	11 (2.3 ± 2.9)	1/1/2-231
Nymphalinae	30.5 ± 9.04	14	30	183.2 (75.8 ± 76.3)	10 (3.5 ± 3.5)	-
<i>Colobura dirce</i> (Linnaeus, 1758)	29.5 ± 2.3	12	30	183.2 (75.8 ± 76.3)	10 (3.5 ± 3.5)	1/1/7-699
<i>Smyrna blomfieldia</i> (Fabricius, 1781)	40.01 ± 2.3	1	-	-	-	1/5/11-391
<i>Tigridia aesta</i> (Linnaeus, 1758)	22.01 ± 2.3	1	-	-	-	3/5/8-370
Satyrinae-Brassolini	52.6 ± 11.8	23	36	422 (124.7 ± 142.1)	17 (3.8 ± 4.9)	-
<i>Caligo illioneus</i> (Cramer, 1775)	65.9 ± 4.0	10	20	75.6 (60.4 ± 21.4)	5 (3.2 ± 3.7)	8/ /12/16-583
<i>Catoblepia berecynthia</i> (Cramer, 1777)	41.01 ± 2.2	3	-	-	-	1/2/2-na
<i>Eryphanis automedon</i> (C. Felder & R. Felder, 1867)	53.9 ± 2.2	5	60	422.8 (237.3 ± 160.8)	17 (4.8 ± 4.6)	4/9/12-351
<i>Opsiphanes invirae</i> (Hübner, [1808])	38.1 ± 2.0	5	30	40.2 (30.1 ± 12.5)	12 (3.2 ± 3.5)	3/17/29-566
Satyrinae-Morphini	59.1 ± 4.1	27	30	142.8 (86.5 ± 44.6)	10 (3.1 ± 3.4)	-
<i>Morpho helenor</i> (C. Felder & R. Felder, 1867)	59.1 ± 4.1	27	30	142.8 (86.5 ± 44.6)	10 (3.1 ± 3.4)	11/30/58-2094
Satyrinae-Satyrini	22.3 ± 7.1	282	15	272.1 (49.2 ± 53.3)	21 (2.3 ± 3.1)	-
<i>Fosterinaria quantius</i> (Godart, [1824])	23.1 ± 0.8	20	-	-	-	1/1/1-na
<i>Pareuptychia ocirrhoe</i> (Fabricius, 1776)	19.9 ± 1.4	174	10	151.9 (41.7 ± 38.5)	18 (3.4 ± 4.3)	1/8/11-359
<i>Cissia phronius</i> (Godart, [1824])	19.7 ± 1.1	47	10	272.1 (100.9 ± 78.7)	21 (3.3 ± 4.6)	1/1/1-na
<i>Paryphthimoides poltys</i> (Prittwitz, 1865)	20.2 ± 0.8	17	10	111.2 (45.1 ± 29.5)	13 (2.5 ± 3.2)	1/1/1-na
<i>Taygetis virgilia</i> (Cramer, 1776)	36.01 ± 1.6	10	-	-	-	2/2/ /2-216
<i>Taygetis laches</i> (Fabricius, 1793)	35.7 ± 1.4	10	30	171.1 (66.9 ± 52.1)	8 (2.1 ± 2.6)	2/2/2-216
<i>Taygetis mermeria</i> (Cramer, 1776)	30.01 ± 1.4	4	-	-	-	1/2/2-200
Total	-	539	30	422.8 (237.3 ± 160.8)	26 (6.3 ± 6.3)	-

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