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Comparative Biology of Three Species of Costa Rican Haeterini

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Comparative Biology of Three Species of Costa Rican Haeterini

A Dissertation

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By

Laura G. Alexander

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Abstract

Documenting life history characteristics of populations, especially of herbivorous insects such as butterflies, is fundamental to the ecological study of tropical rainforests. However, we know relatively little about tropical forest butterflies. Here, I combine information gathered using the mark-release-recapture (MRR) approach with manipulative and observational experiments in a natural environment to explore aspects of the population biology of three closely-related species of Costa Rican fruit-feeding understory butterflies (*Cithaerias pireta*, *Dulcedo polita*, and *Pierella helvina*), specifically: vertical stratification, attraction to and persistence in fruit-baited traps, relative abundance and distribution, movement patterns, probabilities of recapture and daily survival, and factors that affect those probabilities. Among the three focal species there were differences in capturability, recapturability, spatial distribution, and degree of vertical stratification. Males appear to fly within smaller home ranges than females, and *P. helvina* can traverse the entire forest reserve in a single day. These findings have implications for the genetic diversity of these populations and for the risk of local extinction in the face of changing ecological conditions.

Abundance Distribution, Apparent Survival, Capture Probability, *Cithaerias menander, Cithaerias pireta*, Dispersal, *Dulcedo polita*, Escape Rate, Fruit-feeding Butterfly, Home Range Behavior, Mark-release-recapture, Nymphalidae, *Pierella helvetia incanescens, Pierella helvina*, Rainforest, Recapture Probability, Satyrinae, Spatial Distribution, Spatial Heterogeneity, Survival Probability, Temporal Heterogeneity, Trap Persistence, Vertical Stratification

Chapter 1: Life History Characteristics of Three Species of Costa Rican Haeterini

Introduction

Documenting life history characteristics of populations is fundamental to the ecological study of tropical rainforests. Terrestrial invertebrates, especially herbivorous insects in the tropics, are essential to processes that regulate terrestrial ecosystems, and are good indicators of ecological condition (Andersen et al. 2002; Barbosa et al. 2005). The spatial and temporal heterogeneity inherent in the tropics makes generalizations about these ecosystems difficult (Basset et al. 2004), in turn making the study of tropical insect populations particularly valuable. Butterflies are ideal insects for the study of ecologically important topics (Ehrlich 1989; Gilbert 1989), and work on tropical butterflies has been important for understanding population biology and evolutionary ecology (Vane-Wright and Ackery 1989; Brown and Freitas 2000; Boggs, Watt and Ehrlich 2003; DeVries, Austin and Martin 2008; Wahlberg et al. 2009; Bonebrake et al. 2010; DeVries, Penz and Hill 2010; Fordyce 2010; Grotan et al. 2012). Approximately 90% of tropical butterfly species are found only within forest habitats (Beccaloni and Gaston 1995), which are rapidly disappearing (Laurance 1999; Achard et al. 2002). Even in Costa Rica, known for its commitment to protecting natural habitats, 70% of the forest is outside protected areas and the remainder exist primarily as small fragments (Kricher 1997; Sanchez-Azofeifa 2001). This habitat loss makes the study of tropical forest butterflies even more important. However, we know relatively little about them in terms of life history characteristics, mortality and longevity, spatial structure, dispersal, or sex-linked behavioral differences (Carey 2001; Bonebrake et al. 2010).

The published literature has focused on relatively few butterfly genera, many of which comprise temperate meadow and grassland species. Examples include *Maculinea* spp (Lycaenidae) in wet meadows (e.g., Thomas 1984; Meyer-Hozak 2000; Maes et al. 2004;

Table 1.1. Estimates of butterfly species richness by biogeographical realm. Estimates (Robbins and Opler 1996, p. 71) compared with the contribution to the scientific literature of each realm based on a search of mark-release-recapture (MRR) butterfly papers published from 2000 through 2013.

	Species		Published papers	
Biogeographical realm	Estimate	%	Count	%
Neotropical (Central/South America & Caribbean)	7500	41.8	13	9.77
Oriental & Australian (India/Southeast Asia & Australia/New Zealand)	4500	25.1	2	1.50
Ethiopian (Sub-saharan Africa)	3650	20.3	1	0.752
Palearctic (Europe and Asia)	1550	8.64	91	68.4
Nearctic (North America)	750	4.18	26	19.5

Kőrösi et al. 2008; Nowicki and Vrabec 2011; Bonelli et al. 2013), *Melitaea* sp. (Nymphalidae) in dry meadows (e.g., Kuussaari, Nieminen and Hanski 1996; Harrison, Hanski and Ovaskainen 2001; Zheng et al. 2007; Niitepõld et al. 2011; Novotny, Konvička and Fric 2012), and *Parnassius* sp. (Papilionidae) in alpine and sage brush meadows (e.g., Roland, Keyghobadi and Fownes 2000; Adamski 2004; Auckland, Debinski and Clark 2004; Fred and Brommer 2009; Matter and Roland 2013). Of the studies conducted in the tropics, many have focused on species in the genus *Heliconius*. Bonebrake et al. (2010) reference 18 studies on *Heliconius* color pattern mimicry, pollen-feeding, population dynamics and reproductive biology. But *Heliconius* represents only a few of the 7500-8000 estimated tropical forest butterfly species (Beccaloni and Gaston 1995; Robbins and Opler 1996; Tufto et al. 2012).

Non-tropical forest ecosystems are disproportionately reflected in the literature. A recent search of the Web of Science database for mark-release-recapture (MRR) butterfly literature published since 2000 found that for the 133 pertinent results, 116 (88%) of the study habitats were in North America, Europe and Asia (excluding southeast Asia; Table 1.1)

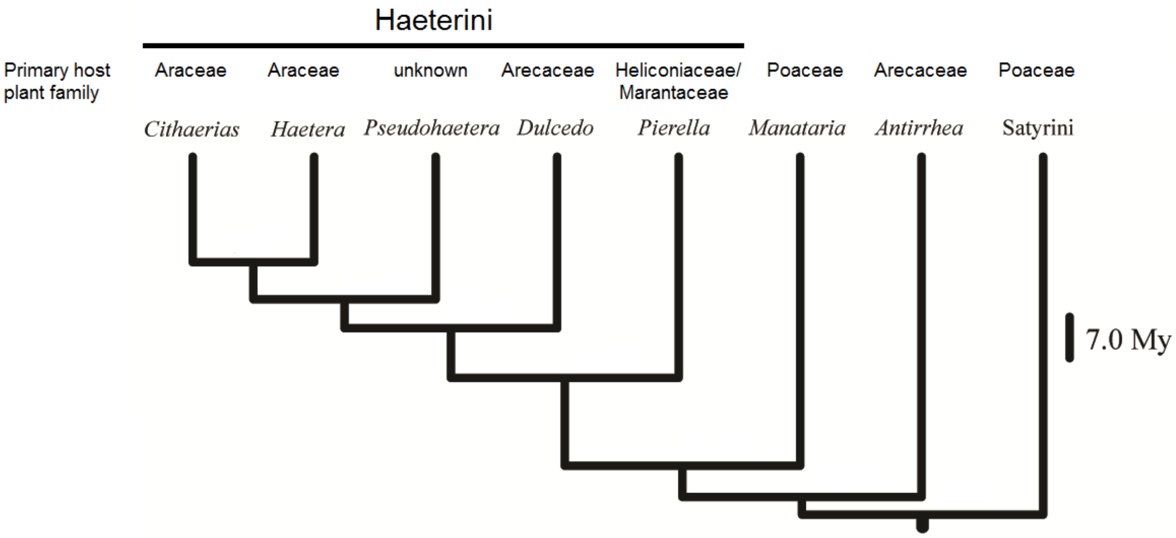


Figure 1.1. Phylogenetic relationships of Haeterini genera. Tree created by A. Cespedes (unpublished) based on recent work by Wahlberg et al. (Wahlberg personal communication) showing the phylogenetic relationships of genera of the tribe Haeterini (Nymphalidae, Satyrinae). Branch lengths and topology were estimated simultaneously in BEAST (v.1.7.4; Drummond and Rambaut 2007; Drummond et al. in preparation). The most recent common ancestor of all taxa were constrained to the age estimated in Wahlberg et al. (2009), and output was analyzed in Tracer (v. 1.4; Rambaut and Drummond 2007) for convergence. References for the host plant families: DeVries 1987; Constantino 1993; Peña 2007; Janzen and Hallwachs 2013. My = millions of years.

even though those regions represent less than 13% of estimated worldwide butterfly species richness (Robbins and Opler 1996). The Neotropical realm comprises almost 42% of butterfly richness (Robbins and Opler 1996) but < 10% of the study regions found in the literature search (Table 1.1). Granted, the literature search used limited search terms and was biased toward MRR papers published in English, and a diverse body of work has been published on tropical species. Researchers have studied spatial, temporal, and species diversity of communities of forest fruit-feeding (Nymphalidae) butterflies in a variety of tropical locations, including Belize (Lewis 2001), Borneo (Hamer et al. 2003; Tangah et al. 2004), Brazil (Barlow et al. 2007), Costa Rica and Ecuador (DeVries et al. 2012, and references therein), Indonesia (Fermon et al. 2005), Southeast Asia (Dumbrell and Hill 2005), and Uganda (Molleman et al. 2006). Nevertheless, given the relative contribution tropical forest butterflies make to the world’s butterfly diversity, in-depth studies of tropical forest species are vastly underrepresented in the scientific literature.

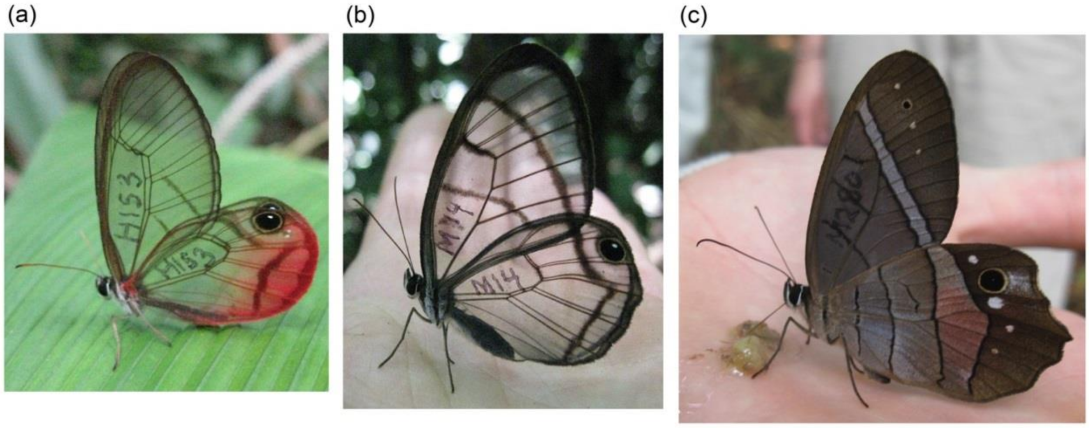


Figure 1.2. Wing marks. Placement of marks on the ventral surface of the left fore- and hindwings of (a) *Cithaerias pireta* and (b) *Dulcedo polita,* and (c) the left and right forewings of *Pierella helvina* (only left side shown). Images are not to scale.

Many questions in ecology and evolutionary biology require detailed information on individuals within populations (Lomnicki 1988; Clutton-Brock and Sheldon 2010), and mark-release-recapture (MRR) is an appropriate way to collect data on tropical forest butterfly populations. MRR allows individuals to be tracked, provides a wide range of demographic information, and produces data that can be analyzed in a statistically rigorous fashion (Elton 1927; Jolly 1965; Seber 2001; Nichols 2005; Haddad et al. 2008). Marking individuals is often the only way to derive estimates of vital population rates, and MRR can be used to estimate species richness and assess wildlife monitoring programs (White and Burnham 1999). Statistical models for MRR data can incorporate individual and group covariates to describe physical condition, genetics or habitat conditions, allowing researchers to explore the role of ecological mechanisms such as competition, habitat quality or weather conditions in population dynamics (Franklin 2001). As a result, MRR methods have been used with a variety of taxa and habitats to answer many population ecology questions (Appendix A). MRR is an excellent tool for use with butterflies when they are robust to marking (Haddad et al. 2008), and there is an extensive literature on its use in butterfly populations (e.g. Ehrlich 1965; Brakefield 1982; Hanski, Alho and Moilanen 2000; Matter and Roland 2013).

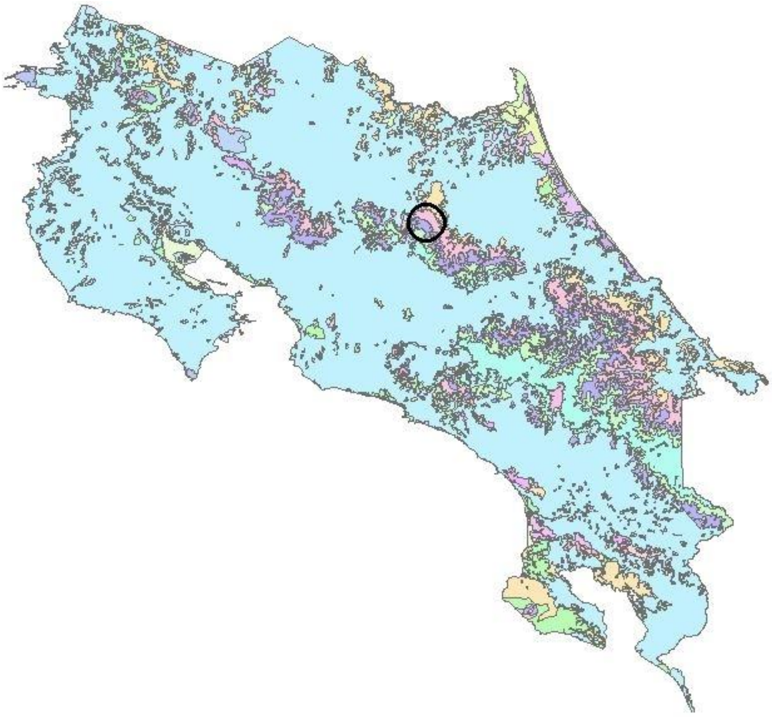


Figure 1.3. Map of Costa Rica showing life zones in various colors. The study region is enclosed in a circle. This map was created by LGA with ArcGIS in November 2007 using regional coverages of the Rio Sarapiquí Watershed made publicly available by the Organization for Tropical Studies, combined with the USGS Hurricane Mitch Program Data: Central American Ecosystem Map, May 2001.

A familiar but largely unstudied group of tropical forest butterflies that lends itself well to the MRR approach is the tribe Haeterini (Nymphalidae, Satyrinae). The Haeterini are fruit-feeding understory butterflies that are common and locally abundant within rainforest habitats (DeVries 1987). They are well-known phylogenetically within the Satyrinae (Freitas and Brown 2004; Peña et al. 2006; Wahlberg et al. 2009), and recent work (Cespedes, Penz and DeVries, unpublished) showed the relationships of all five genera in the tribe (Fig. 1.1). The Haeterini can be sampled in fruit-baited traps, are robust to handling, and can be uniquely and permanently marked on the wings (Fig. 1.2). They also are visually distinctive and in Costa Rica can be unambiguously identified in the field. Three sympatric species of Haeterini (*Cithaerias pireta* Cramer, *Dulcedo polita* Hewitson, and *Pierella helvina* Hewitson) are present year-round in the Sarapiquí River Basin of Costa Rica (DeVries et al. 2012). Here, I combine information gathered using the MRR approach with manipulative and observational experiments in a natural environment to explore aspects of the population biology of these three species, specifically: vertical stratification within the low understory, attraction to and persistence in fruit-baited traps, relative abundance and distribution,

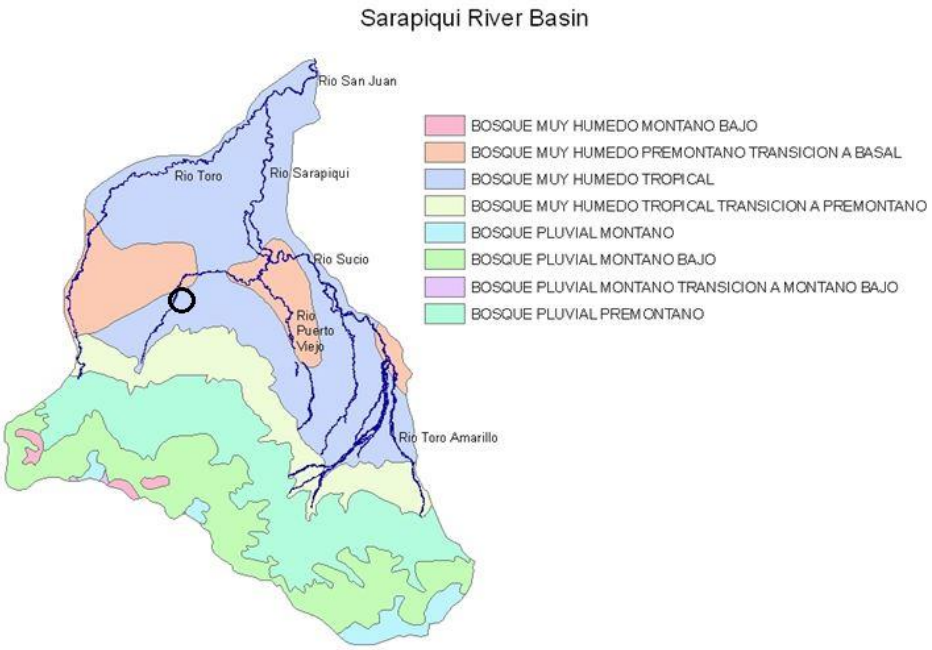


Figure 1.4. Map of the Sarapiquí River Basin. The location of the Tirimbina reserve enclosed in a circle. This map was created with ArcGIS in November 2007 using regional coverages of the Rio Sarapiquí Watershed made publicly available by the Organization for Tropical Studies.

movement patterns, probabilities of recapture and daily survival, and the relative effects of species, sex, rain, abundance, and sampling site on those probabilities.

Study Location

The field work for this dissertation took place in the Sarapiquí River Basin, Heredia Province, a geographic region in the interior of Costa Rica that has been well studied (Janzen 1983; DeVries 1987; Gentry 1990; Rich et al. 1993; McDade et al. 1994; Lieberman et al. 1996; Kricher 1997). Costa Rica contains four mountain ranges, experiences weather systems from two oceans, and is situated on the land bridge between North and South America, all contributing to extremely high biodiversity and life zones (Fig. 1.3; DeVries 1987; Janzen 1983; Longhi 2000; Wainwright 2007). Forests in the Sarapiquí River Basin are classified primarily as Tropical Wet Forest (Bosque Muy Humedo Tropical; Fig. 1.4) comprising undisturbed wet forest, swamp forest, riparian forest, light gaps, and second growth (Frankie, Baker and Opler 1974; Longhi 2000). The study region receives an average of 3.7 to 4.2 m of precipitation per year and has no distinct dry season (Zuchowski 2007, p. 237), although

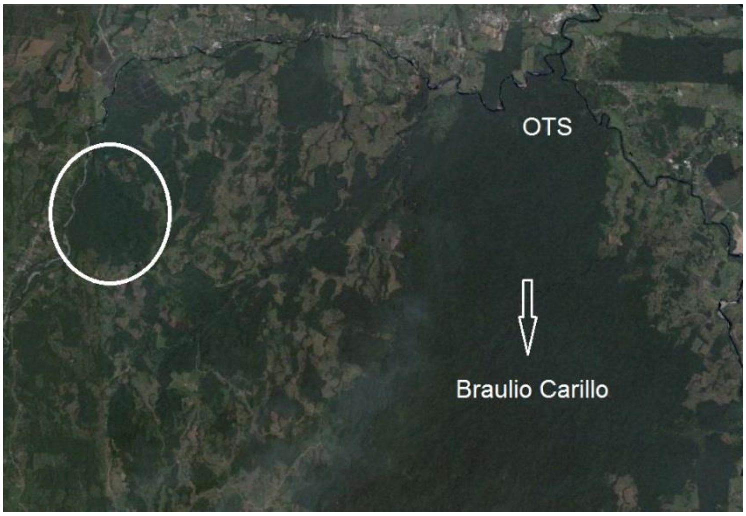


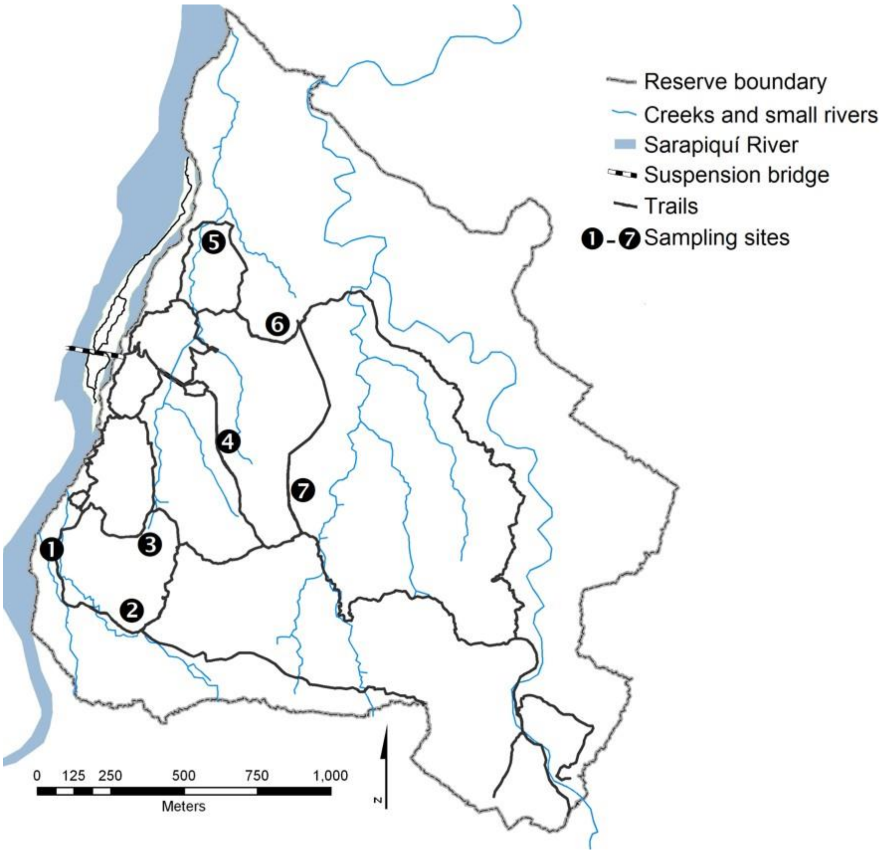
Figure 1.5. GoogleEarth image of the inner portion of the Sarapiquí River basin. Shows the confluence of the Sarapiquí and Puerto Viejo rivers, La Selva Biological Station (OTS), and the forest corridor leading to the 476 sq km Parque Nacional Braulio Carillo. Tirimbina, bordered on its western edge by the Sarapiquí river, is enclosed in an oval. Imagery dates: 2003-2007.

December to April are usually dryer months. This region is characterized by an agriculture-dominated matrix of developed lands and small, privately owned patches of forest used for ecotourism.

Reserva Biológica La Tirimbina, hereafter referred to as Tirimbina, is a private, non-profit wildlife refuge that uses ecotourism to fund educational outreach for local communities. It is situated with the Sarapiquí River along its western border, and is approximately 10 km from the forested corridor that leads north to La Selva Biological Station (OTS) or south to Parque Nacional Braulio Carillo (Fig. 1.5). Tirimbina is 3.4 sq km in size and is 85% primary forest (http://www.tirimbina.org/what-is-tirimbina/physical-description.html; 20 Sep 2010). The forest interior is structurally complex, but is characterized by abundant *Pentaclethra macroloba* trees and many palms species (Marquis and Braker 1994; Longhi 2000; Isidro Chacón personal communication). Tirimbina is criss-crossed by two small rivers and numerous creeks that drain into the Sarapiquí River, and is traversed by a network of paths to accommodate local educational programs and ecotourism visitors (Fig. 1.6).

A nearby forest patch used as a secondary sampling site was similar in forest composition to Tirimbina, but different in size and disturbance level. The nearby patch,

Figure 1.6.
Tirimbina Biological Reserve, Heredia Province, Costa Rica.



hereafter referred to as Pozo Azul, is owned by Hacienda Pozo Azul and used for nature walks. Pozo Azul is separated from Tirimbina by approximately 2 km of roads, agricultural fields, pastures, and small homes and businesses. Although individuals of the butterfly genus *Morpho* have been observed flying along rivers, forest edges, and roads in the study region, butterflies such as the Haeterini are confined to the forest interior and do not traverse open or developed lands or fly across roads (DeVries 1987; personal observation). Thus, the study species were unlikely to move between Tirimbina and Pozo Azul, and the two populations of butterflies were effectively isolated. Pozo Azul was similar to Tirimbina in terms of plants and forest structure, i.e., degree of understory visibility, size and density of trees, and number and size of natural tree gaps, small streams and rivers. However, at 1.6 sq km it was about half the size of Tirimbina, and its boundaries were closer to roads and homes. Furthermore, Pozo Azul was bisected by a dirt road at the northern end so that approximately one-third of the patch was separated from the rest of the reserve. It is unclear whether haeterines would

Figure 1.7. Haeterini wing patterns. Shows (a) pink hindwing coloration in two individuals of *Cithaerias pireta*, one fresh and one with damaged hindwings, feeding on banana adjacent to an individual of *Greta oto* (Ithomiini), (b) the transparent wings lacking bright coloration of a fresh female *Dulcedo polita*, and (c) the vivid red, white and black coloration of an extremely fresh female *Pierella helvina*. Images are not to scale.

cross that interior dirt road, but it is possible that the functional size of Pozo Azul was smaller than 1.6 sq km for the haeterine populations.

Study Organisms

Satyrines comprise the most speciose group of nymphalids, with approximately 2,000 species worldwide (Peña 2004), and the larvae generally feed on monocots like palms, bamboos and grasses in the families Arecaceae and Poaceae (DeVries 1987; Peña et al. 2006; Chacón and Montero 2007). The host shift to grasses is considered a driving mechanism in the diversification of this subfamily (Peña et al. 2006), and many satyrines are meadow or grassland species in temperate zones where they primarily have been studied (Beccaloni and Gaston 1995). However, the Haeterini are part of a clade that diverged from the rest of Satyrinae before its adaptive radiation coincident with the spread of grasses across the globe (Peña 2007; Wahlberg et al. 2009). Larval haeterines feed not on grasses but primarily on philodendrons (Araceae), palms (Arecaceae) and heliconias (Heliconiaceae and Marantaceae; Appendix B), and are considered “primitive” satyrines in this respect (Peña et al. 2006).

Haeterines differ from “typical” satyrines in flight behavior and appearance. Satyrine flight has been described as unsteady, jumpy or bouncy (Weymer 1924; DeVries 1987), but

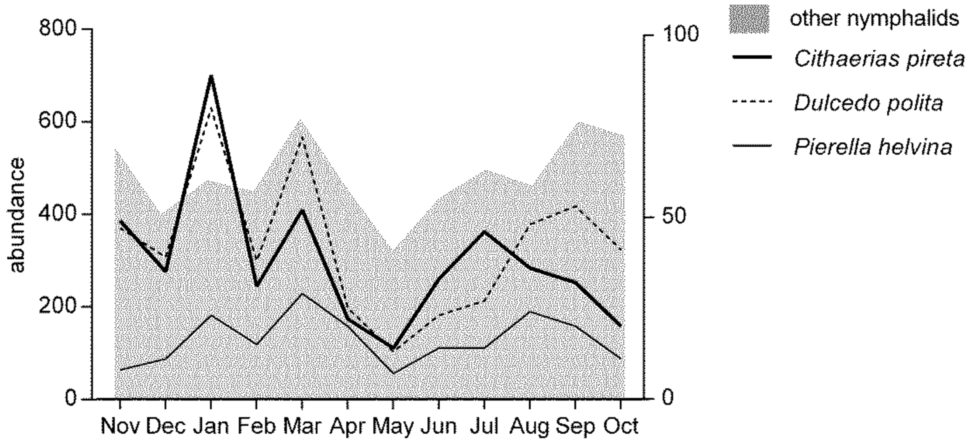


Figure 1.8. Nymphalid butterfly abundance. Monthly abundance for the three focal Haeterini butterflies and 97 other Nymphalidae butterflies captured in fruit-baited traps at Tirimbina from November 2003 through October 2008 (DeVries et al. 2012). The haeterines are plotted against the right y-axis and the other fruit-feeding nymphalids are plotted against the left y-axis.

haeterines have been observed soaring smoothly along trails centimeters above the ground (Weymer 1924; DeVries 1987; Constantino 1992) and gliding from low vegetation to the ground with their wings held in a dihedryl (personal observation). Satyrines may have forewings that are rounded, angled, sickle-shaped or pointed (Weymer 1924; DeVries 1987), but haeterines have comparatively narrow forewings that are rounded at the apex. In appearance, the typical satyrine is small and brown with rows of eye spots on the hindwings (Weymer 1924; DeVries 1987; Chacón and Montero 2007). The genus *Pierella*, the first of the Haeterini to diverge within that clade (Fig. 1.1; Peña et al. 2006; Wahlberg et al. 2009), is closest in wing pattern to the typical satyrine by having brown wings and multiple ocelli (Weymer 1924). However, many members of *Pierella* also have bright patches of color on the hindwing, possibly functioning to direct predator attacks away from vital body parts (Hill and Vaca 2004; Murillo-Hiller 2009). In Costa Rica, *P. helvina* has red hindwing patches (Fig. 1.7). The other genera within Haeterini diverge further from the typical satyrine wing pattern by having slightly iridescent, transparent wings with only one or two eyespots and, except for *Dulcedo*, variously colored hindwing patches. Thus, the Haeterini generally soar or skim rather than bounce in flight, and are bright and/or transparent rather than drab in coloration.

The Haeterini at Tirimbina exhibit a roughly bimodal seasonal pattern in abundance similar to some other nymphalid species, with annual abundance peaks in July-September and January-March (Fig. 1.8; DeVries et al. 2012; Alexander and DeVries b). They also have been observed congregating at fruit falls with other members of the fruit-feeding butterfly guild (Young 1972; personal observation), although the haeterines are usually solitary (DeVries 1987). Daily survival was similar among the focal haeterines and averaged < 0.82, suggesting that less than 82% of the population survives from one day to the next (Alexander and DeVries b). These haeterines also showed similar daily movements in terms of straight-line distances, with most observed movements within 80 m. And for *C. pireta* and *P. helvina* in particular, females tended to disperse while males flew in smaller home ranges (Alexander and DeVries a).

We know almost nothing about mating and reproduction in the haeterines, and what we do know primarily has to do with descriptions of eggs and larvae (not covered here), and brief descriptions of oviposition and larval behavior. This is an important topic because larval survival and development are critical to the life history and could affect characteristics of the adult population (Price et al. 2011, p. 62). For the focal butterflies, we know that all lay eggs singly (DeVries 1986, 1987; Murillo-Hiller 2009; Isidro Chacón personal communication), and one account describes egg-laying behavior for each species plus an account for *Haetera piera* in Colombia (Constantino 1993). Murillo-Hiller (2009) observed a single *C. pireta* lay one egg on the underside of a *Philodendron* leaf close to the central leaf vein at a height of 15 cm. Development time from egg to adult of neotropical butterflies can range from two weeks to three months (DeVries 1987, 1997; Grotan et al. 2012). The *C. pireta* larva reared by Murillo-Hiller (2009) developed in 65 days, whereas the *H. piera* larva reared by Constantino

Table 1.2. Palm-feeding nymphalid butterflies. Eleven species of Satyrinae that have been recorded feeding on palms (Arecaceae) as larvae (DeVries 1987, personal communication).

Species	Tribe	Palm record	Notes
Brassolis isthmia	Brassolini	*Cocos nucifera*	gregarious, nocturnal feeders; can defoliate entire trees
Opsiphanes quiteria quirinus	Brassolini	"palms" *Cocos nucifera*	
Opsiphanes invirae cuspidatus	Brassolini	"palms" *Cocos nucifera*	
Opsiphanes cassina fabricii	Brassolini	*Acrocomia vinifera,* *Cocos nucifera*	
Catoblepia orgetorix championi	Brassolini	"palms"	
Eryphanis aesacus buboculus	Brassolini	"palms"	but *E. polyxena lycomedon* feeds on bamboo (Poaceae)
Dulcedo polita	Haeterini	*Geonoma* sp., *Welfia* sp.	
Antirrhea pterocopha	Morphini	*Calypterogyne* sp.	
Antirrhea miltiades	Morphini	*Geonoma longivaginata*	old mature leaves
Caerois gerdrudtus	Morphini	*Socratea durisima* *Cocos nucifera*	mature leaves
Cissia confusa	Satyrini	*Iriartia* sp., *Geonoma* sp.	most *Cissia* sp. feed on grasses (Poaceae *C. confusa* also observed on *Calathea* sp. (Marantaceae); the only other *Cissia* sp. with a non-Poaceae host plant is *C. calixta*, observed on the sedge *Cyperus lazulae* (Cyperaceae)

(1993) developed in 44 days. It may be that *D. polita* and *P. helvina* also lay eggs close to the ground although this is not included in published accounts, and there are no accounts indicating larval development time for either species. *Dulcedo polita* has been observed laying single eggs more than once on the same plant, while *P. helvina* usually oviposits only once per plant (DeVries 1986). The larvae of both are solitary, with *D. polita* larvae feeding first on new leaves then on old leaves, and *P. helvina* larvae feeding on all leaves (DeVries 1986). There are no published records of male-male interactions or mating behaviors in any of these species.

Table 1.3. Wing lengths. Average forewing length (±SE) calculated from 2,267 living butterflies measured in the field at Tirimbina and Pozo Azul in 2009, 2010 and 2011, and average variation (±SE) in length measurements taken from a subset (n=509) of butterflies for which multiple measurements were available.

		Wing length (mm)		Variation (mm)	
Species	Sex	N	mean ± SE	N	mean ± SE
Cithaerias pireta	♀	170	29.16 ± 0.09	38	0.33 ± 0.04
	♂	258	27.69 ± 0.07	54	0.42 ± 0.06
Dulcedo polita	♀	236	34.04 ± 0.09	53	0.50 ± 0.07
	♂	151	31.1 ± 0.11	30	0.49 ± 0.06
Pierella helvina	♀	435	37.61 ± 0.07	104	0.43 ± 0.04
	♂	494	33.27 ± 0.05	131	0.42 ± 0.03

Other species:

		Wing length (mm)		Variation (mm)	
Species	Sex	N	mean ± SE	N	mean ± SE
Antirrhea miltiades	♀	127	47.11 ± 0.24	22	0.73 ± 0.29
	♂	130	43.35 ± 0.12	29	0.38 ± 0.04
Caligo atreus	♀	66	78.91 ± 0.39	10	0.37 ± 0.09
	♂	52	73.19 ± 0.60	12	1.41 ± 0.92
Caligo eurilochus	♀	42	83.81 ± 0.67	6	0.43 ± 0.10
	♂	59	75.00 ± 0.38	10	0.44 ± 0.08
Caligo illioneus	♀	5	72.84 ± 1.04	0	na
	♂	7	63.75 ± 0.82	0	na
Morpho granadensis	♀	6	67.87 ± 2.37	2	0.13 ± 0.06
	♂	8	64.07 ± 1.08	3	0.21 ± 0.06
Pierella luna	♀	1	37.19	1	na
	♂	5	34.11 ± 0.34	1	na
Taygetis andromeda	♀	2	35.96 ± 0.06	1	na
	♂	13	33.71 ± 0.40	5	0.46 ± 0.13

Host plants from different families have been recorded for the focal haeterines, with relatively few records for *C. pireta* and *D. polita*. As mentioned above, *C. pireta* has been recorded using philodendrons from the family Araceae (DeVries 1987; Janzen and Hallwachs 2009; Murillo-Hiller 2009; Isidro Chacón personal communication). In addition to the single record of *Philodendron herbaceum* observed on the Caribbean slope of Costa Rican lowland rainforest (Murillo-Hiller 2009), there are seven records from multiple forest types of the Guanacaste region of northwestern Costa Rica: six on *Philodendron rhodoaxis* and the

Table 1.4. Movement distances. One-day travel distances observed in selected butterflies marked and released in the years 2009-2011 at Tirimbina. Sampling effort was identical for the focal haeterines, but varied for the other species. N = number of observed one-day distances.

Focal haeterines:	Sex	N	Median (m)	Mean ± SE (m)	Max (m)
Cithaerias pireta	♀	17	43.88	65.8 ± 17.8	269.97
	♂	10	36.91	41.7 ± 10.2	91.63
Dulcedo polita	♀	33	34.07	48.0 ± 13.5	431.65
	♂	17	37.71	43.4 ± 10.2	124.12
Pierella helvina	♀	78	21.74	62.4 ± 21.2	1170.49
	♂	73	17.99	48.1 ± 14.3	872.73

Other Species	Sex	N	Median (m)	Mean ± SE (m)	Max (m)
Antirrhea miltiades	♀	69	0.00	29.5 ± 9.5	508.01
	♂	104	0.00	39.5 ± 11.3	968.41
Caligo atreus	♀	22	17.04	117.0 ± 44.0	804.27
	♂	19	36.62	80.5 ± 30.8	458.02
Caligo eurilochus	♀	10	0.00	47.5 ± 23.5	219.01
	♂	30	0.00	87.2 ± 27.5	559.58
Caligo illioneus	♀	1	na	0.00	0.00
	♂	3	0.00	19.1 ± 19.1	57.25
Morpho granadensis	♀	3	0.00	0.0 ± 0.0	0.00
	♂	5	254.37	296.8 ± 108.6	710.11
Pierella luna	♀	1	na	0.00	0.00
	♂	3	19.90	16.3 ± 3.6	19.90
Taygetis andromeda	♀	2	na	0.0 ± 0.0	0.00
	♂	7	0.00	0.0 ± 0.0	0.00

seventh on *Philodendron sulcatum* (Janzen and Hallwachs 2009). *Dulcedo polita* has been recorded using palms in the genera *Euterpe*, *Geonoma* and *Welfia* (Arecaceae) in Costa Rica, although the palm species have only been identified in Colombia (DeVries 1986, 1987; Beccaloni et al. 2008). There also is a single record for *D. polita* on *Asplundia microphylla*, a palm-like plant from the family Cyclanthaceae, in Guanacaste, Costa Rica (Janzen and Hallwachs 2009).

There are many more host plants records for *P. helvina* than the other two focal species. This may be, in part, because *P. helvina* uses noticeable, ornamental plants that often grow in easily observed successional environments (Kricher 1997; Zuchowski 2007).

Table 1.5. Abundances for *Dulcedo polita* (Nymphalidae, Satyrinae, Haeterini). Observed from November 2003 through October 2008 in the community diversity study using mid-understory traps, and from December 2009 through June 2010 in the MRR study using ground-level traps, both conducted at Tirimbina reserve. Binomial test p-values are two-tailed.

	Female	Male	Total	% Male	P-value	Conclusion
Community diversity study	213	293	506	0.58	$p = 0.0002$	Male-biased
MRR study	197	119	316	0.38	$p < 0.0001$	Female-biased

Observations for *P. helvina* host plants fall primarily into the families Heliconiaceae and Marantaceae, although they have been recorded using plants from other families as well (DeVries 1986, 1987; Janzen and Hallwachs 2009). In Guanacaste, *P. helvina* has been recorded 203 times using 35 plant species in seven families. Six species represent the bulk of the observations (140 records, 69%), with *Heliconia irrasa* (Heliconiaceae) the most commonly observed host species (40 records, 20%), and the remaining five species representing 17-24 records each (8-12% each): *H. latispatha* (Heliconiaceae), and *Calathea marantifolia*, *C. macrosepala*, *Hylaeanthe hoffmannii*, and *Pleiostachya leiostachya* (Marantaceae). The remainder of the host plant records may represent ovipositing “mistakes” or identification errors.

Nutrition for haeterine larvae has not been studied. Generally speaking, leaves in tropical forests relative to those in temperate forests are low in nutrition and protected from herbivory by a variety of secondary metabolites or defensive structures (Coley and Barone 1996). With that said, most host plants recorded for the focal haeterines are not considered particularly toxic (Watson and Dallwitz 1992; Longhi 2000; Murillo-Hiller 2009). Philodendrons in the family Araceae produce cyanogenic glycosides (Grayum 1990), but *Cithaerias* does not appear to be unpalatable to predators and so presumably does not sequester this toxin (DeVries 1987).

All recorded host plant families contain calcium oxalate crystals. Most plants express non-cytoplasmic structures of some kind in their cells, with the expression of silica in grasses

Table 1.6. MRR data for Costa Rican Haeterini. Summary of captures and recaptures for butterflies sampled at Tirimbina during the January-March 2011 post-study. Return rate is the ratio of individuals recaptured to individuals marked.

	Individuals marked			Indivs. recaptured			No. of recaptures			Return rate		
	♀	♂	Total	♀	♂	Total	♀	♂	Total	♀	♂	Total
Cithaerias pireta	20	18	38	1	1	2	1	1	2	0.05	0.06	0.05
Dulcedo polita	28	20	48	3	1	4	4	2	6	0.11	0.05	0.08
Pierella helvina	139	135	274	33	38	71	50	54	104	0.24	0.28	0.26

being a familiar example (Prychid and Rudall 1999). Calcium oxalate crystal is widespread in flowering plants, particularly palms, and often is produced with sharp, pointy ends that act as physical abrasives during feeding and may interfere with digestion (Prychid and Rudall 1999; Zona 2004; Korth et al. 2006). Lepidoptera larvae feeding on plants with abundant calcium oxalate crystals grow more slowly and die more often than when feeding on plants with lower crystal concentrations (Korth et al. 2006). As a result, growth rate may be slower and larval stages longer in palm feeders such as *D. polita* compared to other tropical forest butterflies.

Relatively few satyrine butterflies feed on palms (Peña 2004). DeVries (1987) summarized natural history observations for 532 species of Costa Rican butterflies in the families Papilionidae, Pieridae and Nymphalidae, of which only 11 satyrine species (2.07%) were recorded feeding on palms (Table 1.2). In the Janzen and Hallwachs (2009) online database, 16 Nymphalidae species (4.97%) are recorded as having oviposited on palms out of 322 species for which host plants were recorded. Palms are characteristic of the tropics and subtropics, and the humid forest zone of the Sarapiquí River Basin is rich in palms (Hahn 1997; Longhi 2000). However, in addition to the challenge to herbivores presented by high calcium oxalate crystal concentrations, palms represent a spatially heterogeneous resource. Palm populations are negatively affected by habitat fragmentation due to obligate outcrossing and specialized insect pollination (Arroyo-Rodriguez et al. 2007). Palm density also can vary significantly with soil type (Clark et al. 1995) making palm distributions patchy in spite of their abundance. Therefore, palms may represent a less attractive host plant resource for butterflies than their ubiquity at first glance suggests.

Species Summaries

Cithaerias pireta:

Cithaerias pireta is a familiar inhabitant of the forest floor in the Tirimbina forest. This species primarily has been observed flying just above the forest floor and perching on the ground or on leaf litter (DeVries 1987; personal observation), and as with the other focal haeterines, it is most likely to be captured in traps positioned very close to the ground (Alexander and DeVries 2012). These butterflies are seen on trails and hills, along stream-edges, and in light gaps wherever its host plants – philodendrons – are found (Janzen and Hallwachs 2009; Murillo-Hiller 2009; Isidro Chacón personal communication). The study region is rich in Araceae (Zuchowski 2007), and this may help explain the homogeneous spatial distribution of trap abundance shown for this species in the forest interior (Alexander and DeVries b).

In spite of its relatively cosmopolitan distribution within the reserve, *C. pireta* is more difficult to capture in traps than the other haeterines. Abundances for *C. pireta* were about half that observed for *P. helvina*, which also frequents hills and light gaps (Whittaker 1983; DeVries 1987). The difference in abundance may be due, in part, to lower capture probability. While the other two study species showed about a 50/50 chance of remaining in or escaping from traps in a 24-hr period, *C. pireta* showed a significantly lower chance of remaining in a trap long enough to be marked (Alexander and DeVries 2012). This means that population sizes based on data from trap studies will be underestimated more for this species than for more easily captured species (Hughes, Daily and Ehrlich 1998; Williams, Nichols and Conroy 2002).

Figure 1.9. *Pierella luna* (Nymphalidae, Satyrinae, Haeterini). A female *P. luna* trapped, marked, and photographed March 2010 at site 6 (site E) in the Tirimbina reserve.

Cithaerias pireta is the most petite of the focal species, and flew the shortest maximum distances. The forewing length of *C. pireta* averaged about 28 mm, making it 75-91% of the size of the other butterflies (Table 1.3). Its daily movements were similar in distance to those of the other haeterines, but its maximum distances were shorter (Table 1.4). This may be due to shorter forewing length due to the positive relationship between wing span and dispersal ability (Dudley 2000; Sekar 2012). The maximum single-day distance observed for *C. pireta* was a little over half of that observed for *D. polita*, and less than a quarter of that observed for *P. helvina*.

Males and females of *C. pireta* differed in movement patterns and daily survival. While female *C. pireta* gradually moved away from their initial capture locations, males did not (Alexander and DeVries a). In keeping with this, females have been documented flying near their host plants without remaining for longer than one day (Whittaker 1983; Murillo-Hiller 2009), whereas males may remain in a single location for many days in a row (DeVries 1987). Males have been observed flying up and down trails apparently patrolling territories, although these males were seldom captured in nearby fruit-baited traps and had to be hand netted to be marked (personal observation). Males also had higher estimated daily survival than females (Alexander and DeVries b), presumably due to smaller home range sizes and lower emigration rates as has been found in insects and other butterflies (Watt et al. 1977; Ehrlich 1989; Carey 2001).

With its habit of skimming the forest floor, small body size, and transparent forewings, *C. pireta* appears delicate and fragile. This species is widespread in the philodendron-rich Tirimbina interior but difficult to trap, with males and females showing differences in movement and home range size.

Dulcedo polita:

Dulcedo polita is locally abundant but less often observed at Tirimbina than the other two haeterines. It has transparent wings lacking a bright hindwing patch, so it may be more difficult to see, but the primary explanation probably has to do with its avoidance of sunny locations. Unlike the other two species, *D. polita* is seldom observed in light gaps or on hilltops (DeVries 1987; personal observation), and is associated with swamp forest habitats, especially palm swamps (DeVries 1987). The study region is rich in palms that serve as its host plants (DeVries 1987; Beccaloni et al. 2008; Janzen and Hallwachs 2009), but palms are patchily distributed (Clark et al. 1995). In keeping with this, *D. polita* showed strong heterogeneity in abundance among sampling sites, with the greatest abundances in swampier habitats (Alexander and DeVries b).

Spatial heterogeneity can reduce capture probability since some traps may be positioned in less frequented habitats by random chance (Borchers and Efford 2008). The heterogeneous spatial distribution of *D. polita* may have lowered capture probability and reduced trap abundances. Trap persistence (i.e., the likelihood of an individual remaining in a trap long enough to be marked; Alexander and DeVries 2012) can interact with spatial distribution and affect capture probability. Consider *C. pireta*, in which low trap persistence countered the positive effect of its homogeneous spatial distribution on capture probability and may have resulted in smaller trap abundances. This contrasts with *P. helvina*, in which higher trap persistence plus homogeneous spatial distribution (particularly males) contributed

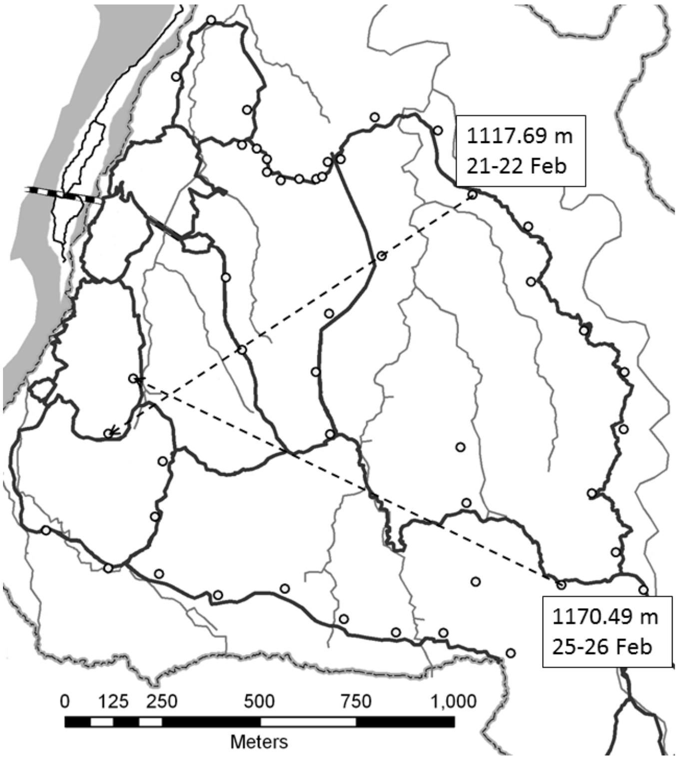


Figure 1.10. Long-distance movements by *Pierella helvina*. In February 2011, two female *P. helvina* were observed flying > 1 km in a single 24-h period, from traps placed along the outer boundaries of the reserve west through the interior.

to higher capture probability and larger trap abundances. As with *P. helvina*, *D. polita* had higher trap persistence, but it was countered by strong heterogeneity in spatial distribution, reducing capture probability and contributing to smaller trap abundances. This suggests that abundance of *D. polita* was likely under-represented relative to more homogeneously distributed species even when they had similar persistence rates within traps.

As with the other focal haeterines, *D. polita* flys near the forest floor, but shows a sex bias in capture height: females were more likely to be captured in lower traps than males (Alexander and DeVries 2012). Thus capture height probably contributed to observed female bias in trap abundance in low traps (Alexander and DeVries b). Compare this to the male bias observed in trap abundance when using mid-understory traps (Table 1.5). More often than the other focal haeterines, *D. polita* was seen perching on vegetation about 1 m above the ground (personal observation). It would be interesting to assess whether these higher-perching individuals are males and, if so, whether they are gaining a vantage point that allows them to locate females visually, as in *Heliconius numata* (Joron 2005).

With its transparent wings, patchy distribution and preference for swampy forest habitats, *D. polita* is less noticeable than the other haeterines. Vertical stratification of the sexes suggests a potential mate-searching behavior in this species.

Pierella helvina:

Pierella helvina is the most noticeable focal species, partly due to its penchant for sunny, easy-to-observe locations. This species frequently has been observed basking in the sun with wings held open, and flying on hilltops and in light gaps (Whittaker 1983; DeVries 1987). Its primary host plants are species of the ubiquitous and often successional genera *Heliconia* (Heliconiaceae) and *Calathea* (Marantaceae) (DeVries 1987). Thus is it not surprising that *P. helvina* was sampled more than five times as often as the other two haeterines in the sunny, disturbed habitats along the reserve boundaries (Table 1.6).

Pierella luna, which has brown and black wings (Fig. 1.9), also was observed at Tirimbina, but at considerably lower numbers. Six individuals of *P. luna* were captured over the entire course of this project. This contrasts with Whittaker's (1983) observations in Corcovado National Park on the Pacific coast of Costa Rica where he hand netted 40 *P. luna* but only four *P. helvina*. The difference in abundance between the two sites could have to do with temporal heterogeneity (Whittaker sampled in July) or climate (the Corcovado site was about 1 km from the ocean).

Of the three focal species at Tirimbina, *P. helvina* showed the most pronounced vertical stratification. When traps were available at both ground-level and mid-understory, a proportion of the other two species entered the higher traps, but *P. helvina* only entered the ground-level traps (Alexander and DeVries 2012). This may be one reason why, when using ground-level traps in the interior of the reserve, *P. helvina* was captured almost twice as often as *C. pireta* and *D. polita* (Alexander and DeVries 2012; Alexander and DeVries b).

Figure 1.11. Vertical trap placement. Photos of butterfly traps showing placement in (a) the mid-understory using a trap hung from an overhead tree branch, and (b) at ground level using a trap strung from a free-standing pole.

Moreover, abundances for *P. helvina* were about four times higher in the MRR study using ground-level traps than in the community diversity study conducted at the same sites using higher trap placement (see section "MRR vs community diversity study"). *Pierella helvina* showed a significant behavioral difference in vertical stratification as it was least likely of the three species to fly and feed higher than ground level.

Females of *P. helvina* flew the farthest. With an average forewing length of over 37 mm, females of *P. helvina* were larger than the other butterflies, including conspecific males (Table 1.3). This may explain why they showed the longest one-day travel distances (Table 1.4; Dudley 2000; Sekar 2012; Alexander and DeVries a). Some females traversed Tirimbina in a single day (Fig. 1.10) and it seems likely that their dispersal was confined by the non-forest matrix surrounding the reserve.

Males of *P. helvina* were evenly distributed, relatively easy to recapture, and flew in smaller home ranges relative to females. While females showed heterogeneity in spatial distribution, the males were homogeneously distributed (Alexander and DeVries b). Males also had the highest recapturability of the focal butterflies (Alexander and DeVries b), suggesting lower dispersal rates (Hill et al. 2001; Prieto, Takegami and Rivera 2005; Tufto et al. 2012). Males moved shorter net distances than females, and tended to return to the location where they were initially captured (Alexander and DeVries a), supporting the hypothesis that females roamed in search of resources such as oviposition sites, and males moved in smaller areas.

Pierella helvina was an abundant, visible, and easily recaptured inhabitant of relatively sunny areas within primary and secondary forest. Its low-to-the-ground flight behavior, combined with fairly even spatial distribution and high recapturability suggest that capture probabilities were highest when sampled near the ground.

Methods

Sampling occasions:

I collected data in Costa Rica on three separate occasions. Pilot studies were conducted January-March 2009, and the main data set was collected December 2009-June 2010. Adjunctive persistence data was collected during ten extra days of sampling in early June 2010, and a follow-up data set was collected February-April 2011. All data, except where noted, were collected at Tirimbina using the same MRR methods, but number, height and spatial configuration of the traps were not identical during the three collection periods (see Trap Placement). Secondary data collection at Pozo Azul was interspersed with collection at Tirimbina in January-March 2010 by alternating ten days of sampling at one site with ten days of sampling at the other site (Appendix C).

Basic methodology:

Butterflies were captured in cylindrical, fabric-net traps (see DeVries 1987 and DeVries and Walla 2001 for design) that were either hung from tree branches or from free-standing poles stuck into the ground (Fig. 1.11). The traps were baited with mashed bananas that had been fermented in a large barrel 48 h prior to use. The bait was refreshed or replaced in each trap as needed, often daily, and traps were checked at 24-h intervals. Butterflies were identified, sexed, and uniquely marked using a non-toxic permanent marker, and released immediately at the trap site unless otherwise noted.

Measuring wing length:

Upon first capture, forewing length was measured to the nearest 0.01 mm using dial calipers (Table 1.3). Measurements were made by grasping the thorax of the butterfly between the left thumb and forefinger and measuring the span of the ventral surface of the left wing from where the wing attached to the thorax to the rounded tip of the wing at the termination of the upper R5 vein. Wing length measurements were made with living butterflies in the field under a variety of weather conditions, so some degree of variability in measurement precision is to be expected. Multiple wing lengths were recorded for a subset individuals, and these records were used to estimate variation in wing length measurements (Table 1.3). To do so, the standard deviation of the measurements for individual butterflies was calculated, then those values were averaged for each species and sex. Relative to the average lengths for each species and sex, intra-individual variation in measurement was small.

Trap placement:

Trap sites were established in seven areas within Tirimbina that encompassed various levels of disturbance and habitat types but mostly primary forest (Fig. 1.6; Appendix D). Twenty-nine to 80 traps were baited at any one time as noted for each trial (see Brief Summaries). Traps were placed in all seven areas during the pilot studies conducted January-March 2009, but site 1 was not sampled thereafter due to low abundance of focal butterfly species. During

Table 1.7. Preliminary MRR analysis results. The 95% confidence set from an analysis of non-covariate time-variation models of apparent daily survival (phi) and recapture probability (p). AIC_c = Aikake Information Criterion corrected for small sample size; Δ = distance from the lowest ranking model; Wt = relative model weight; $\hat{c}$ = median estimated inflation factor.

Model	AIC_c	Δ	Wt	Likelihood	Parameters	$\hat{c}$
Phi(constant) p(attraction)	4508	0.00	0.722	1.000	14	1.00
Phi(attraction) p(attraction)	4511	3.61	0.119	0.164	16	1.00
Phi(attraction) p(constant)	4513	5.16	0.055	0.076	14	1.00
Phi(constant) p(constant)	4513	5.19	0.054	0.075	12	0.96

the ten days of adjunctive sampling in June 2010, traps were placed along a ridge overlooking the Tirimbina River. In February-April 2011, during post-study sampling for assessment of abundance heterogeneity and maximum dispersal capability, traps were placed throughout the reserve, along the boundaries, and in site 6 (site E). Except as described for the height trial during the 2009 pilot, the traps were positioned with the bases approximately 15 cm above the ground and are referred to as low or ground-level traps. They were arranged in groups of ten with adjacent traps 20 to 40 m apart, except for the 2011 post-study in which they were farther apart.

Software choice:

In the last 20 years a variety of computer software packages have been developed to allow researchers and wildlife managers to analyze MRR data. In a list last updated in mid-2011, the USGS Patuxent Wildlife Research Center described 39 software packages designed for the analysis of marked animal populations, 27 of which were specifically developed to estimate parameters such as survival, detectability, population size/density, and spatial distribution (http://www.mbr-pwrc.usgs.gov/software.html). MRR data also can be analyzed in the free software environment R (R Core Team 2013). The MRR software package recommended by Williams, Nichols and Conroy (2002) in their standard work on the analysis and management of animal populations is MARK (White and Burnham, 1999). MARK is capable of performing analyses on many types of data involving marked animals, is particularly powerful when working with data stratified into classes, and uses maximum likelihood and the information-theoretic approach to sort models by AIC values (Cooch 2001; Williams, Nichols and Conroy 2002). MARK also is widely used and well-supported online (http://warnercnr.colostate.edu/~gwhite/mark/mark.htm and http://www.phidot.org) and in the literature (e.g., Anderson and Burnham 1999; Cooch 2001; White, Burnham and Anderson 2001), with a comprehensive software manual (Cooch and White 2008). Program MARK was used to analyze the MRR data in this study.

Time structure analysis:

The information-theoretic approach was used for the covariate-based analysis of the main data set. Prior to analysis, however, it was necessary to choose an underlying time structure, and to do so six non-covariate time-variation models were compared (Appendix E). All six models allowed the parameters for recapture and survival to vary by sex and species, but within each sex/species group the parameters could (1) remain constant over the ten sampling occasions, (2) increase or decrease with each successive 24-h time interval, or (3) differ between the first time interval and the remaining intervals to simulate increased trap attractiveness immediately after baiting, termed the attraction effect (Otis et al. 1978). Four of the models explained 96% of the variation in the model set, and the top three had estimated median $\hat{c}$ values of 1.00 $\pm$ 0.0001 indicating good fit of the models to the data (Table 1.7; Appendix F). The best ranking model, Phi(constant)p(attraction), constrained survival to be constant, and applied the attraction effect to recapture probability.

In general, when using the information-theoretic approach the best model from among a set of models should have a minimum weight of 90% (Burnham and Anderson 2002, p. 176). However, in the above time structure analysis, the best model explained only 72% of

Table 1.8. MRR pilot results. Summary of captures and recaptures for a subset of butterflies sampled at Tirimbina during the January-March 2009 pilot studies. Return rate is the ratio of individuals recaptured to individuals marked.

	Individuals marked			Indivs. recaptured			No. of recaptures			Return rate		
	♀	♂	Total	♀	♂	Total	♀	♂	Total	♀	♂	Total
Cithaerias pireta	20	20	40	2	3	5	2	5	7	0.10	0.15	0.13
Dulcedo polita	30	22	52	5	5	10	6	8	14	0.17	0.23	0.19
Pierella helvina	27	27	54	8	6	14	14	11	25	0.30	0.22	0.26

the variation in the data set. The difference between the best model and its nearest neighbor was > 2 AIC units (3.61 units), implying substantial empirical support in favor of the best model as the most parsimonious approximating model for the underlying time structure. Furthermore, manually changing the value of $\hat{c}$ resulted in no changes to the rankings of the top models, increasing confidence in the choice of best time structure model (Cooch and White 2008).

The likelihood ratio for survival also supports substantial discrimination between the best time structure model and its nearest neighbor. Model likelihoods are good measures of data-based weight of evidence about parameter values, and model likelihood (or AIC weight) ratios are used to estimate the relative importance of variables (Burnham and Anderson 2002, pp. 75 and 167). A ratio = 1 indicates no discernible difference in effect between two variables. In this case, since both top ranking time structure models applied the attraction effect to recapture probability, the question regarding discrimination between them concerned the relative importance of the attraction effect on survival. The likelihood ratio calculated using the four models in the 96% confidence set (Table 1.7) showed that a model with constant survival was 4.5 times more likely to better approximate the data than one in which survival varied according to the attraction effect. This ratio provides additional support for the choice of the best model as the underlying time structure for the covariate-based analysis of the main data set.

MRR analysis of the main data set:

For specifics of the MRR analysis of the main data set, please see Chapter 4.

Nomenclature:

Two of the focal species that occur in Costa Rica have been considered as subspecies: *Cithaerias pireta pireta* and *Pierella helvina incanescens* (see Table 1 of Constantino 1995). Here the nomenclature of Lamas (2004) is employed to refer to these entities as *C. pireta* and *P. helvina*, but readers should be aware of nomenclature used by other authors (e.g., DeVries 1987; Janzen and Hallwachs 2009; DeVries et al. 2012).

Research Summaries

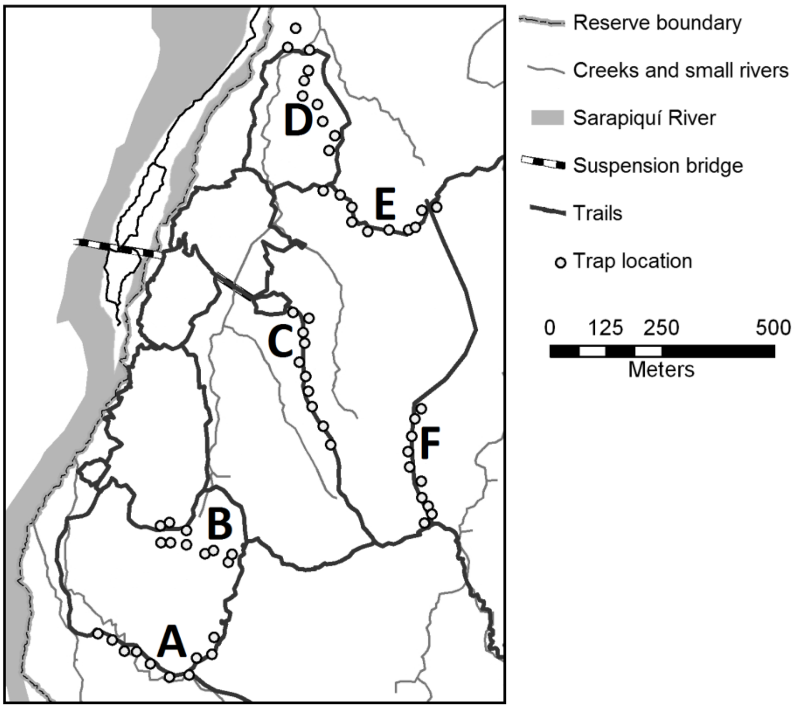
Pilot studies:

From 25 January through 11 March, 2009, I conducted preliminary trials to explore best practices regarding marking and trap placement, look for species- or sex-related differences that might affect capturability, and determine whether return rates would be high enough to make the haeterines a viable system for MRR study (Alexander and DeVries 2012).

Marking was easy in *C. pireta* and *D. polita* due to their scale-free forewings, but because they are transparent I placed the unique identifier in the discal cells of the left forewing and left hindwing so that resighted individuals might be identified from a distance (Fig. 1.2). The forewings of *P. helvina* are lightly scaled and could be marked in the discal cells of both forewings.

All three species were more likely to be captured in traps placed very near the forest floor than 1 m above it, and *P. helvina* entered only the lowest traps. I captured more females than males of *D. polita*, and *D. polita* females were more likely to enter low traps than

Figure 1.12. Sampling sites and trap locations. Sampling sites A-F correspond to sites 2-7 from the pilot studies. The sites pictured were used during the main MRR study conducted December 2009 through June 2010 at Tirimbina. Trap locations within each site are shown.



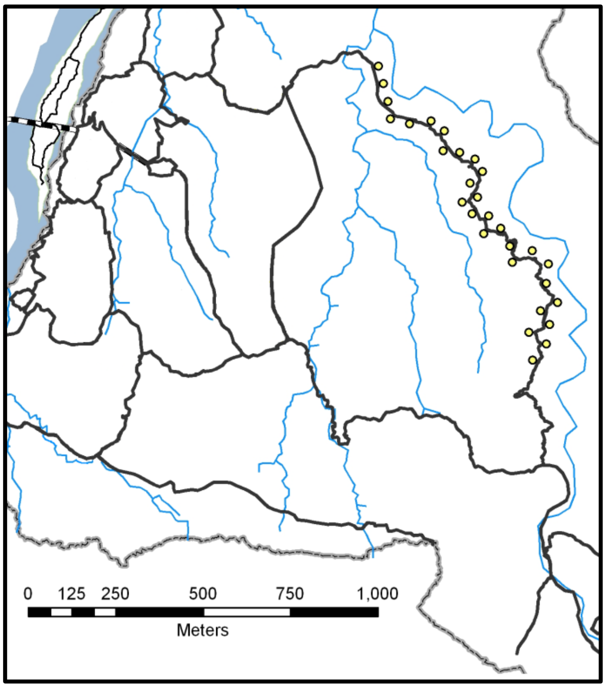
conspecific males. I also found that the odds of *C. pireta* remaining in a trap for 24 hours were significantly lower than for the other two species. Altogether, I captured about twice as many *P. helvina* as the other species (see Table 3 in Alexander and DeVries 2012). Return rates ranged from 0.10 to 0.30 depending on species and sex (Table 1.8).

These pilot studies showed that focal species were easy to handle and mark, exhibited behaviors that could differentially affect their capturability depending on trap placement, species and sex, and were sufficiently abundant within the study area to use the MRR method.

Main study:

To measure relative abundance, examine spatial and temporal distribution, estimate probabilities of recapture and daily survival (Alexander and DeVries b), and explore movement patterns (Alexander and DeVries a), I used the MRR method to sample individual butterflies from December 2009 through June 2010 using 60 traps deployed within six sampling sites (Fig. 1.12). The traps were checked for ten consecutive days (sampling

Figure 1.13. Trap locations along the Ajillo Ridge. Utilized during ten days of adjunctive sampling in early June 2010 at Tirimbina.



occasions) per month in seven consecutive months (sampling periods) as described in Methods.

As in the pilot study sample sizes for *P. helvina* were about twice those of the other species. *Dulcedo polita* and female *P. helvina* were heterogeneously distributed among sampling sites, while *C. pireta* and male *P. helvina* showed spatial homogeneity. All butterflies exhibited attraction effect (Otis et al. 1978), with sample sizes highest in the first few days of sampling each month. All butterflies showed estimated recapture probabilities > 0.10 although recaptures were higher in certain regions of the forest and for male *P. helvina.* Daily survival did not vary markedly among species and averaged 0.815 (± 0.024) per day. While average movement distances did not differ among species, there were significant differences between the sexes, with females dispersing from where they were originally marked and males moving within narrower home ranges.

Table 1.9. Adjunctive sampling results. Summary of individual butterflies marked along the Ajillo Ridge during ten adjunctive days of sampling between the May and June 2010 main sampling periods.

	♀	♂	Total
Cithaerias pireta	6	20	26
Dulcedo polita	2	3	5
Pierella helvina	11	25	36

Adjunctive study:

During ten adjunctive days of sampling in early June 2010 between the main May and June sampling periods, I deployed 29 traps along the Ajillo Ridge overlooking the Pozo Azul river (Fig. 1.13). The goals were to determine what proportions of species would be found in that region of the reserve, whether there would be movement between Ajillo Ridge and other sampling sites, and to collect additional persistence data. Captures observed during this period were not included in MRR analysis.

I captured very few *D. polita* at this site (Table 1.9). The low abundance of this species was no surprise considering the habitat was reminiscent of site 4 (site C) where we sampled fewer *D. polita* than expected (Alexander and DeVries b). There was virtually no movement between this site and the other sampling sites. Only one butterfly that had been previously marked in a different sampling site was recaptured on the Ajillo Ridge: a male *C. pireta* captured by net on 23 May in site 7 (site F). No butterflies marked on the Ajillo Ridge during this adjunctive sampling period were recaptured elsewhere in the reserve during the final June sampling period.

Because traps were checked twice daily, some movement among traps was detected in the adjunctive persistence trial that was not detected in the 2009 pilot trial. Of the 42 individuals included in the adjunctive persistence trial (Table 1.10), 15 persisted (i.e., were in the traps 24 hours later), including a single male *P. helvina* that was marked in the morning, was not present in the trap that afternoon, but returned to the same trap the next morning. Of the 27 individuals that did not persist, 11 were resighted outside of the trap or recaptured in a

Table 1.10. Results of the adjunctive persistence trial. Uses a subset (n=42) of butterflies marked on the Ajillo Ridge between the main May and June 2010 sampling periods. Persisted = alive and in the trap after 24 hrs. Died = found dead. Escaped = seen alive outside of the trap on some future occasion. Unknown = not in trap, unknown if alive or dead.

	Individuals			Persisted			Died			Escaped			Unknown		
	♀	♂	Total	♀	♂	Total	♀	♂	Total	♀	♂	Total	♀	♂	Total
Cithaerias pireta	4	7	11	1	2	3	0	1	1	1	2	3	2	2	4
Dulcedo polita	2	3	5	1	0	1	1	1	2	0	1	1	0	1	1
Pierella helvina	7	19	26	4	7	11	0	3	3	2	5	7	1	4	5

Table 1.11. Pooled results of both persistence trials. The first trial (n=90) conducted in January 2009 in sampling sites 1-6, and the second (n=42) conducted in June 2010 on the Ajillo Ridge. Persisted = alive and in the trap after 24 hrs. Results of independent binomial tests to determine whether the ratio of persisted to not persisted = 50/50 are presented as two-tailed p-values with significant results marked by asterisks.

	Pooled individuals			Persisted			P-value	
	♀	♂	Total	♀	♂	Total	♀	♂
Cithaerias pireta	13	28	41	2	7	9	0.023*	0.013*
Dulcedo polita	20	15	35	8	6	14	0.50	0.61
Pierella helvina	21	35	56	11	13	24	1.00	0.18

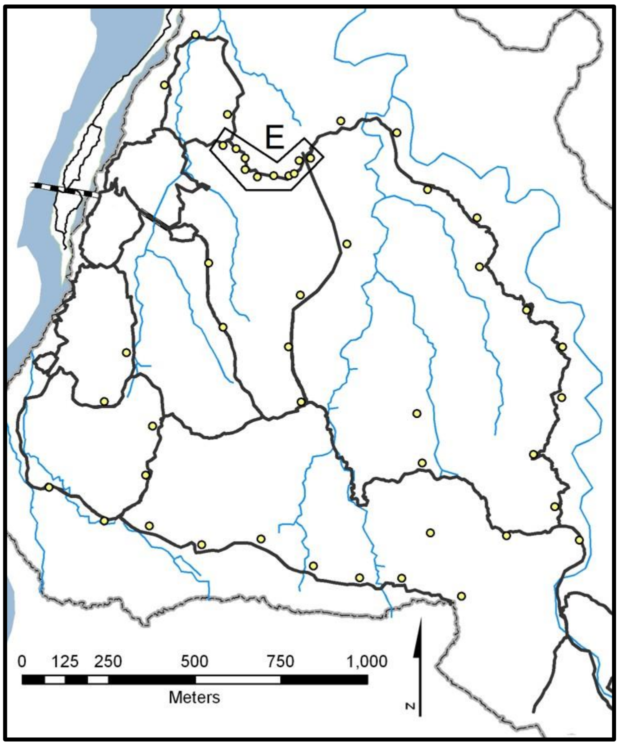
different trap, indicating that at least 40% of the non-persisting individuals were escapees rather than victims of mortality factors. Individual binomial tests conducted using the combined data sets from the 2009 and 2010 persistence trials supported the results from 2009 data alone: about 50% of *D. polita* and *P. helvina* remained in the traps for at least 24 hours while significantly fewer than 50% of *C. pireta* remained (Table 1.11).

This study showed that the three species were not found in all locations in constant proportions, individual butterflies may not have moved among all portions of the reserve, individual butterflies escaped from (and returned to) traps, and individuals of *C. pireta* were less likely to remain in traps for 24 hours than the other species.

Post-study:

To measure maximum dispersal capability of the focal species and explore heterogeneity in abundance between years, I used the MRR method to sample individual butterflies from February through March 2011 using 47 traps deployed throughout the reserve. Ten of the

Figure 1.14. Wide spatial trap placement in 2011. Trap locations along the outer Tirimbina boundaries and within site 6 (site E; marked by a polygon), used from February-April 2011.



traps were deployed in sampling site 6 (site E) at the same GPS coordinates as in 2010 so that butterfly abundances at that site could be compared between 2010 and 2011 for those three months. The remaining traps were spread as evenly as possible around the outer boundary of the reserve and in the reserve interior with the goal of measuring the longest possible straight-line distances travelled by individual butterflies (Fig. 1.14).

Return rates were low (Table 1.6), probably due to the wide-spread placement of traps. The focus was to detect long-range movements, so traps were positioned to cover the perimeter of the reserve and key interior points. Excluding the traps in site 6, the average distance between adjacent traps was about 186 m, too far apart to observe most daily movements. The distance between traps probably also helps explain why return rates were highest for *P. helvina*, which by virtue of its longer wingspan might be expected to fly farther (c.f., Dudley 2000; Sekar 2012) and, thus, be recaptured more often in widely spaced traps. The longest single-day movements observed during the post-study were two *P. helvina*, both captured > 1 km from their starting points (Fig. 1.10). Large movements were not detected in the other two species in any phase of this research (Table 1.4).

Table 1.12. Comparison of abundances between years. Abundances observed in 2010 and 2011 (a) in the MRR study during the months February-April in site 6 (site E) only, (b) in the community diversity study for the entire year and all sampling sites, and (c) also for the entire year in the community diversity study but only for site 6 (site E).

(a) MRR post-study, Feb-Apr, site 6

	2010	2011	2011/2010
Cithaerias pireta	26	4	0.15
Dulcedo polita	73	10	0.14
Pierella helvina	93	28	0.30

(b) Community diversity study, Jan-Dec, all areas

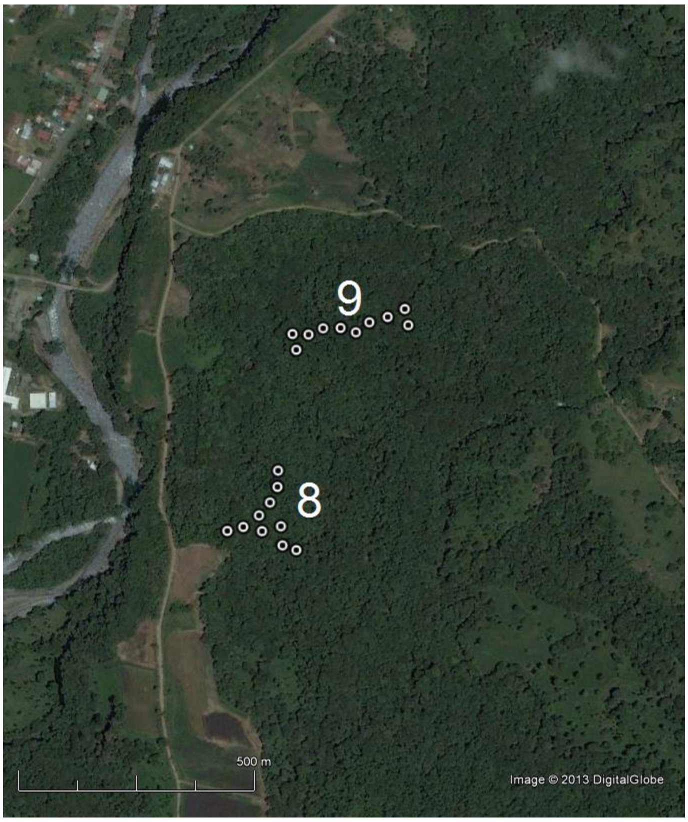
	2010	2011	2011/2010
total species, abundance	1709	1665	0.97
total species, species richness	84	82	0.98
Cithaerias pireta	128	65	0.51
Dulcedo polita	125	84	0.67
Pierella helvina	44	27	0.61

(c) Community diversity study, Jan-Dec, site 6

	2010	2011	2011/2010
total species, abundance	441	359	0.81
total species, species richness	60	53	0.88
Cithaerias pireta	28	9	0.32
Dulcedo polita	73	40	0.55
Pierella helvina	13	6	0.46

Ecological differences between the habitats in the post-study and those in the prior trials might have influenced relative abundances. In the post-study, a larger proportion of the sample than expected was represented by *P. helvina:* 76% (274 individuals) compared to 49% (139 individuals) in the pilot study and 48% (547 individuals) in the main study (Alexander and DeVries 2012; Alexander and DeVries b). For the pilot and main studies, traps were placed in sites that reflected ecological variability, but all were in the interior of the reserve except site 1. In the post-study, traps deployed along the outer boundaries of the reserve were often placed in habitats sunnier than the interior, with more successional plants such as *Passiflora* sp. (Passifloraceae) and *Heliocarpus* sp. (Malvaceae). Since host plants of *P. helvina* are in plant families that tend to occur in successional conditions (Kricher 1997;

Figure 1.15. Secondary sampling sites. GoogleEarth image (imagery dates 2003-2007) showing trap locations within secondary sites 8 and 9 at Pozo Azul.



Zuchowski 2007), it is not surprising this species was more abundant in the post-study traps relative to the other two haeterines.

Butterfly abundance observed in sampling site 6 during the post study was less than a quarter of the abundance observed in 2010 during the same three months (Table 1.12a). To place this into context, consider that the results from the ongoing community diversity study at Tirimbina (e.g., DeVries et al. 2012) showed that total sampled richness and abundance were similar in 2010 and 2011. However, abundances of the three focal species averaged 1.7 times lower in 2011 than in 2010 (Table 1.12b), an effect more pronounced in site 6 (Table 1.12c). These differences support findings of temporal heterogeneity in tropical butterflies (DeVries 1987; DeVries and Walla 2001; Bonebrake et al. 2010; Grotan et al. 2012) and indicate that individual species can exhibit fluctuations that are not necessarily reflected in all species of the same feeding guild, especially if combined with subtle environmental changes in forest microhabitats.

Table 1.13. Secondary MRR results. Captures for butterflies sampled at Pozo Azul from January through March 2010. Return rate is the ratio of individuals recaptured to individuals marked.

	Individuals marked			Indivs. recaptured			No. of recaptures			Return rate		
	♀	♂	Total	♀	♂	Total	♀	♂	Total	♀	♂	Total
Cithaerias pireta	38	53	91	14	20	34	25	44	69	0.37	0.38	0.37
Dulcedo polita	10	11	21	6	3	9	14	4	18	0.60	0.27	0.43
Pierella helvina	36	41	77	14	19	33	31	40	71	0.39	0.46	0.43

Table 1.14. Return rate comparison between sampling areas. Return rates and proportions observed at Tirimbina (December 2009-June 2010, 10 traps per site, six sites) and at Pozo Azul (Jan 2010, 10 traps, one site, plus February-March 2010, 20 traps per site, two sites).

	Return rates		Relative proportions of each species	
	Tirimbina	Pozo Azul	Tirimbina	Pozo Azul
Cithaerias pireta	0.34	0.37	0.24	0.48
Dulcedo polita	0.40	0.43	0.28	0.11
Pierella helvina	0.51	0.43	0.48	0.41

Table 1.15. Abundance comparison between sampling areas. Individuals per trap marked in February and March 2010 at Tirimbina and Pozo Azul, Costa Rica.

	Tirimbina			Pozo Azul			Relative proportion (Tirimbina/Pozo Azul)
	♀	♂	Total	♀	♂	Total	
Cithaerias pireta	1.10	1.22	2.32	1.75	2.20	3.95	0.59
Dulcedo polita	1.65	1.20	2.85	0.40	0.50	0.90	3.17
Pierella helvina	2.42	2.32	4.73	1.30	1.95	3.25	1.46

Secondary sampling sites:

To compare return rates and relative abundances of focal species between forest patches of different sizes, in January-March 2010 I established two secondary sampling sites at Pozo Azul, which is structurally similar to Tirimbina but about half the size. Sampling at Pozo Azul began in January 2010 with ten traps deployed within a single sampling site (site 8) with guidelines as those in the main study. In February and March 2010, I added a second sampling site (site 9; Fig. 1.15).

I captured 189 individuals of the three species at Pozo Azul (Table 1.13). In spite of lower sampling effort at Pozo Azul, return rates were similar to those observed at Tirimbina

(Table 1.14). However, the relative proportions at which the species were captured differed, with observations at Pozo Azul almost equal between *C. pireta* and *P. helvina* (Table 1.14). *Dulcedo polita* was captured three times less often per trap at Pozo Azul than at Tirimbina (Table 1.15). This could be due to random chance given *D. polita*'s spatial heterogeneity, but it also could indicate greater edge effects due to smaller patch size and proximity to roads and housing. *Cithaerias pireta* and *P. helvina* have both been observed more often in light gaps (DeVries 1987), and *P. helvina* in particular uses successional plants as larval food sources (DeVries 1997; Kricher 1997; Zuchowski 2007; Janzen and Hallwachs 2009), so it seems reasonable to expect them to be more abundant in habitats exhibiting edge effects. However, to assess the effects of patch size on abundances, one would need to quantify differences among the reserves and surrounding landscapes and assess factors that might confound detection of species responses to habitat fragmentation (Turner 1989; Ewers and Didham 2006).

Comparison of MRR and removal studies:

A comparison of abundances from the MRR study and an ongoing community diversity study at the same location (e.g., DeVries et al. 2012) supports the hypothesis that while all three species fly and feed at ground level, vertical stratification is most pronounced in *P. helvina*.

In the MRR study, traps were positioned at ground-level, but in the community diversity study, traps were positioned in the mid-understory with the bases approximately 1 m above the ground. The MRR study was conducted December-June 2009/2010. From the community diversity study we used trap abundances observed during the five years from 2003/2004 through 2007/2008, and pooled the pertinent seven months over the five years. In other words, total abundance for December is the sum of December 2003, December 2004 …

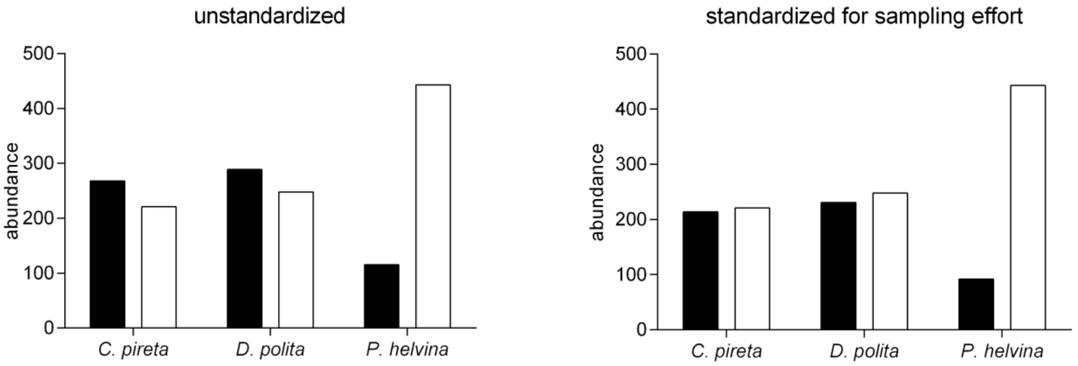


Figure 1.16. Abundance comparison between two studies. Butterfly abundances observed in the community diversity study (black bars) and MRR study (white bars), both as raw data (unstandardized) and standardized for sampling effort.

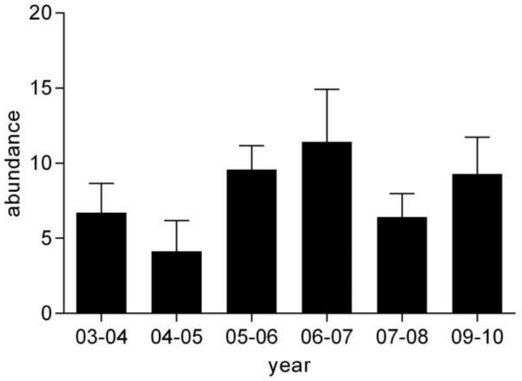
December 2007, etc. Data were only included from the five sampling sites shared between the two studies: sites 2-6 (sites A-E).

Sampling effort was not identical for the two studies, although the difference in effort was not as large as it might seem at first glance. The MRR study was conducted within a single year for ten consecutive days per month using ten traps per site, while the five-year portion of the community diversity study included here was conducted for five consecutive days per month using five traps per site in the understory. The sampling effort in the community diversity study was only 1.25 times that of the MRR study.

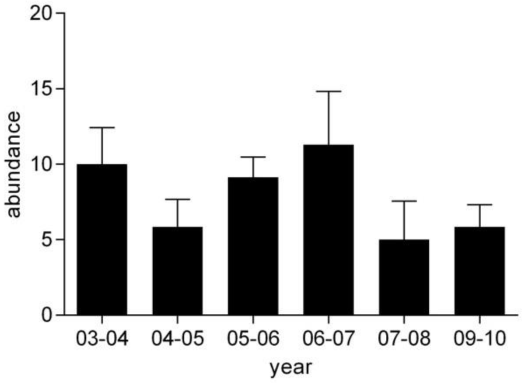
Abundances observed during the community diversity study were a bit higher than from the MRR study for *C. pireta* and *D. polita* (Fig. 1.16). Independent t-tests showed that differences in abundance between the two studies were not significant (*C. pireta*: t=0.593, df=12, p=0.564; *D. polita*: t=0.430, df=12, p=0.675), and differences vanished when results were standardized for sampling effort. However, we captured significantly more *P. helvina* in the MRR study whether considering standardized (t=3.295, df=12, p=0.0064) or unstandardized (t=3.05, df=12, p=0.0101) abundances (Fig. 1.16).

These findings suggest that *C. pireta* and *D. polita* were more likely to fly into mid-understory traps than *P. helvina*. While all three species were trapped more often close to the ground, about a quarter of individuals for *C. pireta* and *D. polita* entered higher traps when

Cithaerias pireta: $F_{5,36}$=1.34, p=0.269



Dulcedo polita: $F_{5,36}$=1.27, p=0.298



Pierella helvina: $F_{5,36}$=1.31, p=0.283

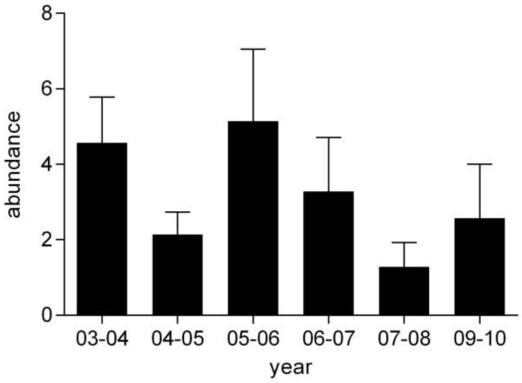


Figure 1.17. Abundance comparison among years. Mean butterfly abundances (±SE) observed in the community diversity study during the months December through June for five consecutive years (2003/2004-2007/2008) and the year 2009/2010, with results of one-way ANOVAs included.

traps were available at both heights (Alexander and DeVries 2012). But zero individuals of *P. helvina* entered higher traps when ground-level traps were also present (Alexander and DeVries 2012). Thus, a likely explanation for the increased sampling of *P. helvina* in the MRR study appears to be vertical stratification.

Two other potential explanations for higher abundance in the community diversity study compared to the MRR study for *P. helvina* were unsupported by the evidence. First, we

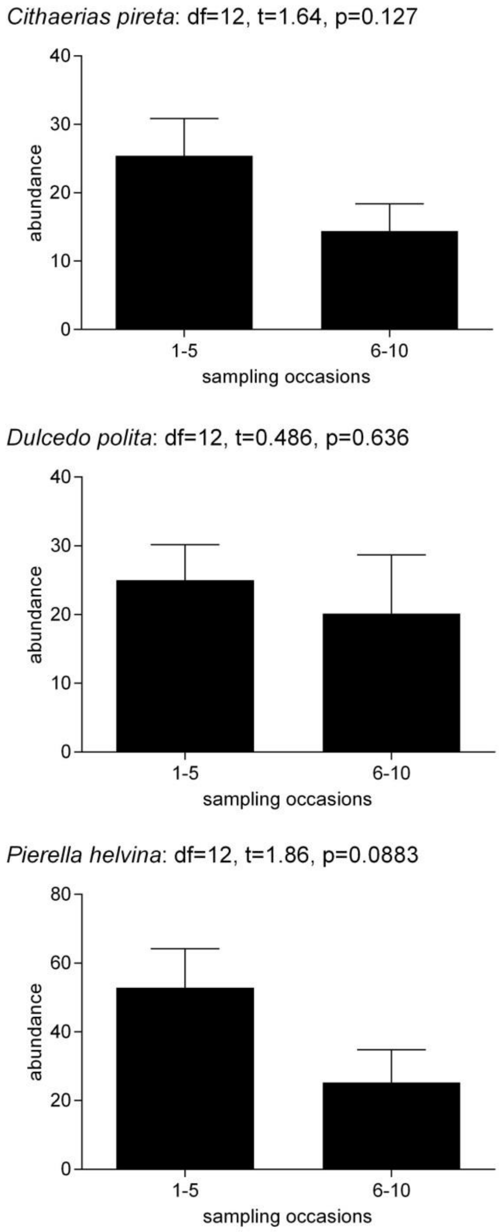


Figure 1.18. Abundance comparison between early and late sampling occasions. Mean butterfly abundance (±SE) observed in the MRR study, stratified by sampling occasion (days 1-5 versus days 6-10), with results of unpaired t-tests included.

thought butterfly abundance might have been higher in the year 2009/2010 compared to the five years used for comparison. To test this, we used a one-way ANOVA for each species to compare mean butterfly abundance from the community diversity study for the year 2009/2010 to mean abundances for each of the five comparison years, but found no significant difference (Fig. 1.17). This suggests that higher *P. helvina* abundances observed in the MRR study cannot be attributed to heterogeneity among years.

Second, we wondered if the five extra sampling days in the MRR protocol contributed more than expected to overall abundance. This was tested using an independent t-test for each

Table 1.16. Summary of non-focal Satyrinae butterflies. Non-haeterine butterflies arked and recaptured at (a) Tirimbina in 2010, (b) Pozo Azul in 2010, and (c) Tirimbina in 2011. Because some *Caligo* sp. butterflies were incorrectly sexed, only total numbers are shown for those butterflies in 2010. **Antirrhea miltiades* was marked beginning in February 2010, not January.

(a) Tirimbina, Jan-Jun 2010, 60 traps

	Indivs. marked			Indivs. recaptured			Indivs. marked per trap per month	Return rate
	♀	♂	Total	♀	♂	Total		
*Antirrhea miltiades**	89	82	171	43	45	88	0.57	0.51
Caligo atreus	-	-	94	-	-	43	0.26	0.46
Caligo eurilochus	-	-	87	-	-	50	0.24	0.57
Caligo illioneus	-	-	23	-	-	11	0.06	0.48
Pierella luna	1	4	5	1	2	3	0.01	0.60

(b) Pozo Azul, Feb-Mar 2010, 20 traps

	Indivs. marked			Indivs. recaptured			Indivs. marked per trap per month	Return rate
	♀	♂	Total	♀	♂	Total		
Antirrhea miltiades	8	6	14	2	2	4	0.35	0.29
Caligo atreus	-	-	18	-	-	9	0.45	0.50
Caligo eurilochus	-	-	15	-	-	8	0.38	0.53
Caligo illioneus	-	-	1	-	-	0	0.03	0.00
Pierella luna	0	1	1	0	1	1	0.03	1.00

(c) Tirimbina, Feb-Apr 2011, 47 traps

	Indivs. marked			Indivs. recaptured			Indivs. marked per trap per month	Return rate
	♀	♂	Total	♀	♂	Total		
Antirrhea miltiades	33	50	83	6	11	17	0.59	0.20
Caligo atreus	33	22	55	9	5	14	0.39	0.25
Caligo eurilochus	20	22	42	4	6	10	0.30	0.24
Caligo illioneus	0	0	0	0	0	0	na	na
Pierella luna	0	0	0	0	0	0	na	na
Morpho granadensis	7	8	15	2	3	5	0.11	0.33
Taygetis andromeda	2	13	15	2	5	7	0.11	0.47

species to compare mean abundance per month observed in the first five sampling days to the second five sampling days, and again found no significant difference (Fig. 1.18). Apparently, higher *P. helvina* abundance observed in the MRR study was not due to the five additional sampling days.

With both large- and small-scale temporal heterogeneity excluded, the abundances observed in these two studies supported the hypothesis that *P. helvina* shows a significant

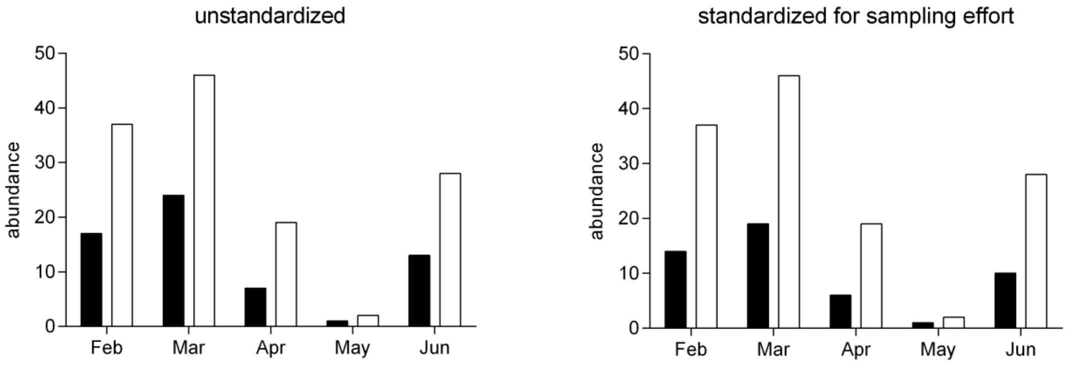


Figure 1.19. *Antirrhea miltiades* (Nymphalidae, Satyrinae, Morphini) abundance. Total abundance of the butterfly *A. miltiades* from the five-year community diversity study (black bars; years 2003/2004 - 2007/2008), and from the 2010 MRR study (white bars), both as raw data (unstandardized) and standardized for sampling effort.

behavioral difference in vertical stratification compared to the other haeterines. *Pierella helvina* was the least likely of the three species to fly and feed higher than ground level.

Non-focal species:

Although three Haeterini species were the focus of this research, other satyrine species were captured in the traps. Beginning in January 2010 I marked the most conspicuous of these thinking they might be appropriate future study subjects. As mentioned elsewhere (see the section on *Pierella helvina*), a fourth member of the tribe Haeterini – *Pierella luna* – was captured rarely. Nevertheless, it was marked along with three species of the Brassolini genus *Caligo*, and a single species from the tribe Morphini, *Antirrhea miltiades* (Table 1.16). In 2011, I also marked another morphine, *Morpho granadensis*, plus a member of the tribe Euptychiini, *Taygetis andromeda*.

Of the marked non-haeterines, *A. miltiades* appeared to spend the most time flying and feeding near the ground. I captured approximately twice as many individuals in ground-level traps during the MRR study compared to mid-understory traps in the community diversity study (Fig. 1.19). In spite of this apparent difference, an unpaired t-test did not find

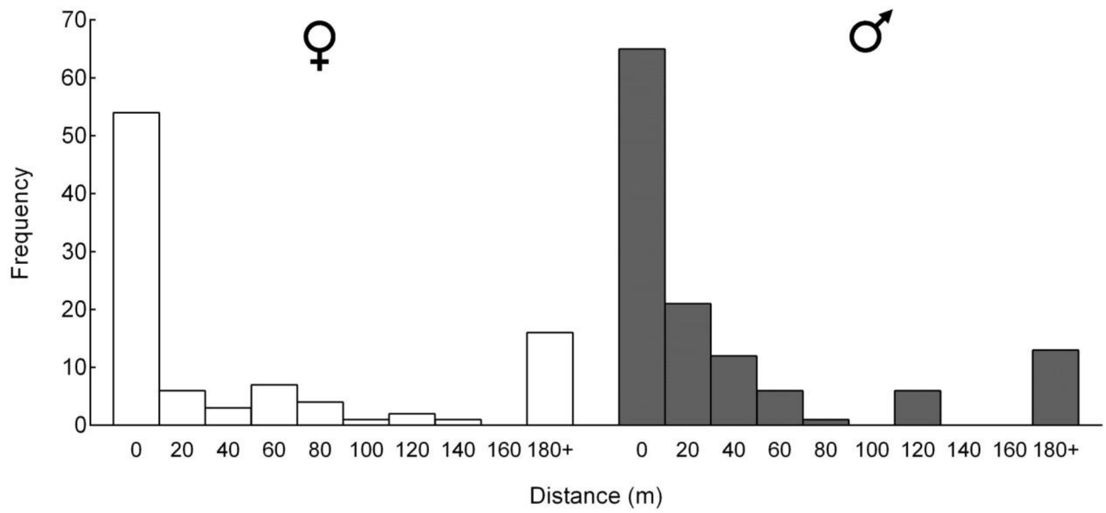


Figure 1.20. *Antirrhea miltiades* movement distances. Distributions of travel distances observed females (n = 43) and males (n = 45) of the butterfly species *A. miltiades* in February-June 2010 at Tirimbina.

a statistically significant difference in abundance between the two studies, whether considering raw abundances (t=1.64, df=8, p=0.141) or abundances standardized for sampling effort (t=2.00, df=8, p=0.0804). This suggests that even if *A. miltiades* spends a large proportion of its time at ground-level, it can be captured as readily in the mid-understory.

Legibly marking the darker colored and more thickly scaled non-haeterines was more challenging than marking the transparent or thinly-scaled haeterines, but non-haeterines were easier to handle due to their larger sizes (Table 1.3). Return rates were high (Table 1.16) suggesting these species would be appropriate subjects for using MRR methods if sampled long enough to achieve adequate sample sizes.

One question that would be interesting to explore is whether the non-focal species show the same sex-based movement patterns as the haeterines. The histograms of distances moved by male and female *A. miltiades,* for example, show that males seemed to move more intermediate distances than conspecific females (Fig. 1.20). This suggests that, unlike haeterines, male *A. miltiades* might be the dispersing sex.

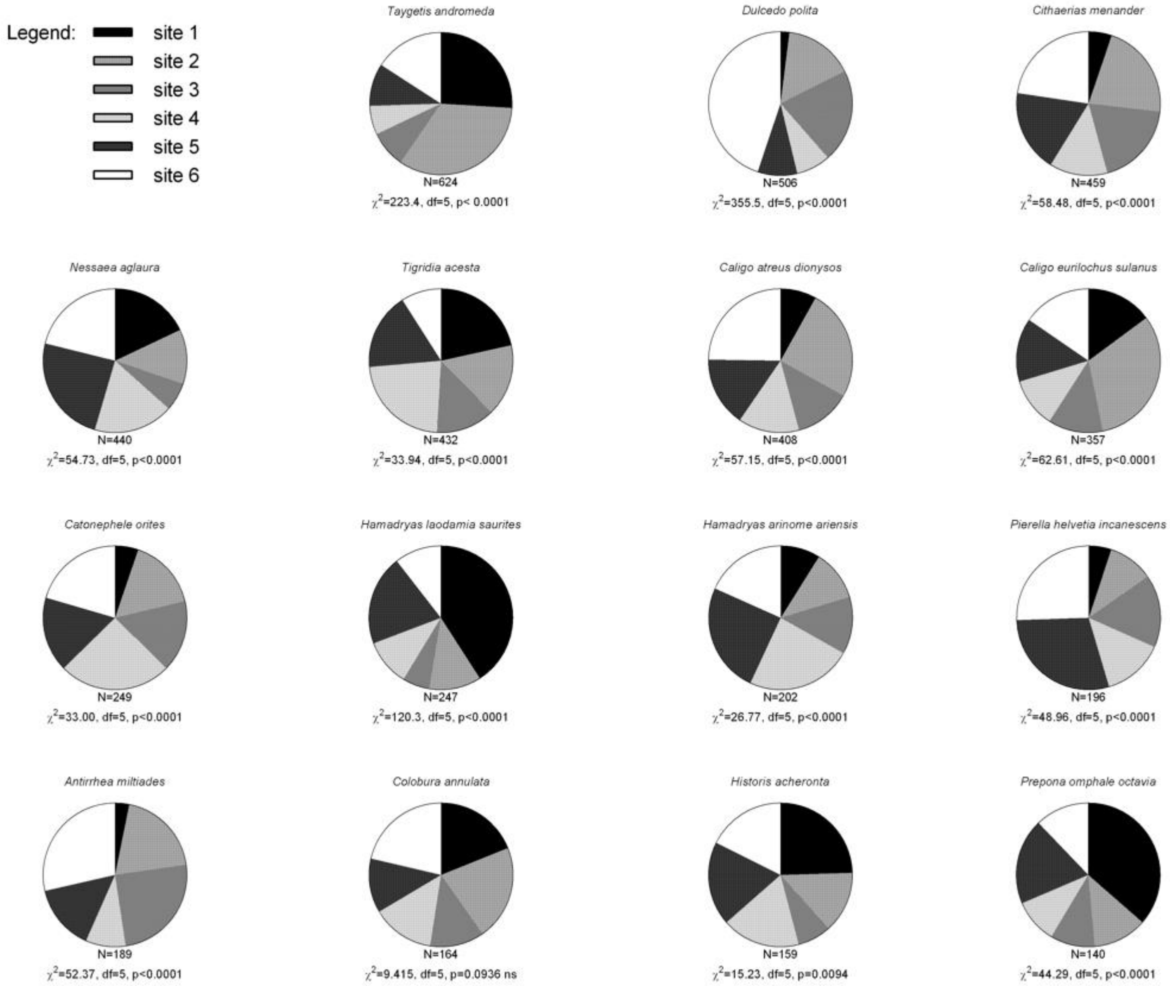


Figure 1.21. Spatial distributions of fruit-feeding Nymphalidae butterflies. Includes 27 species with total abundance ≥ 60 after being sampled monthly by trap for five years (Nov 2003 - Oct 2008). Results of χ^2 tests for homogeneous distribution are shown. P-values are two-tailed. ns = not significant. 15 species shown here; figure continued on next page.

Spatial distribution of Nymphalidae butterflies at Tirimbina:

During the five year period from November 2003 through October 2008, butterflies were sampled in fruit-baited traps in an ongoing community diversity study at Tirimbina (e.g., DeVries et al. 2012). Traps were positioned in the mid-understory in sites 1-6 with five traps per site and checked daily for five consecutive days each month. As described elsewhere (see Appendix D), even though most of the sites were primary forest (Isidro Chacón personal communication), they varied in anthropogenic disturbance, plant composition, hydrology and topography. This variation may have affected average butterfly abundance and species abundances among sites. To explore this, we pooled abundances for all five years within each

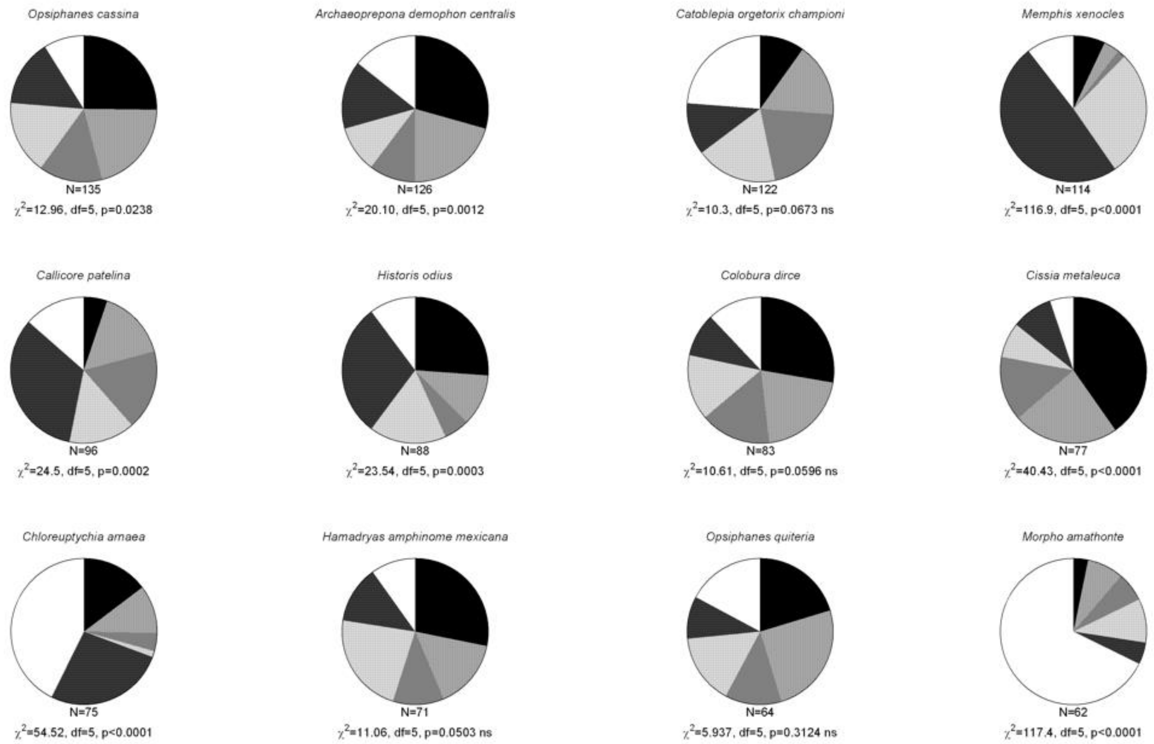


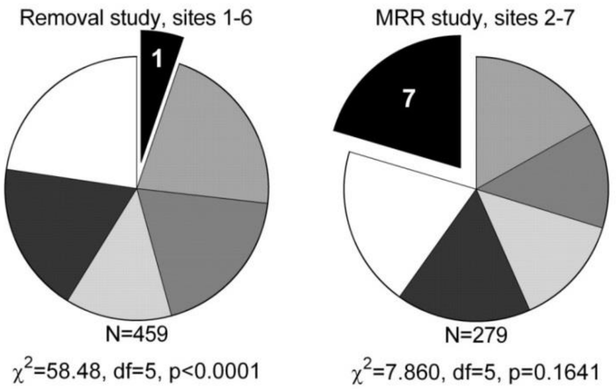
Figure 1.21 – cont.-

species and partitioned them by sampling site (Appendix G). Of the 100 species sampled (n=6984), 27 species (n=5885) had total abundance ≥ 60, an average of ten individuals per site. To avoid effects of small sample size, we used the 27 most abundant species to conduct three analyses:

First, to test the hypothesis that average abundances did not differ among sampling sites, we conducted a one-way ANOVA. Based on the results ($F_{5,156}$=0.8912, p=0.4886, R^2 = 0.02777) we accepted the null hypothesis and concluded that average abundance did not vary by sampling site.

Second, to test the hypothesis that species abundances were distributed homogeneously among sampling sites, we conducted a chi-square test. Based on the results (χ^2=1446, df=130, p<0.0001), we rejected the null hypothesis and concluded that species abundances were heterogeneously distributed among the six sampling sites.

Figure 1.22. Abundance per sampling site for *Cithaerias pireta*. From (a) the community diversity study conducted November 2003 through October 2008 in sites 1-6, and (b) the MRR study conducted December 2009 through June 2010 in sites 2-7. Includes results of χ^2 tests comparing observed and expected abundances.



Due to the significant result of the chi-square test, we wanted to determine which of the 27 species were heterogeneously distributed among sampling sites. To do so, we conducted independent chi-square tests for each species to compare observed versus expected abundances per site, with expected abundance being the average abundance per site for each species. We found that 22 (81.5%) of 27 species were heterogeneously distributed among sampling sites (see Fig. 1.21 for stats).

It is interesting to note that *C. pireta* (=*menander*) was among the heterogeneously distributed species in the community diversity study, but in the MRR study conducted December 2009 through June 2010, it was homogeneously distributed (Fig. 1.22; Alexander and DeVries b). During the MRR pilot studies conducted in early 2009, all focal haeterines were seldom captured at site 1, an old cacao plantation. Thus, for the main MRR study, site 1 was replaced with a more interior site (site 7; Fig. 1.12). Replacement of site 1 with site 7 resulted in a change in the perception of spatial distribution for *C. pireta* from heterogeneous to homogeneous.

It is well known that tropical ecosystems, especially rainforests, are heterogeneous in space and time (Connell 1978; Gentry 1990; DeVries, Walla and Greeney 1999). The findings above reinforce that even when sampled butterfly abundance is homogeneously distributed among sampling sites, species abundances can vary by habitat in small spatial scales.

Conclusion

This dissertation explored the population biology of three butterfly species in Costa Rican forest. The Haeterini are a group of fruit-feeding understory butterflies that share pattern of seasonal abundance, and heterogeneity in spatial distribution as do other tropical Nymphalidae. They differ from other members of the subfamily Satyrinae in larval food resources, flight behavior, appearance, and vertical stratification. Among the three focal species there were differences in capturability, recapturability, spatial distribution, and degree of vertical stratification. Males appeared to fly within smaller home ranges than females. Nevertheless, the ability of *P. helvina* to traverse the entire reserve in a single day suggests that the 3.4 sq km reserve was not large enough to allow full expression of their dispersal capability. This has implications for the genetic diversity of these populations and risk of local extinction in the face of changing ecological conditions. Directions for future research should include mating and reproduction, territoriality and home range size, and landscape-level assessment of patch size on abundances of these unique butterflies. As tropical forests continue to show the effects of anthropogenic pressure and climate change, studies on tropical insects such as butterflies can improve our ecological understanding of diverse forest habitats and our ability to conserve and manage them.

Chapter 2: Variation in Capture Height and Trap Persistence Among Three Costa Rican Understorey Butterfly Species

Abstract

Tropical forest insects are vertically stratified between the canopy and understorey. Using 60 traps set at two heights above the forest floor (30 at 15 cm and 30 at 1 m) we compared abundances in capture height, persistence in traps, and sex of three co-occurring understorey butterflies (*Cithaerias pireta*, *Dulcedo polita*, and *Pierella helvina*) in Costa Rica. We captured, marked and released 283 individual butterflies (65 *C. pireta*, 79 *D. polita*, 139 *P. helvina*) and showed all three species were captured more often in low traps, and P. helvina was captured only in low traps. The probability of remaining in traps for 24 h did not differ significantly for *D. polita* and *P. helvina*, but was significantly lower for *C. pireta*. The odds of trapping either sex did not differ significantly for *P. helvina* and *C. pireta*, but they were significantly lower for *D. polita* males. We experimentally demonstrate that these co-occurring species fly and feed just above the forest floor, but differ with respect to their persistence in traps and attraction to traps by sex. Our study implies that closely related species can exhibit behavioural differences that may influence population abundance estimates in multi-species studies.

Keywords: abundance, *Cithaerias pireta*, *Dulcedo polita*, Haeterini, mark-recapture, Nymphalidae, *Pierella helvina*, population biology, tropical rain forest.

Introduction

Insects have been central to developing a framework for understanding tropical diversification (Grimaldi and Engel 2005, Wilson 1992), and studies on butterflies have been particularly important to illuminating the population biology and evolutionary ecology of tropical insects (Boggs et al. 2003; Bonebrake et al. 2010; Brown and Freitas 2000; DeVries 1987; DeVries et al. 2008, 2010; Fordyce 2010; Vane-Wright and Ackery 1989; Wahlberg et al. 2009). Trap studies of tropical fruit-feeding nymphalid butterflies have demonstrated spatial and temporal variation in species diversity, and vertical stratification between the forest canopy and understorey (DeVries and Walla 2001, DeVries et al. 2012, Dumbrell and Hill 2005, Fermon et al. 2005, Grotan et al. 2012, Hamer et al. 2003). While the importance of sampling both canopy and understorey partitions in tropical fruit-feeding nymphalid communities is now established, little is known about whether some understorey species are more abundant close to the forest floor, or if there are differential behavioural responses to traps among species.

Butterflies in the Neotropical tribe Haeterini (Nymphalidae, Satyrinae) occur in forest habitats in Central and South America with the greatest diversity in the Amazon. All Haeterini fly low to the ground, are easily sampled with fruit-baited traps, and may live over 1 mo in the wild as adults (DeVries 1987; and unpublished data). Of the five species of Costa Rican Haeterini, three (*Cithaerias pireta* Cramer, *Dulcedo polita* Hewitson, *Pierella helvina* Hewitson) are abundant throughout the year in the Sarapiquí River Basin (DeVries et al. 2012). By taking advantage of their local abundance, this study experimentally tested three hypotheses relevant to the behaviour of these three species. Based on field observations, previous long-term studies, and their close phylogenetic relationships, we predicted that these species would: (1) be trapped more frequently near the forest floor than 1 m above it, (2) not differ in the duration individuals stayed in traps (trap persistence), and (3) would exhibit differences in sex-associated sampling bias.

Study Area

This investigation was conducted from 25 January to 11 March 2009 at the Tirimbina Biological Reserve, Heredia Province, Costa Rica. The reserve encompasses an altitudinal range of 180–220 m within c. 345 ha of lowland rain forest in the Rio Sarapiquí river basin (10°29’50.3”S; 76°22’28.9”W). The study site is located within c. 150 ha with some natural and anthropogenic disturbance, but is effectively 85% primary forest. Rainfall records from the nearby La Selva Biological Station indicate this region receives an average of 3.7–4.2 m y-1 precipitation.

Methods

Individuals of *C. pireta*, *D. polita* and *P. helvina* were captured with traps (see DeVries 1987 and DeVries & Walla 2001 for design) baited with mashed bananas that had been fermented in a large barrel 48 h prior to use, and the bait was refreshed or replaced in each trap as needed. Individual trap sites were established in the understorey of seven areas (see Fig. 1.6) that encompassed four levels of disturbance: 1 = old cocoa plantation, most disturbed; 2 = secondary forest with some disturbance; 3-6 = intact forest, least disturbed; and 7 = selectively logged over 40 y ago. All traps were checked at 24-h intervals, and butterflies were identified, sexed, uniquely marked using a non-toxic permanent marker, and released at the trap site.

To test for potential differences in vertical distribution we compared individual abundances of species in areas 1-6 with 60 traps set at two heights: 15 cm and 1 m above the ground. Each area contained ten traps with five of each height interspersed. All traps were checked daily from 10 February to 1 March 2009. Only initial captures were included in the test for differential vertical distribution.

Table 2.1. Vertical distribution of three Costa Rican butterfly species in low and high understorey traps. Species abundances among trap heights were assessed with binomial tests. Adundances between sexes among trap heights were assessed using a Fisher's exact test, with odds ratios calculated for captures in low traps.

	Marked	Captured in low traps	P-value	Odds of capture in low traps
Cithaerias pireta	30	22	0.0161	2.75
Dulcedo polita	32	25	0.0021	3.57
Pierella helvina	89	89	< 0.0001	19.0
C. pireta female	10	5	0.0778	1.00
C. pireta male	20	17		5.67
D. polita female	21	19	0.0318	9.50
D. polita male	11	6		1.20
P. helvina female	33	33	1.00	19.0
P. helvina male	56	56		19.0

Trap persistence was defined as the continued presence of an individual in a trap 24 h after its presence was initially recorded. To evaluate potential differences among species to persist in traps we used the same 60 traps in areas 1-6, plus 20 traps in area 7. Here, trapped individuals were marked, returned to the trap, and the following day the presence or absence of marked individuals was noted. Any marked individuals still present in the traps were released. We continued sampling until trap persistence was determined for 30 individuals of each species, and because *P. helvina* was more abundant than the other species we assessed 30 individuals of each sex separately.

We used binomial tests to assess the null hypothesis that sample abundances were equal with respect to vertical trap height, trap persistence, species, and sex. Relative differences among species were analysed using an odds ratio test with degrees of freedom = 1 (Sokal and Rohlf 1995) and are reported in the text with a chi-square value. We used a Fisher's exact test to assess if trap persistence was affected by sex or vertical placement. Two-tailed P-values are reported for both binomial and Fisher's exact tests.

Table 2.2. Number of individuals remaining in traps 24 h after marking was used to evaluate the effects of species, trap height, and sex on trap persistence in three Costa Rican butterfly species. Species persistence was analyzed with a binomial test. A Fisher's exact test was used to analyze persistence of species among traps heights, and between sexes for *P. helvina*.

	Marked	Persisted	P-value	Odds of persisting	Proportion persisted
Cithaerias pireta	30	4	< 0.0001	0.15	0.13
Dulcedo polita	30	13	0.585	0.76	0.43
Pierella helvina	30	11	0.201	0.58	0.37
All species, high traps	16	7	0.385	0.78	0.44
All species, low traps	74	23		0.45	0.31
P. helvina female	30	14	0.180	0.88	0.47
P. helvina male	30	8		0.36	0.27

Results

We captured, marked and released a total of 283 individual butterflies, of which 151 were included in the height trial, and 120 in the persistence trial. All three species had significantly greater abundances in the low traps (Table 2.1). Because the odds of capture in low traps did not differ significantly between *C. pireta* and *D. polita* ($\chi^2 = 0.19$, $P > 0.05$), we pooled them and found that they were more likely to be captured in the low traps. All *P. helvina* individuals were captured in the low traps. There was no significant difference between the sexes in capture in low traps for *P. helvina* and *C. pireta*, but there was a greater likelihood for female *D. polita* to be captured in low traps (Table 2.1).

The number of individuals persisting in traps for 24 h was three times higher for *D. polita* and *P. helvina* than for *C. pireta* (Table 2.2). Because the odds of persisting did not differ between *D. polita* and *P. helvina* ($\chi^2 = 0.27$, $P > 0.05$), we pooled them and found that persistence did not differ significantly from 0.5 for those two species. Only *C. pireta* exhibited a probability of persistence in the traps significantly less than 0.5. Trap height had no effect on persistence and there was no difference in persistence between sexes of *P. helvina* (Table 2.2).

Table 2.3. Abundance differences between sexes for three Costa Rican butterflies in low and high understorey traps. Abundance differences were assessed using a binomial test, with odds ratios calculated for capture probabilities of males.

	Female	Male	Total	Binomial test P-value	Male capture odds	Male proportion
Cithaerias pireta	28	37	65	0.3211	1.32	0.57
Dulcedo polita	49	30	79	0.0422	0.61	0.38
Pierella helvina	60	79	139	0.1265	1.32	0.57

Only *D. polita* exhibited differential attraction to traps with respect to sex (Table 2.3). The odds of capturing males did not differ for *P. helvina* and *C. pireta*, and when pooled there was no difference in attraction to traps between sexes. The odds of capturing males was significantly lower for *D. polita* compared to the other two ($\chi^2 = 7.91$, $P < 0.01$).

Discussion

Although previous studies of tropical fruit-feeding butterflies have been sampled at heights ranging from 0.5 to 40 m (Barlow et al. 2007; DeVries et al. 2012; Molleman et al. 2006; Tangah et al. 2004), no study has sampled simultaneously at two levels within the lower forest understorey. By comparing the abundances of three closely related butterflies at two understorey levels, this investigation showed that all were trapped near the ground more often than 1 m above it. Members of Haeterini are well-known to fly close to the forest floor (DeVries 1987; DeVries and Walla 2001; DeVries et al. 2012), but here we found that even within the tribe there were differences in capture height. This strongly suggests that seemingly small vertical differences in trap placement can affect species abundance estimates of these butterflies.

Since many other species of fruit-feeding nymphalid also visit rotting fruits on the forest floor (DeVries 1987; personal observation) feeding at ground level is not restricted to the Haeterini. For example, during this study we caught *Morpho granadensis* Felder (Satyrinae, Morphini) and *Caligo atreus* Kollar (Satyrinae, Brassolini) in the lowest traps, but unlike members of Haeterini, these and many other nymphalid species generally fly and perch several metres above the forest floor (DeVries 1987).

All available evidence indicates that members of Haeterini inhabit a unique vertical position within Neotropical forests (i.e. the forest floor). In concert with other work on insect stratification (Brühl, Gunsalam and Linsenmair 1998; Charles and Basset 2005; DeVries et al. 2012) the findings here imply the potential for other, undocumented vertical strata between the forest canopy and understorey. Given the ease of sampling them with traps, we suggest that fruit-feeding nymphalid communities may be useful for exploring species stratification at multiple vertical levels, and help gain a better understanding of species diversity in tropical forests.

We found that the three focal species differed in their probability of staying in traps over a 24-h period, with *C. pireta* most likely to leave. In the persistence trials every individual had been in the trap anywhere from 1 min to 24 h before being removed, marked and returned to the trap. Individual persistence could be affected by length of time in a trap, and future studies of Haeterini could test this by checking traps more frequently as in Hughes et al. (1998). Nevertheless, our study did show that trap persistence varied among these three species, and in concert with trap height this variation may lead to underestimating parameters such as relative abundance.

The present study found no sex differences in abundance for *C. pireta* and *P. helvina*, but we captured significantly more females of *D. polita*. This was unexpected because 5 y of trapping at Tirimbina (DeVries et al. 2012) showed that 39 of 51 abundant species were male-biased while the remainder had no detectable sex bias (unpublished data). It seems unlikely that sex-associated sampling bias in *D. polita* reflects skewed natal sex ratios. Rather, the greater female abundance of *D. polita* in low traps suggests potential sex-specific differences in flight behaviours, temporal activity times, spatial distribution (DeVries, Austin and Martin 2008; DeVries, Penz and Hill 2010), or other factors that may have influenced sampling. In any event, in the present study the males of *D. polita* were likely under-sampled relative to females.

This investigation revealed several behavioural characteristics in three closely related forest understorey butterflies. Compared to traps placed at 1 m or higher, all three species were more abundant in traps closest to the ground. Furthermore, one species, *P. helvina*, only entered the lowest traps, and female *D. polita* were more likely to enter low traps than males. In concert with previous work on fruit-feeding nymphalids (DeVries et al. 2012), this provides experimental evidence suggesting that members of Haeterini most frequently fly and feed in a third stratum found just above the forest floor. We also found sex differences among species with respect to attraction to traps, and differential persistence within traps. This shows that closely related species within the same forest can exhibit significant behavioural differences that may influence estimates of population characteristics derived from multi-species studies.

Chapter 3: Movement in Three Sympatric Rainforest Butterflies Show that Females Disperse and Males Move in Narrower Home Ranges

Abstract

Movement is important to population dynamics and distributions of species within the landscape, but little is known about spatial structure and dispersal capabilities of most tropical butterflies. We present the first study of movement patterns in populations of rainforest butterflies in the tribe Haeterini (Nymphalidae, Satyrinae). We used mark-release-recapture data on *Cithaerias pireta*, *Dulcedo polita*, and *Pierella helvina* to assess movement patterns among species and between sexes in a Costa Rican rainforest.

Overall movement among species did not differ, but there were significant differences between sexes. Female movements were correlated with time between captures, and they moved greater net distances (74.53±8.866 m) than males (45.66±5.855 m). In contrast, male movements were not correlated with time between captures, and they tended to return to where they were first marked. Predicted probabilities of females moving specific distances were best fit by a NEF function, while probabilities of males were better fit by an IPF function. Our analyses indicated that females dispersed from where they were originally marked, supporting the idea that they move through the landscape, potentially searching for oviposition sites. Conversely males moved within narrower home ranges, thus exhibiting a behavior potentially maximizing the likelihood of encountering unmated females.

Keywords: angles of departure, distance distribution, inverse power function (IPF), negative exponential function (NEF), sex differences, tropical forest.

Introduction

Movement is a fundamental characteristic of life. Within the context of population biology organisms are thought to disperse or move away from their places of birth and thus avoid inbreeding and/or colonize new habitats (Wright 1951; Pusey and Wolf 1996). The terms dispersal and movement are sometimes used interchangeably, but movement (i.e., traversal through the landscape) is only one of the stages of dispersal (Van Dyck and Baguette 2005; Ronce 2007; Stevens, Turlure and Baguette 2010). Estimating the movement of individuals within natural populations has become increasingly important to understanding population dynamics and species' distributions (Wilkinson 2003, 2011; Van Dyck and Baguette 2005; Stevens, Pavoine and Baguette 2010; Stevens, Turlure and Baguette 2010). Movement within a habitat can vary in distance and direction depending on the life histories and activities of particular species, e.g. foraging, territoriality, mate seeking, oviposition, predator escape, migration (Drake and Gatehouse 1995; Van Dyck and Baguette 2005; Hapca, Crawford and Young 2009). Movements contribute to individual fitness, heterogeneity within populations in spatial distribution, genetic diversity, and the evolution of life histories (Williams 1957; Kareiva, Mullen and Southwood 1990; Ronce 2007; Price et al. 2011).

Insects have played a critical role in how we perceive biological diversity (DeVries 2000; Grimaldi and Engel 2005; Price et al. 2011), and among insects the butterflies have been an important group for understanding insect population biology, ecology and evolution. Our conceptual underpinning of butterfly spatial movement, however, comes mainly from work on temperate zone species, particularly those occurring in Europe (e.g., Brakefield 1982; Conradt et al. 2000; Asher et al. 2001; Wahlberg et al. 2002; Ehrlich and Hanski 2004; Kuefler and Haddad 2006; Stevens, Turlure and Baguette 2010; and references therein). Although the greatest butterfly diversity is tropical (DeVries 1987, 1997, 2000; and references therein), few studies have focused on spatial movements of tropical species (Mallet and Jackson 1980; Molleman et al. 2006; Tufto et al. 2012). In sum, it is remarkable that even the most basic elements of population biology are unknown for the vast majority of tropical butterfly species (Bonebrake et al. 2010).

Adult butterflies in the family Nymphalidae that feed on the juices of rotting fruit comprise a guild known as fruit-feeding nymphalids. This guild includes members of the subfamilies Charaxinae, Satyrinae, and some genera of Nymphalinae and Biblidinae (Chacón and Montero 2007; DeVries et al. 2012), and can account for over 50% of the nymphalid richness in tropical forests (DeVries 1987; unpublished data). On the whole, these butterflies have been important for elucidating spatial and temporal patterns of tropical insect diversity (Molleman et al. 2006; DeVries et al. 2012; Grotan et al. 2012; Penz, DeVries and Wahlberg 2012; Penz et al. 2013; Tufto et al. 2012; and references therein).

Within the Satyrinae, unusual wing-shapes combined with transparent wings and iridescent coloration make members of the monophyletic tribe Haeterini some of the most visually striking of all Neotropical butterflies (Weymer 1924, DeVries 1987, Constantino 1992). Embracing five genera and over 20 species (Lamas 2004), these butterflies are confined to shaded forest understory and are readily sampled with fruit-baited traps (DeVries 1987). Some of our recent work on sympatric Costa Rican Haeterini (*Cithaerias pireta* Cramer, *Dulcedo polita* Hewitson, *Pierella helvina* Hewitson) showed that they are abundant throughout the year (DeVries et al. 2012), and differ in flight height and persistence within traps (Alexander and DeVries 2012). No studies, however, have documented movements in any species of Haeterini.

The genera *Cithaerias*, *Dulcedo* and *Pierella* are sister taxa within a well-wrought phylogeny (Peña et al. 2006), that differ in color patterns, life histories and geographical distributions (DeVries 1987; Hill and Vaca 2004; Peña et al. 2006; Murillo-Hiller 2009; Alexander and DeVries 2012). Nevertheless, initial field observations on sympatric *C. pireta*, *D. polita* and *P. helvina* in Costa Rica suggested these species differed in their movement patterns. Observations also suggested that females move away from their initial capture locations, whereas males moved among a restricted number of locations. Given there are no

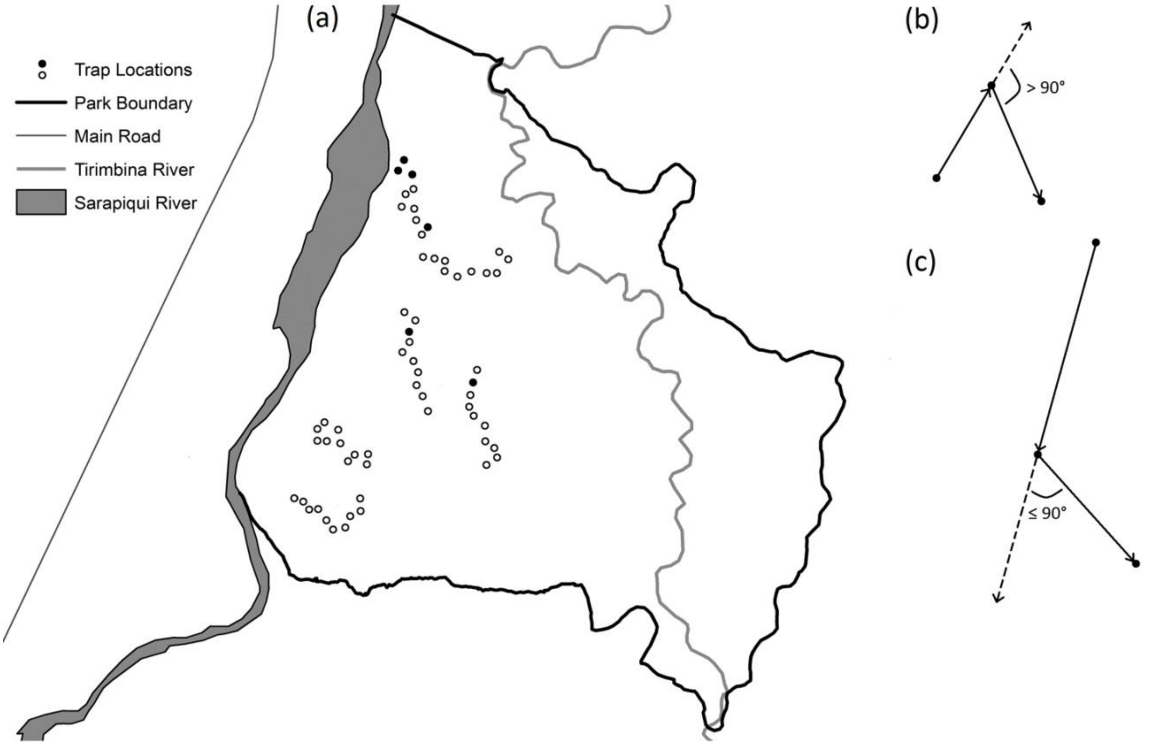


Figure 3.1. Sampling locations and exemplar directional movements by individual butterflies. (a) Six sampling sites each containing ten traps in the Tirimbina Biological Reserve. (b) Movements with an angle > 90° showing a return direction toward where an individual originated. (c) Movements with an angle ≤ 90° showing a forward direction away from where an individual originated. Circles denote trap locations. Solid circles denote trap locations corresponding to angles of departure illustrated in (b) and (c).

empirical measures of movement for these three species, we used mark-release-recapture data to evaluate potential differences in movement among species and between sexes. Accordingly, this study addresses two questions: (1) Do movement patterns differ among species? and (2) Do movement patterns differ between sexes?

Methods

This study was conducted from December 2009 through June 2010 at the Tirimbina Biological Reserve, Heredia Province, Costa Rica (10 ° 29’50.3”S; 76°22’28.9”W). The reserve encompasses an elevation of 180-220 m and approximately 345 hectares of lowland rainforest in the Rio Sarapiquí river basin. The study was conducted within approximately 150 hectares of the reserve, of which 85% is intact forest, the rest having some historical anthropogenic disturbance. The region receives an average of 3.7 to 4.2 m of precipitation per year, with a dry season from December to April.

To sample individuals of *C. pireta*, *D. polita*, and *P. helvina*, we used 60 traps positioned in the low understory (see Alexander and DeVries 2012) and deployed within six sampling sites, ten traps per site (Fig. 3.1a). Within sampling sites, traps averaged 36.5 ± 9.28 m (± SD) from adjacent traps. Traps were baited with mashed bananas and bait was replenished daily. Traps were checked at 24 h intervals for ten consecutive days each month, thus there were no recaptures for time intervals of 10 to 19 days. More details on trap design and sampling protocol are found in Alexander and DeVries (2012) and DeVries et al. (2012).

Butterflies were identified to species, sexed, uniquely marked using a non-toxic permanent marker, and released. In addition we measured forewing length to the nearest 0.01 mm (as a proxy for body size), and assessed potential differences in forewing length among species and sexes with a Kruskal-Wallis ANOVA, using Dunn's pairwise comparisons for *post hoc* exploration of significant results. Here we employ the nomenclature of Lamas (2004) for our three study species, but readers should be aware of nomenclature used by other authors for access to further biological information on them (e.g., DeVries 1987, DeVries et al. 2012). Because the focal species are closely related (Peña et al. 2006), they were pooled when necessary to increase statistical power, but analysed separately wherever possible.

Movement includes two components, time and space. Each recapture is associated with a time in days and a distance in meters between two consecutive captures of an individual. We define movement as occurring when the two consecutive captures were at different locations (traps) so that the distance was > 0 m.

To assess distribution of recaptures among distances for species and sexes, we pooled recaptures into 20 m distance classes (i.e., 0-19.9 m, 20-39.9 m, etc.) and used χ^2 tests. For recaptures with distance > 0 m (i.e., movements), we used the Pearson's correlation

Table 3.1. Butterfly sample sizes and sex ratios. For (a) all butterflies captured and movements observed, and (b) for individuals recaptured at least once and number of recaptures.

	Individuals marked				Movements (> 0 m)			
(a)	♀	♂	Total	♀:♂	♀	♂	Total	♀:♂
Cithaerias pireta	107	172	279	1.0:1.6	24	36	60	1.0:1.5
Dulcedo polita	197	119	316	1.7:1.0	45	29	74	1.6:1.0
Pierella helvina	252	295	547	1.0:1.2	92	115	207	1.0:1.3
Total	556	586	1142		161	180	341	

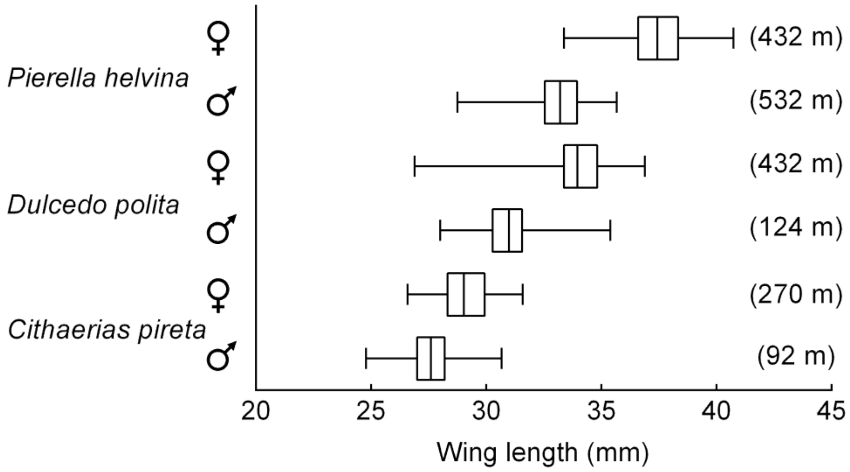
	Individuals recaptured				No. of recaptures			
(b)	♀	♂	Total	♀:♂	♀	♂	Total	♀:♂
Cithaerias pireta	35	61	96	1.0:1.7	63	109	172	1.0:1.7
Dulcedo polita	83	44	127	1.9:1.0	128	71	199	1.8:1.0
Pierella helvina	120	157	277	1.0:1.3	245	365	610	1.0:1.5
Total	238	262	500		436	545	981	

coefficient (r) to assess correlation between the time measured between captures and the associated distance in meters.

We define average distance as the total distance moved by an individual divided by the number of times that individual was recaptured, and net distance as the straight-line distance between the first and last capture locations. Average and net distances were calculated for butterflies recaptured at least once. To test the null hypotheses that average and net distances were equal among species and between sexes, we used two-way analysis of ANOVA.

Homing behavior may be considered the orientation of individuals toward familiar habitat patches (Conradt, Roper and Thomas 2001), and individuals moving within home ranges tend to visit the same locations rather than move away in one particular direction. To characterize the direction of individual movements relative to initial capture location, we calculated angles of departure as in Zimmermann (1979) except we calculated all angles to be between 0° and 180°. The angles were calculated for individuals showing pairs of consecutive captures with distance > 0 m. Angles > 90° were considered a return or backward movement (Fig. 3.1b) and those ≤ 90° as a forward movement (Fig. 3.1c). We used a

Figure 3.2. Box plots comparing median forewing lengths among species and sexes (n = 1142), with maximum one-day distances in parentheses. Whiskers show minimum and maximum wing lengths.

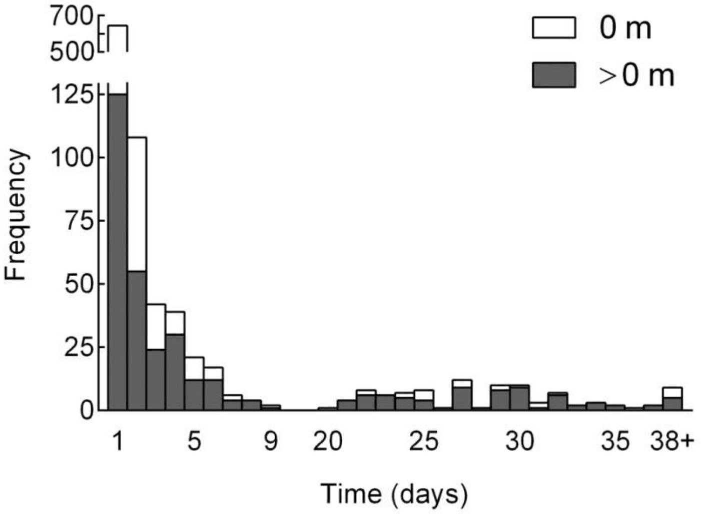


binomial test within each sex to assess the null hypothesis that individuals returned from whence they came equally as often as they moved forward.

When studying animal movement it is often necessary to fit models to predict movements or compare among data sets (Kareiva, Mullen and Southwood 1990; Carey 2001; Wahlberg et al. 2002; Fric and Konvicka 2007; Hamm, Williams and Landis 2013). Negative-exponential (NEF) and inverse-power (IPF) functions are frequently employed to describe butterfly movements (e.g., Hill, Thomas and Lewis 1996; Fric and Konvicka 2007). To compare movement probabilities in males and females, we calculated the probabilities of moving particular distances, linearly transformed those data using either semi-ln (NEF) or double-ln (IPF) plots, and analysed the results using the regression methods of Hill, Thomas and Lewis (1996). To assess model fit, we compared R^2 values and also used a t-test with Welch's correction for unequal variances to compare average magnitudes of variation from the regression line (i.e., the square root of the squared residuals).

For all statistics P-values are two-tailed, where alpha < 0.05 was considered significant. Means are presented with their standard errors (± SE).

Figure 3.3. Distribution of recaptures across time. For pooled species, shows recaptures across one-day time intervals (n = 981). There were no recaptures for time intervals of 10 to 19 days as sampling was done for 10 consecutive days each month. Movements between capture locations (> 0 m) are depicted in gray, and recaptures at the same locations (i.e., with no movement; 0 m) are depicted in white.

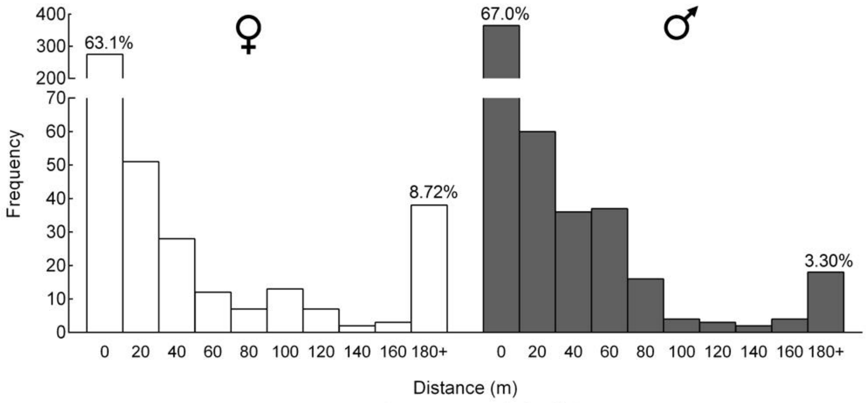


Results

We marked and released 1142 butterflies: 279 *C. pireta*, 316 *D. polita*, and 547 *P. helvina* (Table 3.1a). Median wing lengths differed significantly among species (Fig. 3.2; K-W$_5$ = 988.4, $P < 0.0001$), and between sexes for *D. polita* and *P. helvina* (Dunn's pairwise comparisons, both $P < 0.0001$).

From the total sample, 500 individuals were recaptured at least once, resulting in 981 recaptures (Table 3.1b), and 263 recaptured individuals were observed moving between capture locations, resulting in 341 movements > 0 m (Table 3.1a). Most movements were observed over one- or two-day time intervals (n=180, 52.8%; Fig. 3.3), with the longest time interval by a female *P. helvina* that was recaptured 68 days after initial capture. For distance, the bulk of the movements (n=224, 65.7%) were < 80 m (Fig. 3.4). Of the 56 long-distance movements (> 180 m), six were observed over a one-day interval (Fig. 3.4), but most occurred over many days (Appendix H). Maximum one-day distances for each species and sex ranged from 92-532 m (Fig. 3.2), and although individuals in all three species showed long-distance movements, species with longer forewing lengths tended to move farther.

We found significant heterogeneity in the distribution of recaptures among distance classes for species and sexes ($\chi^2_{20} = 33.45$, $P = 0.0301$). When sexes were pooled, we found



Species	Sex	1-day distances > 180 m
Pierella helvina	♂	532 m
Dulcedo polita	♀	432 m
Pierella helvina	♀	432 m
Cithaerias pireta	♀	270 m
Cithaerias pireta	♀	231 m
Pierella helvina	♀	190 m

Figure 3.4. Distribution of recaptures across distance. For pooled species, shows distributions of recapture intervals across 20 m distance classes in females (n = 436) and males (n = 545), with proportions represented by the 0 m and 180+ m classes given for each sex. Includes the six long-distance movements observed in a one-day interval.

that distribution of recaptures among distances did not differ among species ($\chi^2_8 = 5.657$, P = 0.6856), suggesting that all three species moved similar distances. But when species were pooled, the distribution of recaptures among distances differed significantly between sexes (Fig. 3.4; $\chi^2_4 = 19.80$, P = 0.0005), with males moving shorter distances more often than females, and females moving longer distances more frequently than males. When sexes were compared within individual species, sample sizes were not large enough in distance classes > 0 m to show significant effects in *C. pireta* and *D. polita*. But in *P. helvina*, for which sample size was not an issue, the distribution of movements among distances differed significantly between the sexes ($\chi^2_4 = 17.35$, P = 0.0017), with females moving distances ≥ 80 m more than twice as often as males (males n = 23, 6.30%; females n = 39, 15.9%).

With species pooled the time between captures was positively correlated with distance moved in females (r = 0.3524, P < 0.0001) but not males (r = 0.1334, P = 0.0742). When species were examined separately, this difference held for *C. pireta* (females: r = 0.6453, P = 0.0007) and *P. helvina* (females: r = 0.2578, P = 0.0131). In *D. polita* time between captures and movement distance was positively correlated for both sexes (females: r = 0.4681, P =

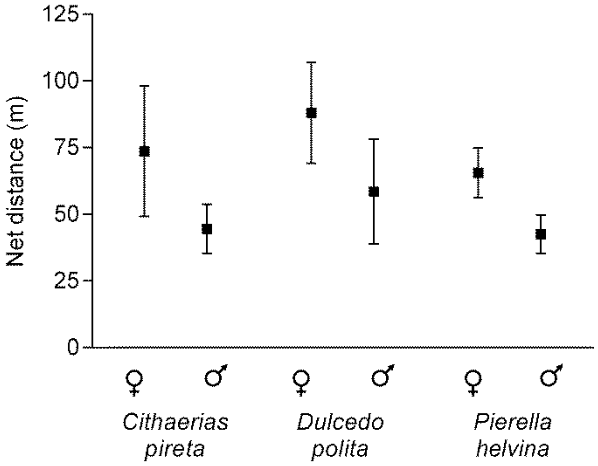


Figure 3.5. Net distances. Mean net distance (± SE) for females and males of each butterfly species (n = 500).

0.0012; males: r = 0.3792, P = 0.0425), although this may be due to a small sample size for *D. polita* males. Our findings indicate that movement distances in male *C. pireta* and *P. helvina* were unrelated to days between captures, but in females the longer the time between captures, the farther away from the initial capture point they had moved.

Average movement distance did not differ among species ($F_{2,494}$ = 1.741, P = 0.1764) or sexes ($F_{1,494}$ = 3.749, P = 0.0534), nor did net distance differ among species ($F_{2,494}$ = 0.9327, P = 0.3942). However, females moved significantly greater net distances than did males (Fig. 3.5; $F_{1,494}$ = 5.221, P = 0.0227). Female net movements averaged 74.53 ± 8.866 m between first and last capture locations, 1.6 times that of males (45.66 ± 5.855 m), indicating that females moved further from their initial capture locations than males.

We were able to calculate relative direction for 80 pairs of consecutive movements, most of which were for *P. helvina* (Table 3.2). For *P. helvina* alone and for the species pooled, 80% of the males returned in the direction where they originated rather than moving in a forward direction (P < 0.0001 and P = 0.0014, respectively). On the other hand, female movements did not differ with respect to return and forward directions. These observations suggest that males in our study may exhibit home range behavior.

Calculated distance probabilities for species and sexes presented in Figure 3.6 were fitted to model functions for sexes with species pooled (Fig. 3.7) and with species separated

Table 3.2. Relative directional movements of the sexes. Based on successive pairs of movements (n = 80). Comparisons done with a binomial test with species pooled, and with *Pierella helvina* analysed separately.

	Sex	Forward (≤ 90°)	Backward (> 90°)	Total	*P*-value
Species pooled	♀	13	22	35	0.1755
	♂	9	36	45	< 0.0001
Pierella helvina	♀	10	16	26	0.3269
	♂	6	24	30	0.0014

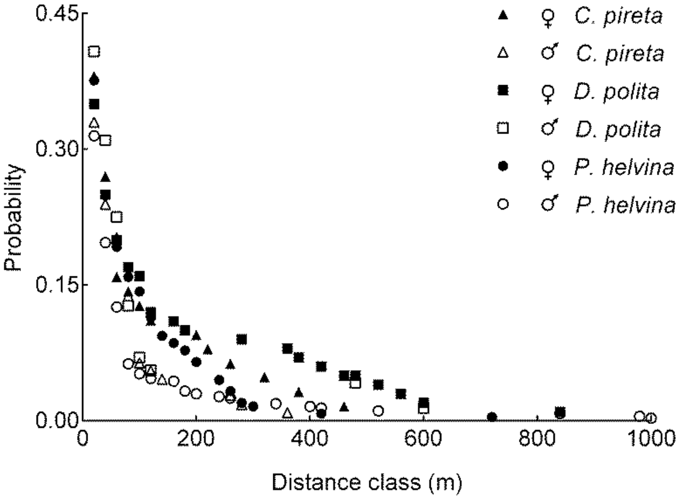
(Appendix I). In all cases, R^2 values were higher for NEF in females and IPF in males. With species pooled the difference in fit was significant for females ($t_{30.86} = 4.156$, P = 0.0002) and males ($t_{37.14} = 2.806$, P = 0.0079), and when species were separated the difference was significant in males of *P. helvina* ($t_{24.63} = 3.609$, P = 0.0014). The lack of significance in separate analyses of *C. pireta* and *D. polita* was likely due to small sample sizes. Based on these results, parameters estimated by fitting the logarithms were used to describe predicted probabilities of the NEF model for females and the IPF model for males, together illustrating distinct movement differences (Fig. 3.8). The probability of moving relatively long distances decreases gradually in females but rapidly in males, thus supporting observations that females move further from initial capture locations than males.

Discussion

By sampling individuals with fruit-baited traps and employing a combination of mark-release-recapture methods and fitted models, here we elucidated empirical and probable spatial movements in three closely related Neotropical forest butterflies, *C. pireta*, *D. polita*, and *P. helvina*. This investigation is one of the few studies of spatial movements in Neotropical butterflies (Cook, Thomason and Young 1976; Mallet and Jackson 1980; Mallet 1986; Tufto et al. 2012), and the only study to document spatial movements in members of the tribe Haeterini.

Maximum movement distances appeared to differ among species, and may be related to body size as maximum movement increased roughly with forewing length (Fig. 3.2). There

Figure 3.6. Movement probabilities. Probability of movement within 20 m distance classes among species plotted as the inverse cumulative proportion of movements.



were, however, no significant differences found among species in the spatial distribution of movements, average and net distances moved, relative direction moved, nor movement probability densities. Similarities in these species may stem from their shared ancestry (Peña et al. 2006), but similarities in movement among close relatives should not be assumed *a priori* (Wahlberg et al. 2002).

An important finding stemming from the present work is the significant difference in movements between sexes. In general, species were typically observed over one- and two-day time intervals (Fig. 3.3) moving < 80 m per day (Fig. 3.4), and although individuals were often recaptured multiple times at the same location (Appendix H), the distance between captures increased with time for females, not males. Females showed larger net distances (Fig. 3.5) and moved away from their initial capture locations. In contrast, males of *C. pireta* and *P. helvina* tended to return to the location where they were initially captured (Table 3.2), a characteristic of home range behavior (Conradt, Roper and Thomas 2001; Börger, Dalziel and Fryxell 2008).

The abundant short movements and correlation of time between captures and movement distance helps explain why female predicted probability distributions were best fit by the NEF (Fig. 3.7), a method used for modelling short, within-habitat movements (Hill,

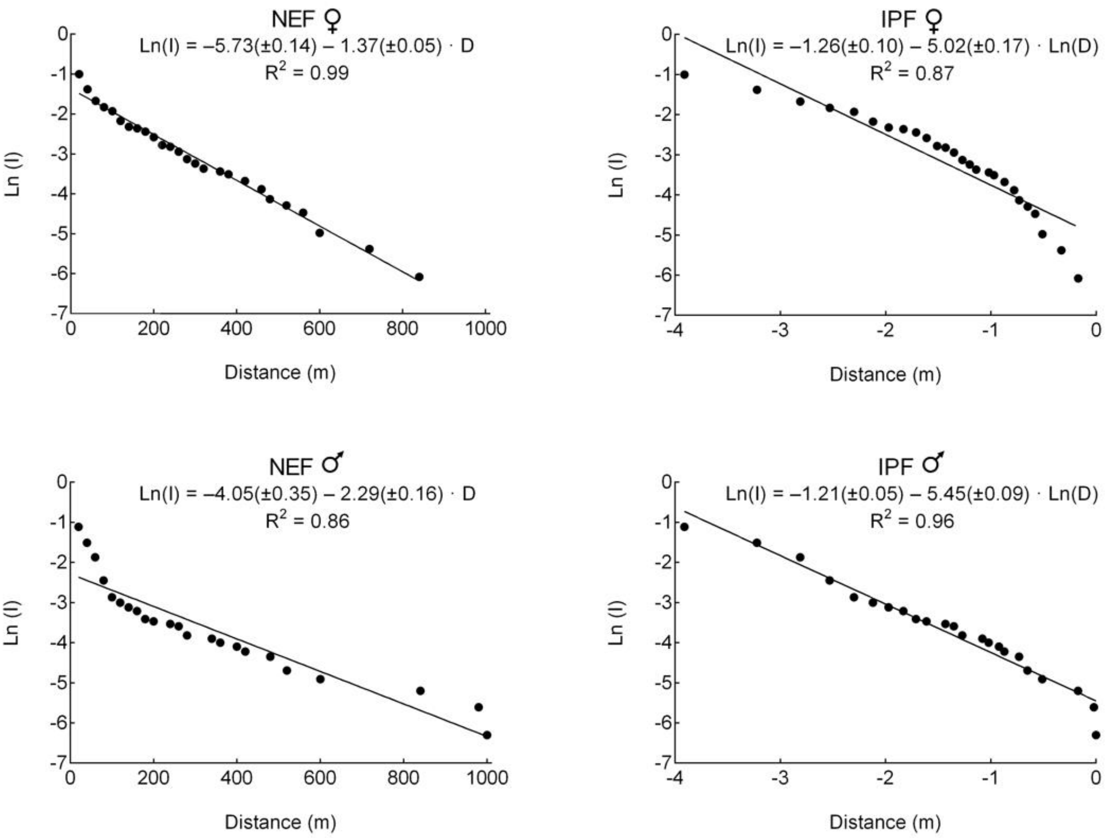


Figure 3.7. Comparative movement probabilities. Females = upper plots. Males = lower plots. Expressed as negative-exponential (NEF) and inverse-power function (IPF) plots. Regression lines show the functions Ln(I) = ln(a) – k•D and Ln(I) = ln(C) – n•ln(D), where I is the probability of moving distance D.

Thomas and Lewis 1996). The lack of correlation between time and male movement distance likely explains why the male distribution was best fit by the IPF, which is better at estimating long-distance movements that occur at very low probabilities (Fric and Konvicka 2007). This is in keeping with the observation that males moved shorter distances than females (Fig. 3.4).

Differential movement patterns in butterflies have been attributed to sex-specific life history traits (Ehrlich 1965; Brussard, Ehrlich and Singer 1974; Kingsolver 1983; Beccaloni 1997; Brakefield 1982; Szymanski, Shuey and Oberhauser 2004; Joron 2005; Grill et al. 2006; DeVries, Penz and Hill 2010; Junker and Schmitt 2010). Ehrlich (1989) viewed tropical butterflies as continuous dispersers, with the distribution of nutritional resources as a major factor that structures non-migrating butterfly populations. Considering that Central American rainforest understory fruit is likely available throughout the year (Frankie, Baker

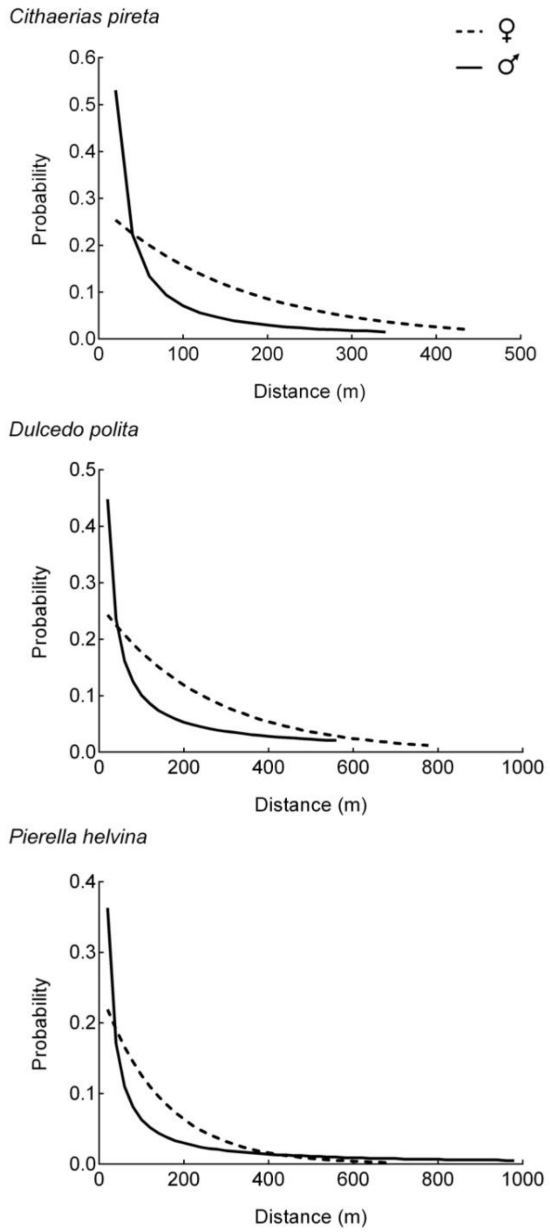


Figure 3.8. Probabilities of movement partitioned by species and sex. Comparisons are expressed as a function of distance predicted by the negative-exponential function (NEF) for females and the inverse-power function (IPF) for males.

and Opler 1974), it seems likely that the distribution of oviposition sites should be equally, if not more important to population structure in fruit-feeding butterflies (DeVries 1987; Grotan et al. 2012; and references therein).

One basic optimal foraging strategy for efficient individuals to avoid re-searching areas is to meander in a habitat until a resource is encountered (Zimmermann 1979). This strategy can be applied to female butterflies searching for critical oviposition sites. Our results suggest that female Haeterini meander through the forest – a behavior that could increase their encounter rates of useable oviposition sites, and move them away from their initial capture locations, thus reflecting the concept of dispersal away from natal locations (Ronce 2007; Stevens, Turlure and Baguette 2010). In contrast, male Haeterini by and large appeared to move within narrower home ranges. Here, potential male home range behavior could maximize the likelihood of encountering new, unmated females (e.g. Börger, Dalziel and Fryxell 2008; Mallet and Jackson 1980). We suggest future work on these species should assess home ranges by documenting the size and shape of home ranges, and the effects of population density on their spatial movements.

It has been suggested that movements of adult butterflies shape butterfly population structure (Ehrlich 1989), and population structure is governed, in part, by reproductive strategies of the sexes (Boggs and Watt 1981). In the face of widespread tropical habitat destruction, documenting sex-specific differences in movement is critical for understanding and conserving population structure of rainforest butterflies, particularly since the population biology for the vast majority of tropical butterflies is unknown. We acknowledge that inferences here are limited by the physical configurations of traps within sampling sites, different sample sizes among species and sexes, and the variation of in time spans among individuals for estimating of movement distances. However, given the paucity of data on movements of tropical forest butterflies, this study provides a window into the life histories of these butterflies, and represents a first step toward exploring their population dynamics that can provide a better understanding of differential movements of the sexes through time and space.

Chapter 4: Recapture Probability and Daily Survival for Three Fruit-Feeding Understory Butterfly Species

Abstract

Butterflies population characteristics have been studied only for a small number of species. We used mark-release-recapture data to estimate recapture probability and daily survival for three sympatric rainforest understory butterfly species in Costa Rica (*Cithaerias pireta*, *Dulcedo polita*, P*ierella helvina*). Sampling sites influenced the estimated recapture probabilities, with more recaptures observed in two sites. This suggested there were lower dispersal rates in those sites. Male *P. helvina* had the highest average recapture probability (0.232 ± 0.007), followed by pooled females (0.160 ± 0.005) and male *C. pireta* and *D. polita* (0.109 ± 0.004). Monthly butterfly abundance influenced the estimation of daily survival, which was sensitive to sample size. Daily survival did not vary among species and averaged 0.815 (± 0.024) per day, implying strong daily turnover in these populations. Variation in abundance among sampling occasions suggests greater movement within the reserve than previously thought. This has potential implications for interpreting movement patterns, local population densities, and temporal and spatial heterogeneity in the distances over which species respond to resources. Continued work on these species will improve our understanding of the ecology of tropical butterfly populations and increase our ability to conserve and manage rainforest organisms.

Keywords: Attraction distance, attraction effect, *Cithaerias pireta*, Costa Rica, *Dulcedo polita*, Haeterini, mark-release-recapture, Nymphalidae, *Pierella helvina*, rainforest, Satyrinae

Introduction

Estimating population structure among closely related species in natural communities is a fundamental underpinning in ecology. Critical to the development of population ecology as a field has been the use of mark-release-recapture (MRR) for estimating population parameters such as abundance, dispersal, recapture probability and survival (Elton 1927; Jolly 1965; Seber 2001; Nichols 2005; Vlasanek, Sam and Novotny 2013; and references therein). Recapture probability is important because it can influence estimates for other parameters, it is affected by individual survival status, and it may provide insights into relevant behavioral traits (Barker and White 2004; Szymanski, Shuey and Oberhauser 2004). Information on adult insect survival is practically nonexistent for most species (Carey 2001), despite survival being a direct component of fitness (Zimmerman, Gutiérrez and Lahaye 2007) and important to understanding and predicting population dynamics (Williams, Nichols and Conroy 2002).

The analysis of MRR data generally assumes homogeneity in recapture and survival probabilities within populations (Mallet et al. 1987, Burnham and Anderson 2002, Nichols 2005). However, these probabilities may vary among species (Samways and Lu 2007, Fric et al. 2010), sex (Brussard, Ehrlich and Singer 1974), habitat (Vlasanek, Sam and Novotny 2013), sampling occasion (Konvička et al. 2005), movement type (Van Dyck and Baguette 2005), and handling method (Mallet et al. 1987). Thus, documenting heterogeneity in recapture and survival probabilities is fundamental to studies seeking to understand the population ecology of all focal species (Amstrup, McDonald and Stirling 2001; Alldredge et al. 2007; Haddad et al. 2008).

Terrestrial species diversity is accounted for largely by insects, yet basic population biology studies are confined to relatively few species (Cornell and Hawkins 1995; Price et al. 2011). Among insects, population ecology in the wild is perhaps best known in the butterflies (Ehrlich 1989, Gilbert 1989, Boggs, Watt and Ehrlich 2003). Although most butterfly species are tropical (DeVries 2000; DeVries and Walla 2001), studies estimating butterfly recapture and survival probabilities derive almost entirely from MRR work performed on a handful of temperate zone butterflies. These include the North American grassland *Euphydryas editha* (Ehrlich 1965, Brussard, Ehrlich and Singer 1974; Harrison, Murphy and Ehrlich 1988; Junker and Schmitt 2010; Zimmermann et al. 2011a,b), migratory *Danaus plexippus* (Brower 1958; Calvert, Hedrick and Brower 1979; Masters, Malcolm and Brower 1988; Brower and Boyce 1991; Dockx et al. 2004; Lyons et al. 2012), North American members of *Colias* (Watt et al. 1977; Kingsolver 1983; Karowe 1990; Buckley and Kingsolver 2012), and metapopulations of European *Melitaea cinxia* (Hanski, Kuussaari and Nieminen 1994; Kuussaari, Nieminen and Hanski 1996; Hanski, Alho and Moilanen 2000). The high species diversity and structurally complex habitats in the tropics (Connell 1978; Janzen 1983, Kricher 1997; Sparrow et al. 1994) makes the estimation of demographic parameters especially important for tropical populations (Haddad et al. 2008), although few studies have estimated recapture probability and daily survival in tropical butterflies (Owen, Owen and Chanter 1972; Mallet and Jackson 1980; Molleman et al. 2007; Tufto et al. 2012; Li et al. 2013).

Butterflies in the family Nymphalidae that feed on juices of rotting fruit as adults form a feeding guild termed fruit-feeding nymphalids, and include members of the subfamilies Charaxinae, Satyrinae, and some genera of Nymphalinae and Biblidinae (DeVries et al. 2012). In many lowland tropical forests these butterflies account for over 50% of the nymphalid species richness, and they are readily sampled with traps (DeVries 1987). For this reason fruit-feeding nymphalids have been important for exploring patterns of tropical spatial and temporal diversity (DeVries and Walla 2001; Hamer et al. 2003; Dumbrell and Hill 2005; Fermon et al. 2005; DeVries et al. 2012; Grotan et al. 2012; Molleman et al. 2006; Penz, DeVries and Wahlberg 2012; Tufto et al. 2012; Penz et al. 2013; and references therein).

Confined to lowland forest understory habitats, the fruit-feeding nymphalids in the monophyletic satyrine tribe Haeterini (Peña et al. 2006) represent some of the most distinctive of all Neotropical butterflies (DeVries 1987; and unpublished data). Recent work on three sympatric Costa Rican species (*Cithaerias pireta* Cramer, *Dulcedo polita* Hewitson, *Pierella helvina* Hewitson) showed them to be abundant throughout the year (DeVries et al. 2012), and that there are differences among species and sexes in flight height, persistence within traps and movement behaviors (Alexander and DeVries 2012; Alexander and DeVries a). Nevertheless, no study has investigated the population biology for any member of Haeterini. The present investigation uses MRR to estimate recapture probability and daily survival in *C. pireta*, *D. polita*, and *P. helvina*, and assess the effects of species, sex, rain, abundance, and sampling site on those probability estimates. Therefore, this study addresses two questions: (1) How do recapture and daily survival probabilities differ among species and sexes? and (2) Do these probabilities vary based on total rainfall during sampling, monthly butterfly abundance, and sampling site/habitat?

Methods

Study Area: This study was conducted from December 2009 through June 2010 at the Tirimbina Biological Reserve, Heredia Province, Costa Rica (10°29’50.3”S; 76°22’28.9”W), an area encompassing an elevation of 180-220 m within approximately 3.4 sq km of lowland rainforest in the Rio Sarapiquí basin. The investigation was performed within approximately 1.5 sq km of forest at the Tirimbina Biological Reserve that has some natural and anthropogenic disturbance, but is essentially 85% primary forest. The area receives an average of 3.7 and 4.2 m of precipitation per year, with no distinct dry season (Zuchowski 2007) although it tends to be dryer from December to April.

Study Species: This study included three species of Haeterini that co-occur year-round at the study area: *Cithaerias pireta* Cramer, *Dulcedo polita* Hewitson, and *Pierella helvina* Hewitson. Here we use the nomenclature of Lamas (2004), but readers should be aware of older nomenclature in the literature (*Cithaerias menander* and *Pierella helvetia incanescens*) for access to more biological information on these butterflies (see DeVries 1987; Janzen and Hallwachs 2009; DeVries et al. 2012).

Sampling Methods: Individuals were sampled using 60 fruit-baited traps that were deployed within six sampling sites, each with 10 traps placed about 36 m apart and 15 cm above the forest floor (see Fig. 1.12). All traps were baited with mashed bananas taken from a large reservoir, and checked at 24 h intervals for ten consecutive days (sampling occasions) for seven consecutive months (sampling periods). To maintain consistency throughout each sampling period, the bait in traps was refreshed as needed, often daily. In the interest of efficiency the traps were checked in consecutive order within each sample site, but to approximate a haphazard sampling design the starting sample site was alternated each month. For example the site order was A B C F E D in December, D E F C B A in January, and so forth. Individual butterflies were identified to species, sexed, uniquely marked with a number using an indelible marking pen, and released. Further details on trap designs and sampling protocols are found in Alexander and DeVries (2012) and DeVries et al. (2012).

MRR Analysis: We used 10-day binary capture histories and an open population approach in version 6.0 of the program MARK (White and Burnham 1999) to estimate two parameters: recapture probability (p), the probability that a marked individual will be captured again, and daily survival (phi), the probability that a marked individual is alive and available for further recapture (i.e., apparent survival). For parameter estimation, we used an underlying model structure in which recapture probability (p) and daily survival (phi) could vary with species and sex (Eberhardt 1969). Recapture probability also could vary depending on whether an individual had been trapped the day before (Appendix E), and the recapture probability estimated for the first recapture occasion (i.e., sampling occasion 2) was allowed to vary separately from the remaining occasions to simulate the attraction effect (Otis et al. 1978).

The initial goal of analysis was to estimate recapture and survival probabilities over the entire observed lifespans of these butterflies. However, most individuals were observed over a single sampling period (month), and the data set that included multi-month observations was too sparse to produce estimates with reasonable confidence intervals (Burnham and Anderson 2002). Thus, to increase data density and improve model fit, we treated marks as temporary, lasting for a single month, so that marked butterflies captured in more than one sampling period were considered “new” the first time they were captured in a subsequent month. We assessed model fit of the underlying model structure using the median ĉ procedure within MARK and found that ĉ = 1.00 (± 0.0001), which indicates we achieved a good fit to the data using 10-day capture histories.

We hypothesized that, in addition to species and sex, three other variables would affect the estimation of recapture and survival probabilities: 1) rainfall: total rainfall during the 10 sampling occasions of each sampling period, 2) abundance: total abundance of individuals captured during each sampling period, and 3) site: the sampling site where the first capture occurred in each capture history. To assess the degree to which these variables influenced parameter estimates, and to improve the accuracy of the estimates themselves, we included combinations of these three variables as covariates to the underlying model structure using a balanced design, and assessed the outcomes. A total of 16 models were formulated (Appendix J). Relative model fit among those 16 models was determined using Akaike’s Information Criterion (AIC_c) corrected for small sample size (Burnham and Anderson 2002), and results were reported for the 95% confidence set.

Table 4.1. MRR results. Summary of captures and recaptures for (a) individuals and (b) ten-day capture histories where capture histories > 1 contain more than one capture.

	Individuals			Indivs. recaptured			Return rate			Total recaptures		
(a)	♀	♂	Total	♀	♂	Total	♀	♂	Total	♀	♂	Total
Cithaerias pireta	107	172	279	35	61	96	0.33	0.35	0.34	63	109	172
Dulcedo polita	197	119	316	83	44	127	0.42	0.37	0.40	128	71	199
Pierella helvina	252	295	547	120	157	277	0.48	0.53	0.51	245	365	610
Total	556	586	1142	238	262	500	0.43	0.45	0.44	436	545	981

	Capture histories			Cap. histories > 1			Return rate			Total recaptures		
(b)	♀	♂	Total	♀	♂	Total	♀	♂	Total	♀	♂	Total
Cithaerias pireta	108	180	288	36	59	95	0.33	0.33	0.33	62	101	163
Dulcedo polita	205	126	331	80	42	122	0.39	0.33	0.37	120	64	184
Pierella helvina	280	340	620	114	148	262	0.41	0.44	0.42	217	320	537
Total	593	646	1239	230	249	479	0.39	0.39	0.39	399	485	884

Statistical Analysis: We used a non-parametric Kruskal-Wallis test to assess whether median rainfall differed among sampling periods, and report the K-W statistic and P-value, and used independent Pearson's correlation tests to assess correlation of 1) rainfall and butterfly abundance, rainfall and lifespan, and 2) butterfly abundance and lifespan. Lifespan was estimated using the number of days from first to last capture in each capture history (Brussard, Ehrlich and Singer 1974; Cook, Thomason and Young 1976). Butterfly abundance was the number of new marks each month. For Pearson's tests we report the coefficient (r), R^2 value and P-value.

Chi-squared tests were used to compare abundance distributions among sampling periods and sampling sites, with species and sexes analyzed independently. To assess the null hypothesis that recaptures for species and sexes were distributed homogeneously among sampling occasions, i.e., to test for marking effect, trap dependence, and handling effect, we used χ^2 tests in the RELEASE section of Program MARK, and report only significant results. For all tests we report the χ^2 statistic, degrees of freedom and P-value.

Table 4.2. The 95% confidence sets. From (a) the original mark-release-recapture (MRR) analysis and (b) post hoc analysis. The abundance covariate influenced estimation of daily survival (phi), and the site covariate influenced estimation of recapture probability (p).

(a)	Delta AIC_c	AIC_c Weights	Model Likelihood
Phi (abundance) p(sampling site)	0.00	0.93	1.00
Phi (abundance) p( )	7.13	0.03	0.03
(b)			
Phi (abundance) p(sampling site) revised for 3 groups in p	0.00	0.94	1.00
Phi (abundance) p(sampling site)	5.68	0.05	0.06

We used a one-way analysis of variance (ANOVA) to determine whether mean recaptures per day (sampling occasion) were the same among sampling sites. Here, species and sexes were pooled, then analyzed independently. We report the F-statistic, degrees of freedom and P-value.

For all statistics, P-values are two-tailed and alpha < 0.05 was considered significant, and means are given with their standard errors (± SE).

Results

A total of 1142 individual butterflies were captured and marked, and recaptures occurred in 500 (43.8%) individuals for a total return rate of 0.44 (Table 4.1a). In other words, 44% of marked individuals were recaptured 981 times. Ninety-one marked individuals were captured in more than one sampling period, yielding 1239 ten-day capture histories (Table 4.1b). Because many of these multi-month individuals were captured only once per sampling period, the number of capture histories that contained recaptures was < 500 (n = 479, 38.7%), resulting in a slightly lower return rate of 0.39 and 884 total recaptures.

In all but 34 of the capture histories, individuals were recaptured within the same sampling site, indicating that the site covariate accurately reflected site of capture for the majority of capture histories. The best fit model explained 93% of the variation in the model

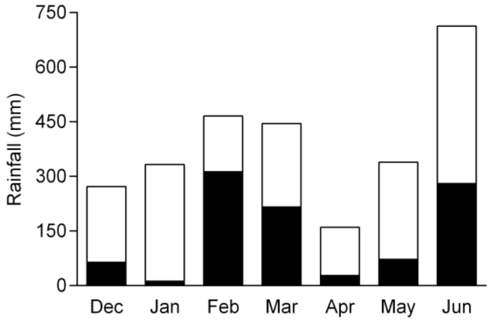


Figure 4.1. Total rainfall (mm) for each sampling period (month). Rainfall during the ten sampling occasions depicted in black, and the non-sampling days in white.

set, and included site as a covariate for recapture probability and abundance as a covariate for daily survival (Table 4.2).

Rainfall was not part of any model in the 95% confidence set. Median rainfall did not differ significantly among monthly sampling periods (Fig. 4.1; K-W statistic = 12.39, P = 0.0537), but did differ when looking only at rainfall during the 10 sampling occasions (days) each period (K-W statistic = 17.86, P = 0.0066). We found no correlation between monthly abundance and total monthly rainfall (r = 0.2991, R^2 = 0.08947, P = 0.5146) or rainfall during the 10 sampling days (r = 0.6220, R^2 = 0.3869, P = 0.1358). There also was no correlation between lifespan and total monthly rainfall (r = 0.1009, R^2 = 0.01017, P = 0.8297) or rainfall during the 10 sampling days (r = 4445, R^2 = 0.1976, P = 0.3177).

Butterfly abundance varied significantly among sampling periods (χ^2 = 80.68, df = 30, P < 0.0001), but all species and sexes showed similar monthly patterns of abundance distribution, with 52% (594 individuals, 648 capture histories) of new captures occurring in February and March (Fig. 4.2). Abundance also varied significantly among sampling sites (χ^2 = 56.24, df = 25, P = 0.0003), largely due to abundance variation in both sexes of *D. polita* and female *P. helvina* (Fig. 4.2).

Mean daily recaptures varied by sampling site (Fig. 4.3; $F_{5,54}$ = 9.891, P < 0.0001) with species and sexes pooled. When species and sexes were analyzed independently, mean daily recaptures were homogeneously distributed among sampling sites for females of *C. pireta* ($F_{5,54}$ = 1.352, P = 0.2570) and males of *P. helvina* ($F_{5,54}$ = 1.737, P = 0.1418), and

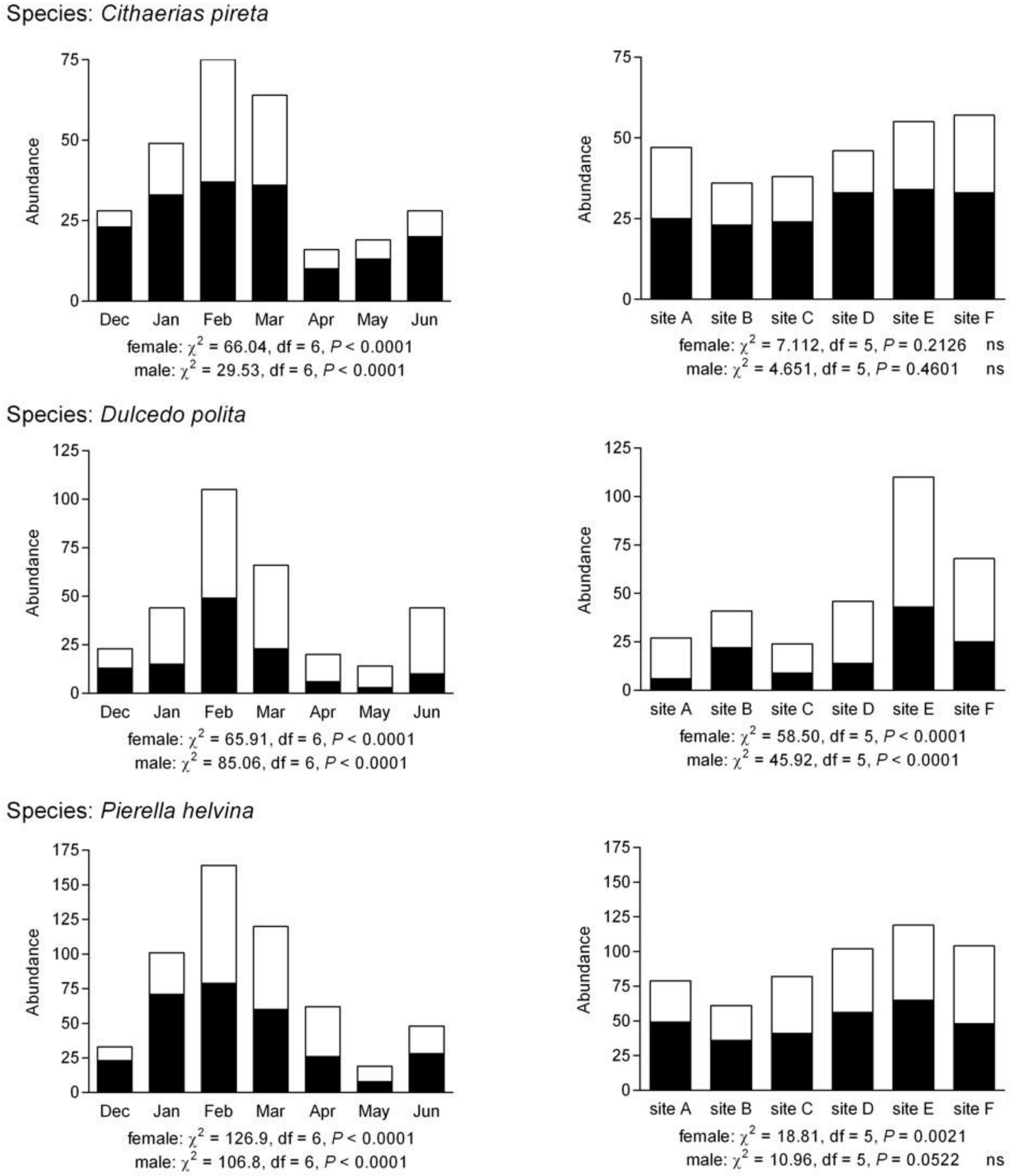


Figure 4.2. Butterfly abundance distributions among months and sites. Distribution of each butterfly species showing distribution of abundance (new captures) among sampling periods and sampling sites. Results of χ^2 tests for homogeneity of distribution are given below each bar chart. Male abundance is depicted in black, and female abundance in white. ns = not significant

heterogeneously distributed for males of *C. pireta* ($F_{5,54}$ = 4.242, P = 0.0025), both sexes of *D. polita* (females: $F_{5,54}$ = 8.068, P < 0.0001, R^2 = 0.4273; males: $F_{5,54}$ = 6.493, P < 0.0001), and females of *P. helvina* ($F_{5,54}$ = 19.32, P < 0.0001). Notably, almost half of all recaptures (48.7%, n=478) were observed at sites E and F.

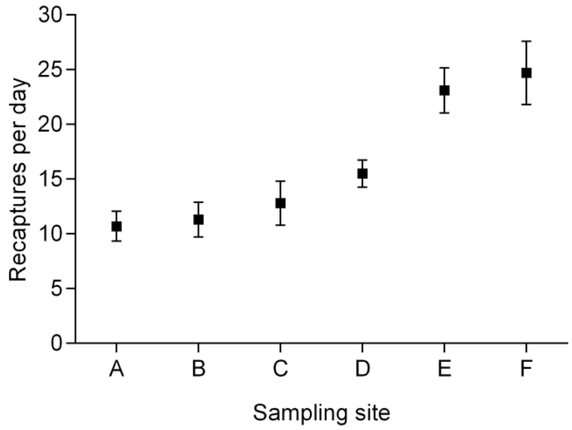


Figure 4.3. Mean daily recaptures (± SE) per site. Species and sexes are pooled.

Estimated recapture probabilities were highest on the first recapture occasion (sampling occasion 2) in all species and sexes, then decreased steadily, and leveled off by recapture occasion six (Fig. 4.4). Overall, recapture probabilities were highest in male *P. helvina*, lowest in males of *C. pireta* and *D. polita*, and all female recapture probabilities were distributed between the males (Fig. 4.4a; Appendices K andL). A *post hoc* model was developed to constrain recapture probability to vary in three groups: (1) male *P. helvina*, (2) male *C. pireta* and *D. polita*, and (3) pooled females for of all species, and the *post hoc* model provided the best fit of for the revised model set (Table 4.2b). The resulting estimates, averaged over the nine occasions showed that male *P. helvina* had the highest average recapture probability (Fig. 4.4b; 0.232 ± 0.007), followed by pooled females (0.160 ± 0.005) and male *C. pireta* and *D. polita* (0.109 ± 0.004).

Median lifespans ranged from 2 to 4 days, and 56.7% of observed lifespans were 3 days or less (Table 4.3). Most individuals showing lifespans ≤ 9 days were initially captured and marked by sampling day 2 or 3 (Table 4.4a), while most multi-month individuals were marked on sampling days 3-9 (Table 4.4b), suggesting that the reason many of these individuals were observed in more than one month was because they were initially captured late in the sampling period. The maximum observed lifespan was 68 days in an individual female *P. helvina*. On average, individuals lived 3.57 (± 0.977) to 12.0 (± 1.23) days, and

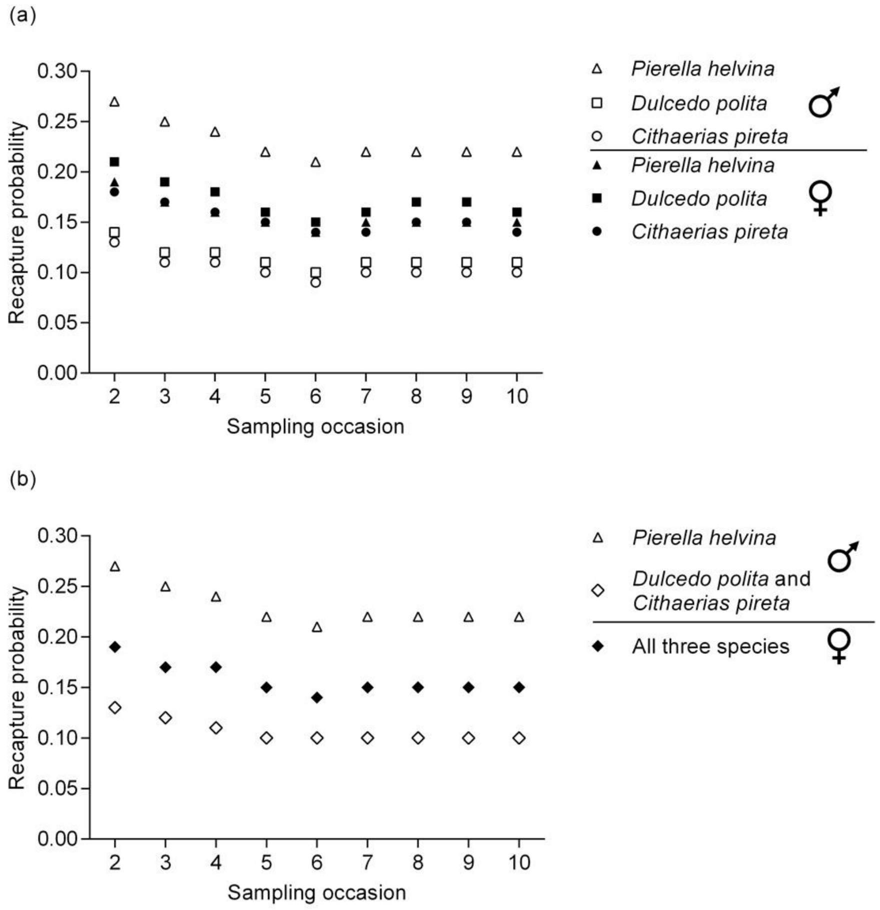


Figure 4.4. Butterfly recapture probabilities. Estimated from a) the original best fit model where recapture probability was allowed to vary with sex and species, and (b) the *post hoc* model where recapture probability was constrained to vary in the three groups depicted.

average monthly lifespans were positively correlated with monthly abundance (Fig. 4.5; r = 0.7989, R^2 = 0.6382, P = 0.0312). Depending on species and sex, estimated daily survival ranged from 0.751 (± 0.049) to 0.896 (± 0.041), and averaged 0.815 (± 0.024) per day (Fig. 4.6; Appendices M and N), suggesting that about 81.5% of these populations survived each day.

More than half (614 individuals, 686 capture histories) of all new captures occurred within the first three sampling occasions (Fig. 4.7). When species and sexes were examined separately, the frequency of new captures among sampling occasions was highest in the first few capture occasions, except when sample sizes were very small (Appendix O). The butterflies also exhibited trap dependence, which means they were recaptured more often

Table 4.3. Lifespans. Average, median and maximum lifespans for three species of Costa Rican understory butterfly (n=500).

		Lifespan (days)		
Species	Sex	Average (± SE)	Median	Max
Cithaerias pireta	♀	3.57 (± 0.977)	2	35
Cithaerias pireta	♂	6.59 (± 1.20)	3	37
Dulcedo polita	♀	5.02 (± 1.15)	2	62
Dulcedo polita	♂	6.73 (± 1.55)	2	33
Pierella helvina	♀	9.93 (± 1.31)	3	68
Pierella helvina	♂	12.0 (± 1.23)	4	64

Table 4.4. Day of first capture. Abundance, median sampling day on which butterflies were marked (first captured), and median lifespan for individuals showing lifespans of (a) ≤ 9 days and (b) > 9 days. *Actual sampling day and observed lifespan is given for the single female *C. pireta* observed in (b).

	Individuals (≤ 9 days)			Median day marked			Median lifespan		
(a)	Female	Male	Total	Female	Male	Total	Female	Male	Total
Cithaerias pireta	34	53	87	2	3	3	2	2	2
Dulcedo polita	76	37	113	2	3	3	2	2	2
Pierella helvina	94	115	209	3	2	2	2	3	2

	Individuals (> 9 days)			Median day marked			Median lifespan		
(b)	Female	Male	Total	Female	Male	Total	Female	Male	Total
Cithaerias pireta	1	8	9	2*	9	8	35*	30	32
Dulcedo polita	7	7	14	6	7	7	33	30	31
Pierella helvina	26	42	68	4	3	3	32	31	31

than expected when they had been trapped and released the day before ($\chi^2 = 153.51$, df = 60, $P < 0.0001$).

Discussion

This study estimated recapture probability and daily survival in three sympatric species of Costa Rican understory butterflies in the tribe Haeterini (Table 4.1). Using mark-release-recapture methods and evaluating potential environmental influences on populations, this is one of the few studies to assess recapture and survival probabilities in tropical butterflies

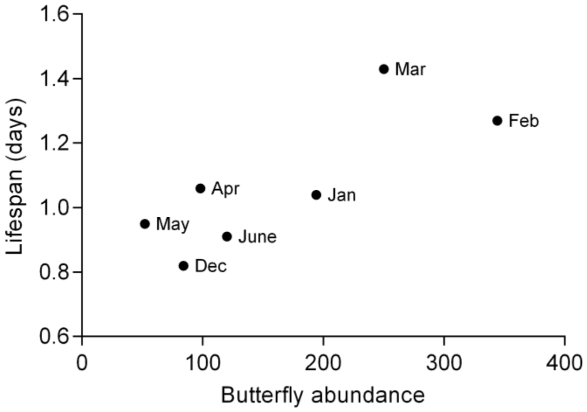


Figure 4.5. Lifespan and abundance. Correlation between monthly abundance and average number of days from first to last capture, an estimator for lifespan in the field. Here, the maximum lifespan is 9 days (n=1239).

(Mallet and Jackson 1980; Fleming, Serrano and Nassar 2005; Molleman et al. 2007; Tufto et al. 2012). The findings here are relevant to estimating population characteristics such as abundance, individual movements, longevity, and illuminating behavioral differences among closely-related species in this distinctive group of butterflies.

We evaluated the effect of rainfall, sampling site and monthly abundance on butterfly recapture probability and daily survival (Table 4.2) and found that site and abundance were influential covariates, but rainfall was not. Despite its variation among sites (Fig. 4.1), models including rainfall as a covariate achieved extremely low likelihoods, and did not correlate with butterfly abundance or with lifespan, strongly implying that rainfall did not influence recapture probability and daily survival. Other studies indicate that tropical butterfly abundance is not strongly influenced by rainfall. For example, DeVries et al. (2012) found no correlation between rainfall (or temperature) and monthly abundance of 101 species of fruit-feeding butterflies. The study of *Morpho sulkowskyi* by Prieto, Takegami and Rivera (2005) also found no correlation between rainfall and abundance, but they did find that temperature and abundance were correlated. This implies that temperature may be a useful environmental covariate for assessing influences on recapture probabilities and daily survival for some tropical insects.

We found that recapture probabilities of our study species varied among sample sites. Recaptures in some tropical butterflies may be lower in second growth habitats compared to

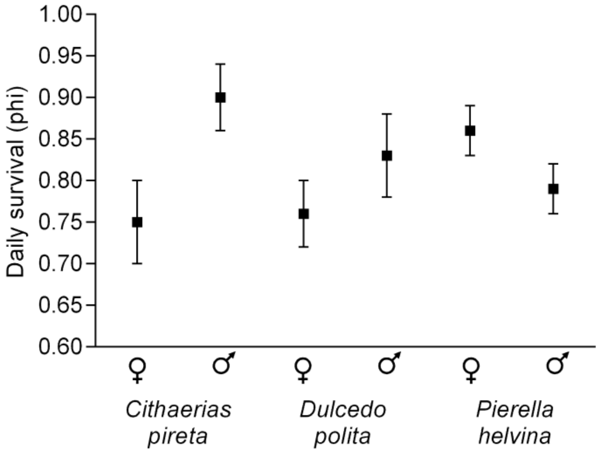


Figure 4.6. Estimates of daily survival (phi ± SE) for the three butterfly species.

primary rainforest (Vlasanek, Sam and Novotny 2013). In the present work, our sampling sites were all within primary forest (Isidro Chacón personal communication), but each site may have manifested subtle microhabitat differences that influenced abundance and recapture probabilities (Figs 4.2 and 4.3). For example, almost half of all individuals and twice the daily recaptures were observed in sites E and F. Higher recapture rates in these two sites suggest greater site fidelity and lower dispersal rates (Hill et al. 2001; Tufto et al. 2012), especially for *D. polita*.

The recapture probabilities found here were similar to those estimated for other butterflies (e.g., Schtickzelle, Le Boulenge and Baguette 2002; Wahlberg et al. 2002; Fleming, Serrano and Nassar 2005; Konvička et al. 2005; Fric et al. 2010), but varied among species and sexes (Fig. 4.4b). Male *P. helvina* had higher recapture probabilities than males of *C. pireta* and *D. polita*, whereas female recapture probabilities were similar in all species. Even though closely related taxa may show significant behavioral differences among both sexes, it is not uncommon to see larger behavioral differences among species for males than females (Shuster and Wade 2003). With a sample size of three species, it is impossible to tell from the present work whether that is the case here. Future work should focus on estimating recapture probabilities for more tropical forest satyrines so that we can assess whether males exhibit more variability among species than females. Variation in recapture probability could

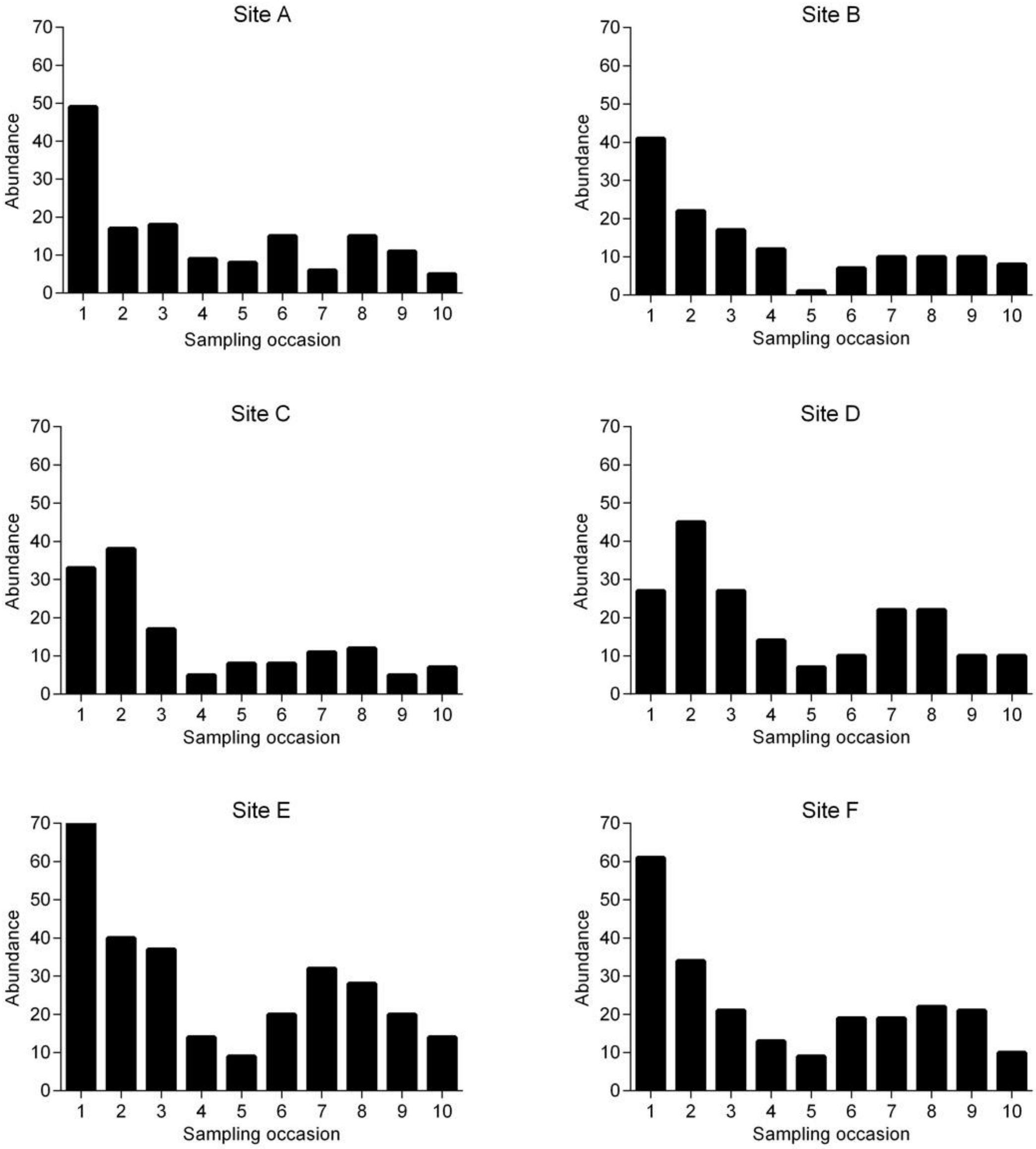


Figure 4.7. Butterfly abundance distribution among sampling days. Distribution of butterfly abundance (new captures) among sampling occasions within each sampling site for 1142 individuals. Species and sexes are pooled.

indicate differences in a wide variety of traits that have not yet been studied in these species, including feeding frequency (Molleman et al. 2005), movement rate (Brussard, Ehrlich and Singer 1974), and home range size (Chew 1981).

Daily survival was affected by abundance, highlighting the inherent stochasticity of MRR observations (Williams, Nichols and Conroy 2002). Monthly butterfly abundance was positively correlated with lifespan (Fig. 4.5), most likely because the probability of observing longer lifespans increased with sample size. The effect of abundance on estimation of daily survival also reflected significantly higher abundances in February and March (Fig. 4.2). Given that temporal heterogeneity in abundance is common in tropical butterfly populations (e.g., DeVries, Walla and Greeney 1999), and assuming data dense enough to support extra parameterization (Burnham and Anderson 2002), future studies might incorporate controls for abundance into underlying model structure. The results here, however, cannot safely be interpreted with respect to density-dependent effects because we could not eliminate the possibility that survival in the focal species may have been constant across sample periods.

The survival estimates here imply potentially large daily population shifts. Most individuals apparently died within a week (Table 4.3), although comparison of initial capture days between single-month and multi-month individuals suggests that median lifespan may be between 2 and 33 days (Table 4.4b). Daily survival probabilities ranged from 0.75 to 0.90 per day (Fig. 4.6), and given that the probability of individual survival is closely related to the proportion of animals in a population that survive (Williams, Nichols and Conroy 2002), the implication is that 75-90% of these butterfly populations survived each day, thus 10-25% did not. Although these survival probabilities likely underestimate true daily survival due to their inability to discriminate between actual mortality and emigration (Tufto et al. 2012), they nonetheless represent significant daily turnovers.

The distribution of new captures among sampling days (Fig. 4.7) suggests the presence of novel individuals within sampling sites in the early days of sampling each month. All available evidence suggests that members of Haeterini do not fly outside of the forest (DeVries 1987), and here we also assumed they stayed within fairly small areas rather than ranging freely across the entire reserve. Because bait was kept fresh consistently, higher than expected numbers of new captures early in sampling suggest a response to new food resources (Muirhead-Thomson 1991). Otis et al. (1978) referred to this as the attraction effect, namely temporary higher sampling density at a new food source. Samples of butterflies marked before the attraction effect subsided had larger proportions of unsampled individuals compared to later samples (Appendix O), suggesting greater movement within the reserve than previously assumed. In other words, individuals appeared to respond to the newly baited traps by temporarily redistributing themselves within the landscape.

The attraction effect interacted with trap dependence to influence daily recapturability, with implications for our understanding of local butterfly densities. To correct for the attraction effect we allowed the first recapture probability to vary independently, but the tendency for butterflies to be recaptured immediately after initial capture (trap dependence) caused the remaining recapture probabilities to decrease incrementally over several days (Fig. 4.4). A way to stabilize attraction effect in the field is by pre-baiting (Otis et al. 1978), and in the present study the first few days of sampling essentially fulfilled the function of pre-baiting. This suggests that abundances observed during the later sampling occasions may more accurately reflect true butterfly densities at each sampling site, a finding important for understanding spatial abundance distribution and local population sizes.

The attraction effect also may interact with attraction distance. The distance over which an insect will respond to an attractant may be species-specific (Finch 1980; Tufto et al. 2012). In general using MRR data to measure attraction distance is problematic because recapturing marked individuals released at known distances from a source point indicates only how far those individuals moved (Finch 1980). But, Tufto et al. (2012) used a Bayesian method to calculate attraction distance of some common fruit-feeding nymphalids, including a distance of about 20 m for the satyrine *Bia actorion* (tribe: Brassolini; Peña et al. 2006), an understory species similar in wing length to the Haeterini studied here. Knowing the attraction distance of a species affords the potential to estimate local population densities using some fairly simple calculations if the overlap in attraction area among traps is low

(Tufto et al. 2012). However, the temporary induction of higher than expected density immediately after baiting implies that the distance across which a butterfly can detect a food source is not always equivalent to the distance across which it will respond. Temporal and spatial heterogeneity in functional attraction distance is potentially an important consideration for estimating population densities within prescribed areas, and for understanding movement and demography.

This work analyzed 10-day capture histories instead of full capture histories to improve model fit and reduce sampling variances (Burnham and Anderson 2002). We captured over 100 individuals of each species/sex pair and more than a thousand individuals, with recapture rates sufficient for the chosen MRR methods (Table 4.1). However, while the study spanned almost 200 days, median lifespans were two to four days (Table 4.3). When individual lifespans are shorter than the study duration and resulting capture histories are sparse, i.e., dominated by zeros, models can be underfitted, making biologically relevant effects difficult to detect (Burnham and Anderson 2002). Here, less than 8% of the butterflies were captured in more than one sampling period, so the 10-day capture histories incorporated the full lifespans and recaptures of the majority of individuals with minimal loss of data. Thus, although recapture probability and daily survival were slightly underestimated, analyzing 10-day histories allowed us to use fitted models.

Using MRR methods on three closely related butterflies, *C. pireta*, *D. polita*, and *P. helvina*, this study is the first to formally estimate probabilities of recapture and daily survival for populations of members of the tribe Haeterini. Habitat heterogeneity and monthly butterfly abundance, but not rainfall, were influential in the estimation of these parameters, and we found daily survival was sensitive to stochasticity in the data. Recapture probability was highest in certain sampling sites, in the first few days of sampling, and for male *P. helvina*, and daily survival did not differ markedly among species, suggesting large daily turnover. Our findings also point to an attraction effect and suggest that functional attraction distance to fruit baits varies in time and space. Basic elements of population ecology such as those estimated here remain obscure for the vast majority of tropical butterfly species (Bonebrake et al. 2010). It is therefore important to continue work on members of the Haeterini to advance our understanding of tropical butterfly population biology in species confined to forests, and increase our ability to conserve and manage rainforest organisms.

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Appendix A: Examples of Mark-Release-Recapture (MRR) Studies (on Various Taxa, Habitats, Geographic Regions, and Questions)

Species	**Order: Family**	**Study habitat**	**Study region**	**Question**	**Reference**
Allium amplectens	Asparagales: Amaryllidaceae	dry, sunny slopes	North America	What are the annual rates of prolonged dormancy in a perennial wild onion?	Hawryzki, Allen and Antos 2011
18 species	various	savanna and gallery forest mosaic	Sub-saharan Africa	What are effects of rain, fire and age on survival of savanna tree seedlings?	Gignoux et al. 2009
Polythore gigantea	Odonata: Polythoridae	tropical streams	South America	What are the effects of stream vegetation variables on population size of a tropical dragonfly?	Altamiranda and Ortega 2012
Chorthippus pullus	Orthoptera: Acrididae	alpine river gravel banks	Europe	How does historical landscape management impact patch occupancy and gene flow in a metapopulation of endangered grasshoppers?	Maag, Karpati and Bollmann 2013
Agriotes lineatus, A. obscurus	Coleoptera: Elateridae	organic research farm	Europe	What is the range of attraction (distance) of a pest click beetle to pheromone traps?	Sufyan, Neuhoff and Furlan 2011
Luciola lateralis	Coleoptera: Lampyridae	restored paddy fields	East Asian Pacific Ocean (Japan)	How does adult detectability, recruitment, and survival rate vary seasonally in a declining populations of firefly?	Koji, Nakamura and Nakamura 2012
Zaspilothynnus gilesi, Z. nigripes	Hymenoptera: Thynnidae	open sandy areas within woodlands	Australia	How do male wasp pollinators search for mates, and what is the effect of that behavior on pollen movement in a sexually deceptive orchid?	Menz et al. 2013
87 species	Lepidoptera: various	seminatural broad-leaved forests	Europe	How do life-history traits and landscape characteristics affect distribution/movement of macro-moths among forest fragments?	Slade et al. 2013
Papilio polyxenes	Lepidoptera: Papilionidae	grasslands and woodlands	East Asian Pacific Ocean (Japan)	Does bird predation significantly impact monthly density of black swallowtail butterflies?	Kiritani, Yamashita and Yamamura 2013

(table cont.)

Lutzomyia longipalpis	Diptera: Psychodidae	urban area	South America	What are the dispersal distance, population size, and daily survival of a fly disease vector?	De Oliveira et al. 2013
Anguilla anguilla	Anguilliformes: Anguillidae	river	Europe	What is the mean growth rate of the European eel, and how does body size correlate with habitat/seasonality?	Chadwick et al. 2007
Eleutherodactylus coqui	Anura: Leptodactylidae	native forest and eucalyptus plantation	West Indies/ Caribbean	How do population densities, movements, and habitat use differ in native forests versus non-native eucalyptus plantation for a common frog?	Fogarty and Vilella 2003
Trachemys scripta scripta	Testudines: Emydidae	barrier island wetlands	North America	What is the population density and size class distribution of a habitat generalist turtle on barrier islands?	DeGregorio, Grosse and Gibbons 2012
Oligosoma maccanni	Squamata: Scincidae	dry scrub habitat	southwestern Pacific Ocean (New Zealand)	Does marking method affect short-term recapture probability of a skink?	Jones and Bell 2010
Tadorna variegata	Anseriformes: Anatidae	hill country and flat coastal plains	southwestern Pacific Ocean (New Zealand)	What is the temporary emigration and year-to-year survival of a game duck?	Barker, White and McDougall 2005
Petrochelidon pyrrhonota	Passeriformes: Hirundinidae	cliffs, bridges and culverts	North America	Is there a correlation between annual survival and oscillation in morphological traits under directional selection in cliff swallows?	Brown, Brown and Roche 2013
Deomys ferrugineus	Rodentia: Muridae	primary rainforest and fallow land	Sub-saharan Africa	How does habitat affect survival and movement of the Congo forest mouse?	Kennis et al. 2012
Arctocephalus gazella	Carnivora: Otariidae	coastal breeding colony	Antarctica	How does age-targeted predation affect population size of Antarctic fur seals?	Schwarz et al. 2013
Ursus maritimus	Carnivora: Ursidae	the southern Beaufort Sea	Arctic Ocean	Are there differences in detection/capture probability between two populations of polar bears?	Amstrup, McDonald and Stirling 2001
Cheirogaleus medius	Primates: Cheirogaleidae	tropical forest	western Indian Ocean (Madagascar)	Are there seasonal changes in body mass and behavioral traits in a small, nocturnal, tropical-forest lemur?	Fietz and Ganzhort 1999

(table cont.)

Phaeosphaeria nodorum	Pleosporales: Phaeosphaeriaceae	experimental fields of winter wheat	Europe	What are the relative contributions of immigration, sexual reproduction, and asexual reproduction of a pathogenic fungus to wheat epidemics?	Sommerhalder et al. 2010

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Appendix B: Hostplant Families for Three Species of Costa Rican Haeterini

Araceae (philodendrons)

The host plants used by *Cithaerias pireta* in the family Araceae are abundant and common. Araceae is an exceptionally diverse and widespread family of tropical/subtropical monocotyledonous shrubs, herbs and vines. They are mostly pollinated by beetles and flies, and usually produce fleshy fruits (Watson 1992; Gentry 1993; Grayum 1990; Longhi 2000). *Philodendron herbaceum*, one of three host plant species recorded for *C. pireta*, is a slender twining herb of low, damp sites in primary forest near streams, swamp-forest, and at the edges of light-gaps and trails (Grayum 1996). Atypically of the genus, it may reproduce more often by vegetative multiplication than by insect pollination. It exhibits a southern Central America/Pacific South America distribution pattern in common with many other tropical plants, and is abundant in the Atlantic lowlands of Costa Rica, but unlike other closely related *Philodendron* species, has not been found in the Pacific lowlands of that country (Grayum 1996). *Philodendron rhodoaxis*, also recorded as a host plant for *C. pireta* (Janzen and Hallwachs 2009), is a member of the same natural subgroup as *P. herbaceum* but is found on both Atlantic and Pacific slopes (Grayum 1996), as is the third recorded host plant species, *Philodendron sulcatum* (Janzen and Hallwachs 2009). Philodendrons flower during the wetter months, sometimes en masse, and are common and abundant throughout their distributions (Grayum 1996), probably contributing to the homogeneous spatial distribution observed in *C. pireta* (Alexander and DeVries b).

Arecaceae (palms)

Cyclanthaceae and Arecaceae are the host plant families observed for *Dulcedo polita*, although the single observation on a cyclanth may represent an oviposition mistake.

Cyclanthaceae is a diverse Neotropical family found in lowland rain forests from southern Mexico to the Atlantic Forest of southern Brazil, and contains a variety of structural forms including some that are palm-like (Leal and Forzza 2012). Both cyclanths and the true palms of Arecaceae are flowering perennials with compound leaves that produce fleshy fruits (Watson 1992). In spite of some superficial similarities, cyclanths and palms are not particularly closely related and differ in many respects (Tomlinson and Wilder 1984). Cyclanths grow in wet, protected areas, are non-spiny, and may be terrestrial or aerial, while palms grow in diverse habitats including some that are exposed and sunny, are often spiny, and are never strictly epiphytic (Tomlinson and Wilder 1984). *Dulcedo polita* is most often observed in wet swampy habitats where cyclanths may be found alongside palms, so an accident either in oviposition or in plant identification would be understandable.

Heliconiaceae (heliconias) and Marantaceae (calatheas)

Heliconiaceae and Marantaceae, the host plant families used by *Pierella helvina*, both contain understory herbs that are common and abundant in wet forest, along streams and edges, and in secondary forest (Gargiullo et al. 2008). The primarily Neotropical family of Heliconiaceae contains a single genus, *Heliconia*, comprising 80 species of large, erect perennial herbs that are abundant and common, with large conspicuous leaves, brightly colored bracts, and hummingbird-pollinated flowers (Watson 1992; Gentry 1993; Longhi 2000; Zuchowski 2007). Many species of *Heliconia* are sun-loving species that grow along roadsides, streams or gaps, and in second-growth, although a few are semi-shade or forest species (Zuchowski 2007). As with Heliconiaceae, plants within the family Marantaceae are noticeable components of tropical forests (Gentry 1993). Marantaceae has 31 genera and about 535 species in warm temperate and tropical parts of the world, with 14 genera in the New World (Prince and Kress 2006). Members of this family are cultivated for a variety of products and as landscape and potted plants (Prince and Kress 2006). Also in common with *Heliconia*, many species of Marantaceae are weedy and grow in sunny or disturbed locations (Prince and Kress 2006).

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Appendix C: Sampling Calendars for 2009/2010

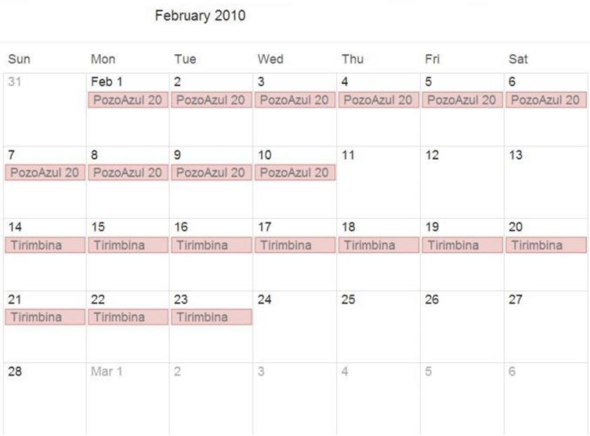
Calendars showing dates of sampling at the Tirimbina and Pozo Azul reserves during the main study period from December 2009 through June 2010. “PozoAzul 10” and “PozoAzul 20” refer to the use of ten and twenty traps, respectively, at Pozo Azul. “Adj-Tirimbina” refers to additional sampling at Tirimbina in June 2010.

December 2009

Sun	Mon	Tue	Wed	Thu	Fri	Sat
29	30	Dec 1	2	3	4	5
6	7	8	9	10	11	12
13	14	15	16	17 Tirimbina	18 Tirimbina	19 Tirimbina
20 Tirimbina	21 Tirimbina	22 Tirimbina	23 Tirimbina	24 Tirimbina	25 Tirimbina	26 Tirimbina
27	28	29	30	31	Jan 1	2

January 2010

Sun	Mon	Tue	Wed	Thu	Fri	Sat
27	28	29	30	31	Jan 1	2 PozoAzul 10
3 PozoAzul 10	4 PozoAzul 10	5 PozoAzul 10	6 PozoAzul 10	7 PozoAzul 10	8 PozoAzul 10	9 PozoAzul 10
10 PozoAzul 10	11 PozoAzul 10	12	13	14	15 Tirimbina	16 Tirimbina
17 Tirimbina	18 Tirimbina	19 Tirimbina	20 Tirimbina	21 Tirimbina	22 Tirimbina	23 Tirimbina
24 Tirimbina	25	26	27	28	29	30
31	Feb 1	2	3	4	5	6



February 2010

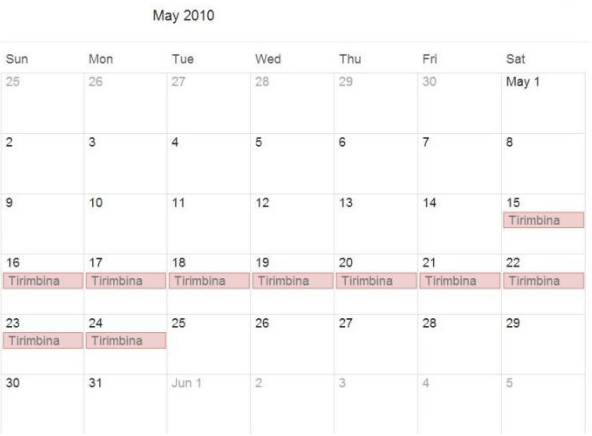
Sun	Mon	Tue	Wed	Thu	Fri	Sat
31	Feb 1 PozoAzul 20	2 PozoAzul 20	3 PozoAzul 20	4 PozoAzul 20	5 PozoAzul 20	6 PozoAzul 20
7 PozoAzul 20	8 PozoAzul 20	9 PozoAzul 20	10 PozoAzul 20	11	12	13
14 Tirimbina	15 Tirimbina	16 Tirimbina	17 Tirimbina	18 Tirimbina	19 Tirimbina	20 Tirimbina
21 Tirimbina	22 Tirimbina	23 Tirimbina	24	25	26	27
28	Mar 1	2	3	4	5	6

March 2010

Sun	Mon	Tue	Wed	Thu	Fri	Sat
28	Mar 1	2	3 PozoAzul 20	4 PozoAzul 20	5 PozoAzul 20	6 PozoAzul 20
7 PozoAzul 20	8 PozoAzul 20	9 PozoAzul 20	10 PozoAzul 20	11 PozoAzul 20	12 PozoAzul 20	13
14	15	16 Tirimbina	17 Tirimbina	18 Tirimbina	19 Tirimbina	20 Tirimbina
21 Tirimbina	22 Tirimbina	23 Tirimbina	24 Tirimbina	25 Tirimbina	26	27
28	29	30	31	Apr 1	2	3

April 2010

Sun	Mon	Tue	Wed	Thu	Fri	Sat
28	29	30	31	Apr 1	2	3
4	5	6	7	8	9	10
11	12	13	14	15 Tirimbina	16 Tirimbina	17 Tirimbina
18 Tirimbina	19 Tirimbina	20 Tirimbina	21 Tirimbina	22 Tirimbina	23 Tirimbina	24 Tirimbina
25	26	27	28	29	30	May 1



May 2010

Sun	Mon	Tue	Wed	Thu	Fri	Sat
25	26	27	28	29	30	May 1
2	3	4	5	6	7	8
9	10	11	12	13	14	15 Tirimbina
16 Tirimbina	17 Tirimbina	18 Tirimbina	19 Tirimbina	20 Tirimbina	21 Tirimbina	22 Tirimbina
23 Tirimbina	24 Tirimbina	25	26	27	28	29
30	31	Jun 1	2	3	4	5

June 2010

Sun	Mon	Tue	Wed	Thu	Fri	Sat
30	31	Jun 1 Adj-Tirimbina	2 Adj-Tirimbina	3 Adj-Tirimbina	4 Adj-Tirimbina	5 Adj-Tirimbina
6 Adj-Tirimbina	7 Adj-Tirimbina	8 Adj-Tirimbina	9 Adj-Tirimbina	10 Adj-Tirimbina	11	12
13	14 Tirimbina	15 Tirimbina	16 Tirimbina	17 Tirimbina	18 Tirimbina	19 Tirimbina
20 Tirimbina	21 Tirimbina	22 Tirimbina	23 Tirimbina	24	25	26
27	28	29	30	Jul 1	2	3

Appendix D: Brief Descriptions of the Sampling Sites Used During Various Phases of the 2009-2011 MRR Study of Costa Rican Haeterini

Generally speaking, the forest at Tirimbina is characterized by the nitrogen-fixing tree *Pentaclethra macroloba* (Fabaceae) and many types of palms (Isidro Chacón personal communication). However, there is a great deal of habitat heterogeneity at a fine resolution within the reserve, and the vegetation, insolation and topography around the traps in each sampling site are variable. Site descriptions provided here are compilations of the shared features from individual trap locations within each site observed in March 2010. Based on advice by Isidro Chacón, Associate Researcher and Lepidoptera Curator at Instituto Nacional de Biodiversidad (INBio), I focused on five general characteristics to describe the sampling sites:

1. Tree size
2. Degree of visibility through the understory
3. Presence of logs and old tree trunks
4. Presence and size of woody vines
5. Abundance, species richness and size of palms

Site 1:

Site 1 is located within an abandoned cacao plantation. This area floods severely during heavy rains, and contains many old *Theobroma cacao* (Sterculiaceae) trees along with some other large tree species on the perimeter. The understory is largely clear with very good visibility except for some weedy patches along the streams and river that enclose the area. The understory contains comparatively few palms, and is characterized by ferns (Blechnaceae) and spike mosses (Selaginellaceae).

Site 2 (site A):

Site 2 is rather swampy and mostly shady, except for one large recent tree fall where it is very sunny. The area contains large trees and large logs from old tree falls, with relatively clear understory and good visibility. There are some palms, but many non-palm herbs. The site is bordered by a stream. Trap 6 is on a bluff above a wide stream separating this site from the old cacao plantation and site 1.

Site 3 (site B):

This site contains many large trees and small to medium palms. Trap 12 is on a hill, but the site leading up to it is swampy with moderately dense to relatively clear understory and many palms. Trap 15 is near an old tree fall and receives more sunshine than the rest of the site, with dense, thicket-like undergrowth composed of many non-palm plants including ferns and herbs.

Site 4 (site C):

Site 4 runs along a ridge and is breezier, less deeply shaded and drier than the other sites. There are small to medium size trees including many *Euterpe precatoria* (Arecaceae) and *Pentaclethra macroloba* (Fabaceae), and broad-leaved saplings of Fabaceae or Moraceae. The undergrowth is moderately dense with small palms and herbs.

Site 5 (site D):

This site generally has low visibility through the thick undergrowth, many palms almost to the exclusion of other understory plants, many woody vines of small to large diameter (although see the description of trap 21), many small samplings, a few large trees, and evidence of trees selectively cut in the past (some old, large tree trunks). Trap 21 is on a ridge above the Rio Sarapiquí, with the river audible but not visible. The terrain around trap 21 is different from the rest of the site, with more large trees and large vines, and more non-palm understory plants, including ferns and erect, showy herbs (Heliconiaceae and Marantaceae).

Site 6 (site E):

Site 6 has trees of all sizes and large saplings, some logs from old tree falls, and two broad open areas from very recent tree falls containing large logs and thick undergrowth. This site contains a mild decline, at the bottom of which is quite swampy. The understory includes many palms and palm-like plants, especially in the swampy interior, but also plants from the families Melastomaceae, Araceae (e.g., *Anthurium*, *Philodendron*), and Blechnaceae (ferns).

Site 7 (site F):

The terrain in this site is steeply sloped in places, with a small ravine that drains rainwater, and a swampy portion at one end. There is extensive evidence of selective logging in the past, with many old, large tree stumps and the remains of an unpaved logging road that serves as a rain sluice. The remaining trees are mostly medium sized, and the area is well-shaded with moderate visibility and many palms and palm-like plants in the understory.

Ajillo Ridge:

The adjunctive study was conducted on this ridge overlooking the Pozo Azul River along the northern boundary of the Tirimbina reserve. The site is reminiscent of site 4 (site C) in that it is elevated, with the river valley on one side and a deep stream valley on the other. At spots the ridge is quite narrow and steep, and throughout is relatively dry and breezy, with many small to medium size trees and broad-leaved saplings. The understory visibility is clear to moderately obscured.

The outer trails (2011 post-study):

The trails along the boundary of the Tirimbina reserve, specifically along the eastern and southern borders, are often located in more disturbed habitats than in the interior, as evidenced by patches of thick undergrowth, sunny spots, and successional plants such as passion flowers (Passifloraceae) and majagua trees (Malvaceae).

Pozo Azul (sites 8 and 9):

Traps were established at two sites in the Pozo Azul reserve. Ten traps were initially established in site 8, which was close to the entrance to the reserve. It contained many small samplings and a few large trees, had good to moderately obscured understory visibility, and contained a mixture of palms, herbs, and successional plants. In the second month of sampling at Pozo Azul (February 2010), another ten traps were established in site 9 deeper within the reserve. Compared to site 8, site 9 was notably wetter with more large trees, fewer saplings and small trees, and a conspicuous presence of philodendrons.

Appendix E. Preliminary MRR Models: Underlying Time Structure

Six non-covariate time-variation mark-release-recapture (MRR) models were tested prior to evaluating covariates and estimating final probabilities. Probabilities of daily survival (phi) and recapture (p) were allowed to vary with sex and species, but otherwise were held constant, constrained by attraction effect, or allowed to vary independently.

	phi		p		
Model	Constant	Attraction effect	Constant	Attraction effect	Varying
1	*		*		
2	*			*	
3	*				*
4		*	*		
5		*		*	
6		*			*

Appendix F: Goodness of Fit, Median $\hat{c}$, and Trap Dependence

The information-theoretic approach to data analysis is founded on the assumption that the data being analyzed are relevant and appropriately collected (Burnham and Anderson 2001, p. 112), and that at least one model in the model set provides a reasonable fit to the data (Nichols 2005, p. 98). One of the most difficult parts of the analytical process is designing the models, and each model in the set should represent a biologically plausible scientific hypothesis based on knowledge of the system being studied (Burnham and Anderson 2002, pp. 15-16; McDonald et al. 2005, p. 222). The goal of analysis is to find the simplest model that accurately reflects the data so that inferences can be made about the sample population (Burnham and Anderson 2002, p. 143). To formulate appropriate models, it is necessary to determine the level of complexity the data will support (Burnham and Anderson 2002, p. 143). In other words, it is important to formulate models that are neither underfitted (ignore important aspects of the data and fail to identify effects supported by the data) nor overfitted (have poor estimator precision and identify features that are unique only to the data at hand; Burnham and Anderson 2002, pp. 32-33). Poor fit can be caused by lack of independence in the data, such as when the fate of one animal influences the fate of another, heterogeneous parameters (probabilities) within classes, or other unknown factors that cause the data to be more complicated than the model predicts (Barker 2005, p. 160; McDonald et al. 2005, p. 236).

The recommended way to assess model fit is by estimating the single variance inflation factor (c) of the most general or underlying model (Burnham and Anderson 2002, p. 68). The estimated statistic $\hat{c}$ measures the extent to which the model fails to represent the data (Barker 2005, p. 160) using the ratio of the observed variation in the data to the variation expected given the model (Manly, McDonald and Amstrup 2005, p. 19). Therefore, $\hat{c} = 1$ indicates perfect fit and $\hat{c}$ > or < 1 indicates over- or under-dispersion.

There are two ways to estimate the variance inflation factor (Barker 2005). The approach recommended by White, Burnham and Anderson (2001, p. 374) uses the parametric bootstrap method in which the model being evaluated for goodness-of-fit is used to generate bootstrap data sets. For perfect fit of the model to the data, the ratio of the observed deviance and the expected deviance (represented by the mean of the simulated deviances) should equal 1. A more recent approach using the bootstrap method termed the median $\hat{c}$ procedure (Cooch and White 2008, section 5.6.1) can be accessed in the program MARK (White and Burnham 1999) and was employed to assess goodness-of-fit for the present project. This procedure uses simulation and resampling to generate an estimate of $\hat{c}$, and is based on the premise that the best estimate of $\hat{c}$ is the value for which the observed deviance $\hat{c}$ falls exactly halfway in the distribution of all simulated deviances under the hypothesis that a given value of c is the true value (Cooch and White 2008, section 5.6.1). The halfway point of that distribution is the median $\hat{c}$, and it can be used to account for model selection uncertainty (Cooch and White 2008, section 5.9.1).

The median $\hat{c}$ is robust when the primary source of lack of fit is simple extra-binomial variation (Cooch and White 2008, section 5.7), so it is important to assess structural problems in the model. This is possible using a series of χ^2 tests in the RELEASE section of program MARK that answer three questions:

1. Did marking affect whether an individual was ever seen again (marking effect or survival effect)?
2. Did marking affect when that individual was seen again (trap dependence)?
3. Did when an individual was last captured affect when that individual was seen again (handling effect)?

We conducted all three sets of χ^2 tests for this project but reported results only for trap dependence since results were non-significant for marking effect and handling effect. Structural issues in the data, when they exist, can be corrected by stratifying the data into classes or by using covariates. We stratified the data by species and sex, and used covariates to correct for trap dependence.

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Appendix G: Distribution Among Sampling Sites of Fruit-Feeding Nymphalids

Abundances of 100 fruit-feeding Nymphalidae butterfly species (n=6984) sampled in mid-understory fruit-baited traps (i.e., with the trap base positioned approximately 1 m above the ground) at Tirimbina from November 2003 through October 2008 (e.g., DeVries et al. 2012), sorted from most to least abundant.

		Sampling site						
Species	Subfamily	1	2 (A)	3 (B)	4 (C)	5 (D)	6 (E)	Total
Taygetis andromeda	Satyrinae	162	210	52	41	60	99	624
Dulcedo polita	Satyrinae	10	79	106	39	45	227	506
Cithaerias menander = pireta	Satyrinae	24	99	87	60	85	104	459
Nessaea aglaura	Biblidinae	79	54	28	79	107	93	440
Tigridia acesta	Nymphalinae	93	70	57	98	75	39	432
Caligo atreus dionysos	Satyrinae	33	102	52	56	64	101	408
Caligo eurilochus sulanus	Satyrinae	53	114	44	40	51	55	357
Catonephele orites	Biblidinae	13	40	40	63	42	51	249
Hamadryas laodamia saurites	Biblidinae	101	29	15	26	50	26	247
Hamadryas arinome ariensis	Biblidinae	18	23	26	48	50	37	202
Pierella helvetia incanescens = helvina	Satyrinae	10	20	32	27	57	50	196
Antirrhea miltiades	Satyrinae	6	37	47	17	28	54	189
Colobura annulata	Nymphalinae	31	35	20	23	20	35	164
Historis acheronta	Nymphalinae	39	22	12	28	30	28	159
Prepona omphale octavia	Charaxinae	51	17	14	14	27	17	140
Opsiphanes cassina	Satyrinae	34	28	19	22	20	12	135
Archaeoprepona demophon centralis	Charaxinae	37	26	13	13	19	18	126
Catoblepia orgetorix championi	Satyrinae	12	20	25	22	14	29	122
Memphis xenocles	Charaxinae	8	4	2	32	56	12	114
Callicore patelina	Biblidinae	5	15	17	14	32	13	96
Historis odius	Nymphalinae	23	10	5	15	26	9	88
Colobura dirce	Nymphalinae	23	17	13	12	8	10	83
Cissia metaleuca	Satyrinae	31	18	11	6	7	4	77
Chloreuptychia arnaea	Satyrinae	11	8	3	1	20	32	75
Hamadryas amphinome mexicana	Biblidinae	20	11	8	16	9	7	71
Opsiphanes quiteria	Satyrinae	13	16	8	10	6	11	64
Morpho amathonte	Satyrinae	2	5	4	6	3	42	62
Archaeoprepona demophoon gulina	Charaxinae	8	11	8	8	8	16	59
Catonephele numilia esite	Biblidinae	9	13	3	7	13	6	51
Archaeoprepona camilla	Charaxinae	5	9	4	13	8	11	50
Caligo oedipus	Satyrinae	35	6	1	1	5	2	50
Morpho granadensis polybaptus	Satyrinae	1	6	7	2	10	24	50
Opsiphanes invirae cuspidatus	Satyrinae	9	9	4	12	10	6	50
Archaeoprepona meander amphimachus	Charaxinae	3	13	12	10	0	11	49
Memphis orthesia	Charaxinae	6	4	6	8	9	15	48
Morpho peleides limpida	Satyrinae	14	6	7	3	2	15	47

(table cont.)

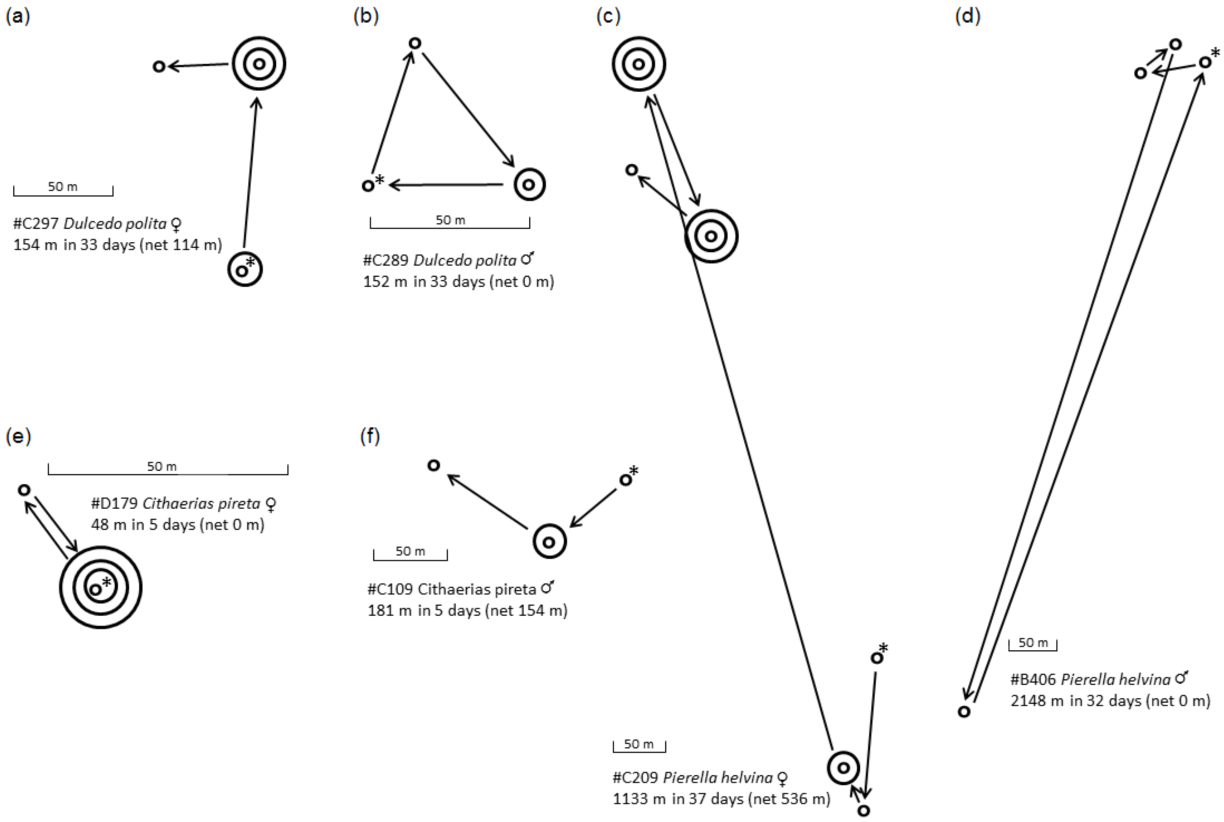
Caligo illioneus oberon	Satyrinae	28	6	4	3	3	2	46
Memphis cleomestra	Charaxinae	8	10	1	7	11	6	43
Baeotus baeotus	Nymphalinae	0	2	4	5	6	15	32
Callicore lyca aerias	Biblidinae	9	6	2	6	1	6	30
Memphis chrysophana	Charaxinae	19	1		1	6		27
Opsiphanes bogotanus	Satyrinae	9	8	1	3	3	2	26
Nica flavilla canthara	Biblidinae	10	6	3		2	2	23
Agrias amydon	Charaxinae	3	3		5	7	5	23
Memphis morvus boisduvali	Charaxinae	3	2	3	3	8	4	23
Memphis eurypyle confusa	Charaxinae	13	5		2	2		22
Smyrna blomfildia datis	Nymphalinae	6	3	2	4	4	3	22
Taygetis virgilia rufomarginata	Satyrinae	3	4	3	3	6	3	22
Myscelia leucocyana smalli	Biblidinae	14	2	2	1	1	1	21
Taygetis salvini	Satyrinae			2	2	16	1	21
Zaretis itys	Charaxinae	2	6	1	2	6	3	20
Hypna clytemnestra clytemnestra	Charaxinae	1	1	3	2	6	3	16
Manataria maculata	Satyrinae	1	6	2	3	2	2	16
Megeuptychia antonoe	Satyrinae	1	2		7	5	1	16
Myscelia cyaniris cyaniris	Biblidinae	7	3		2	2	1	15
Cissia hesione	Satyrinae	8	4				1	13
Temenis laothoe agatha	Biblidinae	7	2	1			1	11
Consul fabius cecrops	Charaxinae	7	1	1		2		11
Cissia usitata	Satyrinae	5		2		1	2	10
Prepona dexamenus	Charaxinae	1	3	1	2	2		9
Caerois gerdrudtus	Satyrinae	1	1		3		4	9
Ectima rectifascia	Biblidinae	2	2	1		2	1	8
Memphis proserpina	Charaxinae	1	4		2	1		8
Taygetis celia keneza	Satyrinae		1	1	5	1		8
Consul panariste jansoni	Charaxinae	1		1		3	2	7
Cissia confusa	Satyrinae	2	2		2	1		7
Cissia pseudoconfusa	Satyrinae	2	2		1	2		7
Callicore peralta	Biblidinae	1	1	1	3			6
Memphis aureola	Charaxinae	1			3	1	1	6
Siderone marthesia	Charaxinae		2		2	1		5
Morpho cypris	Satyrinae	1	3				1	5
Cissia similis	Satyrinae	2				1	1	4
Agrias aedon	Charaxinae		1	2				3
Memphis chaeronea indigotica	Charaxinae	2	1					3
Opsiphanes tamarindi	Satyrinae		1			1	1	3
Taygetis zimri	Satyrinae	1	2					3
Catonephele mexicana	Biblidinae	2						2
Hamadryas feronia ferinulenta	Biblidinae		1		1			2
Hamadryas guatemalena guatemalena	Biblidinae	1			1			2
Hamadryas ipthime ipthime	Biblidinae				2			2
Memphis artacaena	Charaxinae				1	1		2
Caligo memnon memnon	Satyrinae	1		1				2
Cissia agnata	Satyrinae		1		1			2
Cissia labe	Satyrinae		1			1		2
Euptychia mollis	Satyrinae		2					2
Morpho theseus aquarius	Satyrinae	1			1			2
Taygetis mermeria excavata	Satyrinae				1	1		2
Callicore pacifica bugaba	Biblidinae		1					1
Myscelia pattenia	Biblidinae	1						1

(table cont.)

Panacea procilla lysimache	Biblidinae						1	1
Memphis aulica	Charaxinae				1			1
Memphis centralis	Charaxinae					1		1
Memphis oenomais	Charaxinae					1		1
Memphis pithyusa	Charaxinae					1		1
Catoblepia xanthicles xanthicles	Satyrinae				1			1
Cissia hermes	Satyrinae			1				1
Cissia libye	Satyrinae					1		1
Cissia terrestris	Satyrinae	1						1
Eryphanis aesacus buboculus	Satyrinae	1						1
Eryphanis polyxena lycomedon	Satyrinae					1		1

Appendix H. Examples of Movement Patterns in Three Costa Rican Haeterini

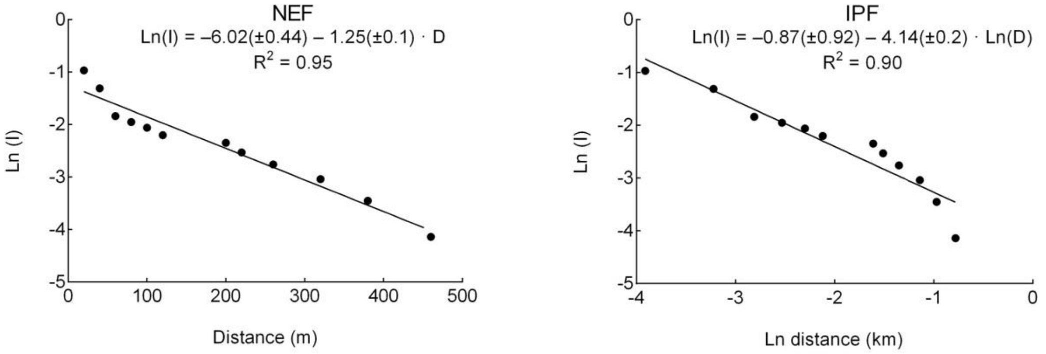
Individual butterflies are identified by their unique identifying number, species, sex, total distance moved, total time during which movements were observed, and net distance from first to last capture. Symbols: Open circle = a capture location. Multiple circles = multiple captures at the same location. Asterisk = position of first capture. Arrow = direction of movement. Scale bar = 50 m.



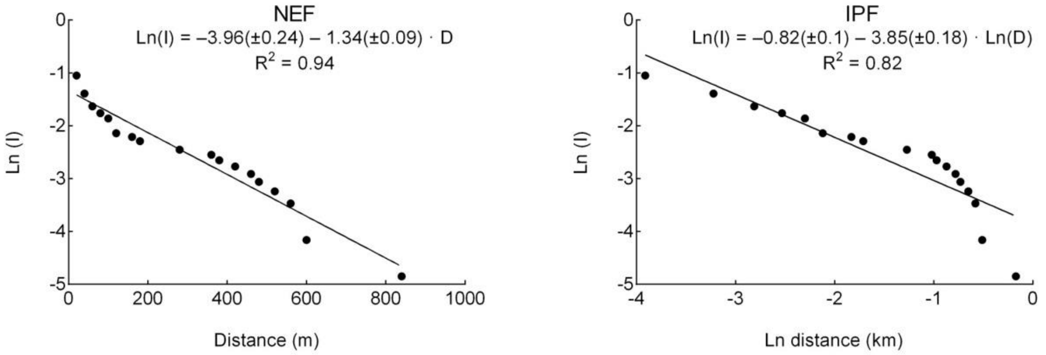
Appendix I. Comparative movement probabilities for three Costa Rican butterflies.

Movement probabilities for females and males of *C. pireta* (upper plots), *D. polita* (middle plots), and *P. helvina* (lower plots) expressed as negative-exponential (NEF) and inverse-power function (IPF) plots. Regression lines show the functions Ln(I) = ln(a) – k·D and Ln(I) = ln(C) – n·ln(D), where I is the probability of moving distance D.

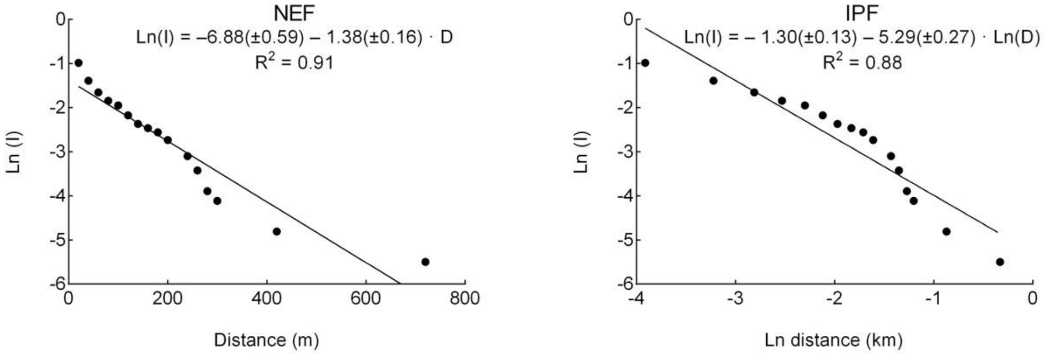
Cithaerias pireta ♀



Dulcedo polita ♀

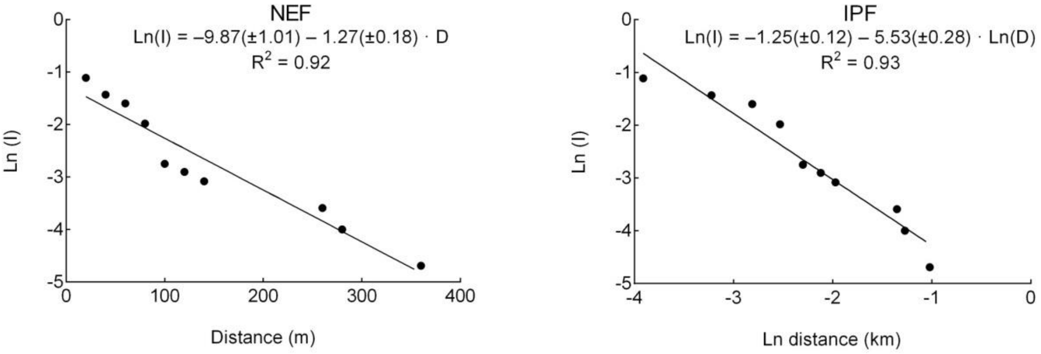


Pierella helvina ♀

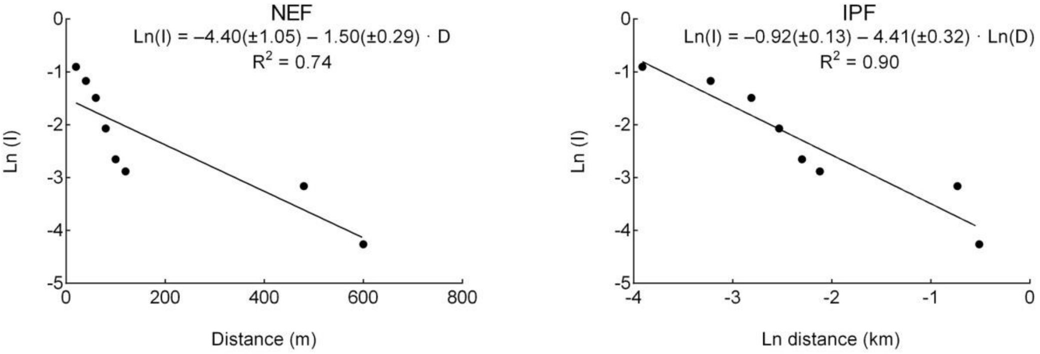


(cont.)

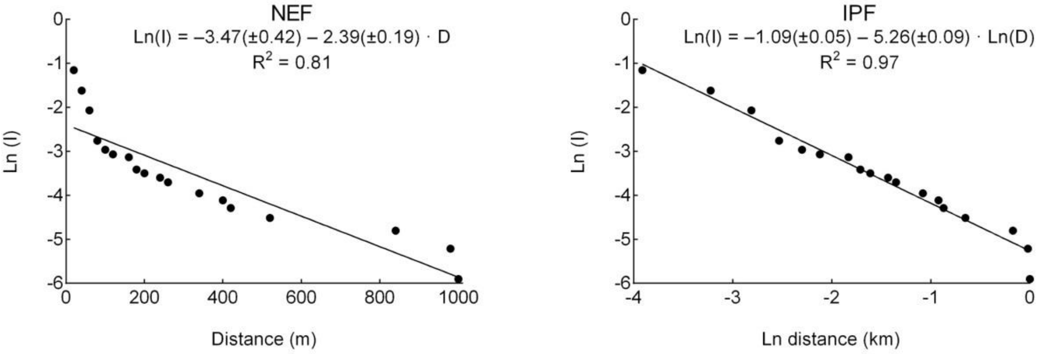
Cithaerias pireta ♂



Dulcedo polita ♂



Pierella helvina ♂



Appendix J. MRR Models with Covariates

Sixteen mark-release-recapture (MRR) models based on the best fit model from the first phase of analysis (see model 2 in Appendix I) were tested in the second phase of analysis in which two group covariates (rain and abundance) and one individual covariate (sampling site) were incorporated.

	phi			p		
Model	Rain	Abundance	Site	Rain	Abundance	Site
2.1	*			*		
2.2	*				*	
2.3	*					*
2.4	*					
2.5		*		*		
2.6		*			*	
2.7		*				*
2.8		*				
2.9			*	*		
2.10			*		*	
2.11			*			*
2.12			*			
2.13				*		
2.14					*	
2.15						*
2.16						

Appendix K. Estimated Recapture Probabilities

Recapture probability (p) estimated for three species of understorey rainforest Nymphalidae (Satyrinae) in Costa Rica. SE = standard error. LCI and UCI = lower and upper boundaries for the 95% confidence interval.

Species	**Sex**	**Sampling interval**	**p**	**SE**	**LCI**	**UCI**
Cithaerias pireta	♀	1	0.18	0.05	0.11	0.29
		2	0.17	0.04	0.11	0.25
		3	0.16	0.04	0.10	0.24
		4	0.15	0.03	0.09	0.23
		5	0.14	0.03	0.09	0.22
		6	0.14	0.03	0.09	0.22
		7	0.15	0.03	0.09	0.23
		8	0.15	0.03	0.09	0.23
		9	0.14	0.03	0.09	0.22
	♂	1	0.13	0.03	0.08	0.19
		2	0.11	0.02	0.08	0.16
		3	0.11	0.02	0.08	0.16
		4	0.10	0.02	0.07	0.15
		5	0.09	0.02	0.06	0.14
		6	0.10	0.02	0.07	0.14
		7	0.10	0.02	0.07	0.15
		8	0.10	0.02	0.07	0.15
		9	0.10	0.02	0.07	0.14
Dulcedo polita	♀	1	0.21	0.04	0.14	0.29
		2	0.19	0.03	0.13	0.26
		3	0.18	0.03	0.13	0.25
		4	0.16	0.03	0.11	0.23
		5	0.15	0.03	0.11	0.22
		6	0.16	0.03	0.11	0.23
		7	0.17	0.03	0.12	0.23
		8	0.17	0.03	0.12	0.23
		9	0.16	0.03	0.11	0.23
	♂	1	0.14	0.03	0.08	0.22
		2	0.12	0.03	0.08	0.19
		3	0.12	0.03	0.08	0.18
		4	0.11	0.02	0.07	0.16
		5	0.10	0.02	0.07	0.16
		6	0.11	0.02	0.07	0.16
		7	0.11	0.02	0.07	0.17

(table cont.)

		8	0.11	0.02	0.07	0.17
		9	0.11	0.02	0.07	0.16
Pierella helvina	♀	1	0.19	0.03	0.13	0.26
		2	0.17	0.02	0.13	0.22
		3	0.16	0.02	0.12	0.21
		4	0.15	0.02	0.11	0.19
		5	0.14	0.02	0.10	0.19
		6	0.15	0.02	0.11	0.19
		7	0.15	0.02	0.11	0.20
		8	0.15	0.02	0.11	0.20
		9	0.15	0.02	0.11	0.19
	♂	1	0.27	0.04	0.20	0.36
		2	0.25	0.03	0.20	0.31
		3	0.24	0.03	0.19	0.30
		4	0.22	0.03	0.17	0.28
		5	0.21	0.03	0.16	0.27
		6	0.22	0.03	0.17	0.28
		7	0.22	0.03	0.17	0.28
		8	0.22	0.03	0.17	0.28
		9	0.22	0.03	0.17	0.28

Appendix L. *Post Hoc* Estimated Recapture Probabilities

Recapture probability (p) as in Appendix K, but estimated from the *post hoc* best fit model. SE = standard error. LCI and UCI = lower and upper boundaries for the 95% confidence interval.

Species	**Sex**	**Sampling interval**	**p**	**SE**	**LCI**	**UCI**
Cithaerias pireta, Dulcedo polita and *Pierella helvina*	♀	1	0.19	0.03	0.14	0.26
		2	0.17	0.02	0.14	0.22
		3	0.17	0.02	0.13	0.21
		4	0.15	0.02	0.12	0.19
		5	0.14	0.02	0.11	0.18
		6	0.15	0.02	0.12	0.19
		7	0.15	0.02	0.12	0.20
		8	0.15	0.02	0.12	0.20
		9	0.15	0.02	0.12	0.19
Cithaerias pireta and *Dulcedo polita*	♂	1	0.13	0.03	0.09	0.19
		2	0.12	0.02	0.09	0.16
		3	0.11	0.02	0.08	0.15
		4	0.10	0.02	0.07	0.14
		5	0.10	0.02	0.07	0.13
		6	0.10	0.02	0.07	0.14
		7	0.10	0.02	0.08	0.14
		8	0.10	0.02	0.08	0.14
		9	0.10	0.02	0.07	0.14
Pierella helvina	♂	1	0.27	0.04	0.20	0.36
		2	0.25	0.03	0.20	0.31
		3	0.24	0.03	0.19	0.30
		4	0.22	0.03	0.17	0.28
		5	0.21	0.03	0.16	0.27
		6	0.22	0.03	0.17	0.28
		7	0.22	0.03	0.17	0.29
		8	0.22	0.03	0.17	0.29
		9	0.22	0.03	0.17	0.28

Appendix M. Daily Survival Probabilities

Daily survival (phi) estimated as described for recapture probability in Appendix K. SE = standard error. LCI and UCI = lower and upper boundaries for the 95% confidence interval.

Species	**Sex**	**phi**	**SE**	**LCI**	**UCI**
Cithaerias pireta	♀	0.76	0.06	0.61	0.86
	♂	0.90	0.05	0.77	0.96
Dulcedo polita	♀	0.74	0.04	0.65	0.82
	♂	0.82	0.06	0.68	0.91
Pierella helvina	♀	0.87	0.03	0.80	0.92
	♂	0.79	0.03	0.73	0.83

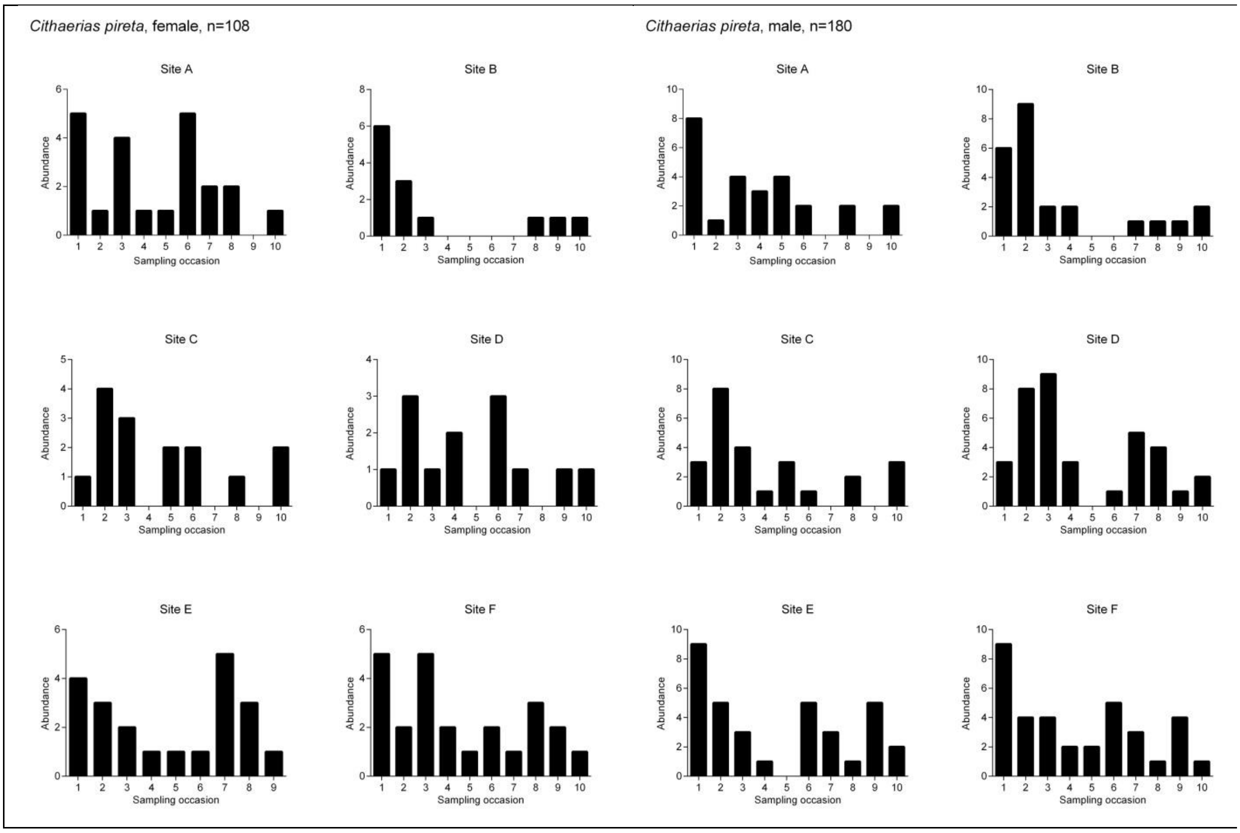
Appendix N. *Post Hoc* Estimated Daily Survival Probabilities

Daily survival (phi) as in Appendix M, but estimated from the *post hoc* best fit model. SE = standard error. LCI and UCI = lower and upper boundaries for the 95% confidence interval.

Species	**Sex**	**phi**	**SE**	**LCI**	**UCI**
Cithaerias pireta	♀	0.75	0.05	0.64	0.83
	♂	0.90	0.04	0.79	0.95
Dulcedo polita	♀	0.76	0.04	0.68	0.82
	♂	0.83	0.05	0.71	0.91
Pierella helvina	♀	0.86	0.03	0.80	0.91
	♂	0.79	0.03	0.73	0.83

Appendix O. Distribution of Butterfly Abundance Among Sampling Occasions

Abundance (new captures) for 1142 individual butterflies of three species distributed among sampling occasions, with sampling periods pooled, and species and sexes partitioned.



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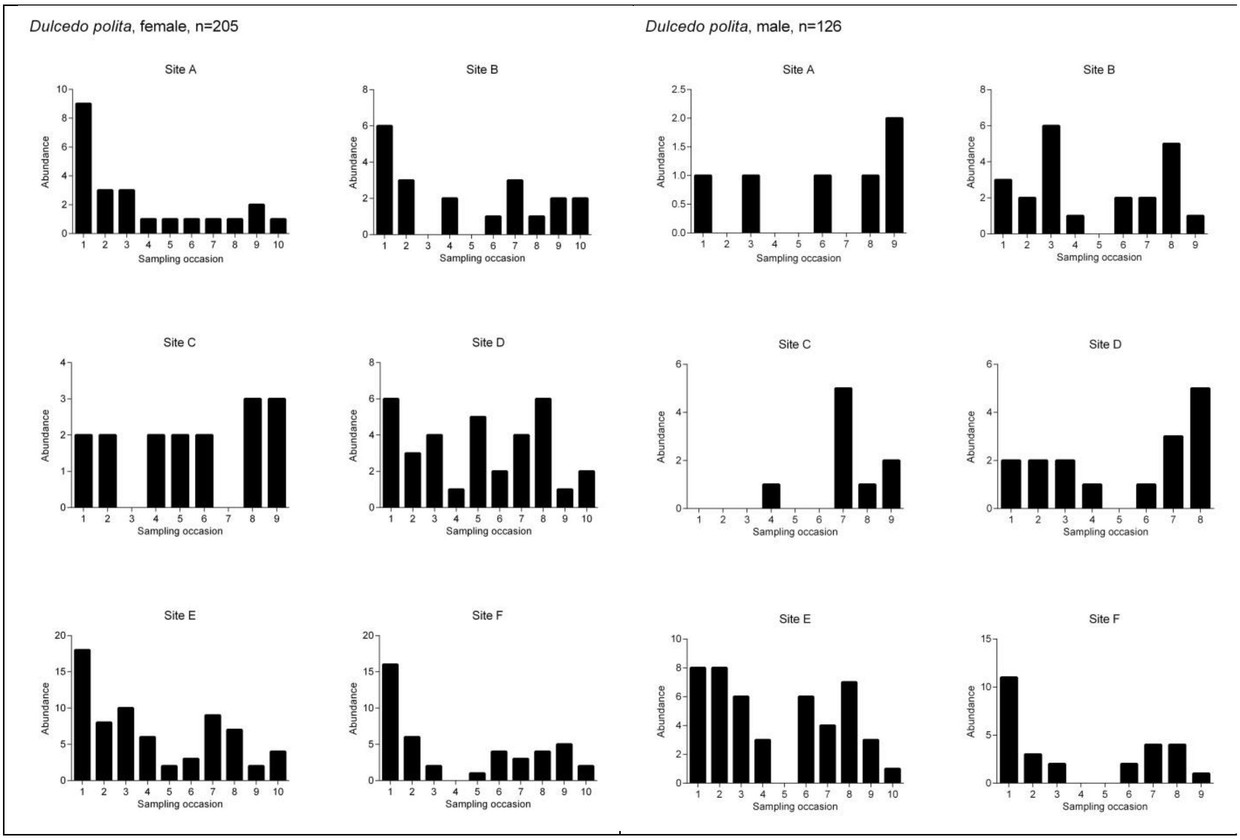
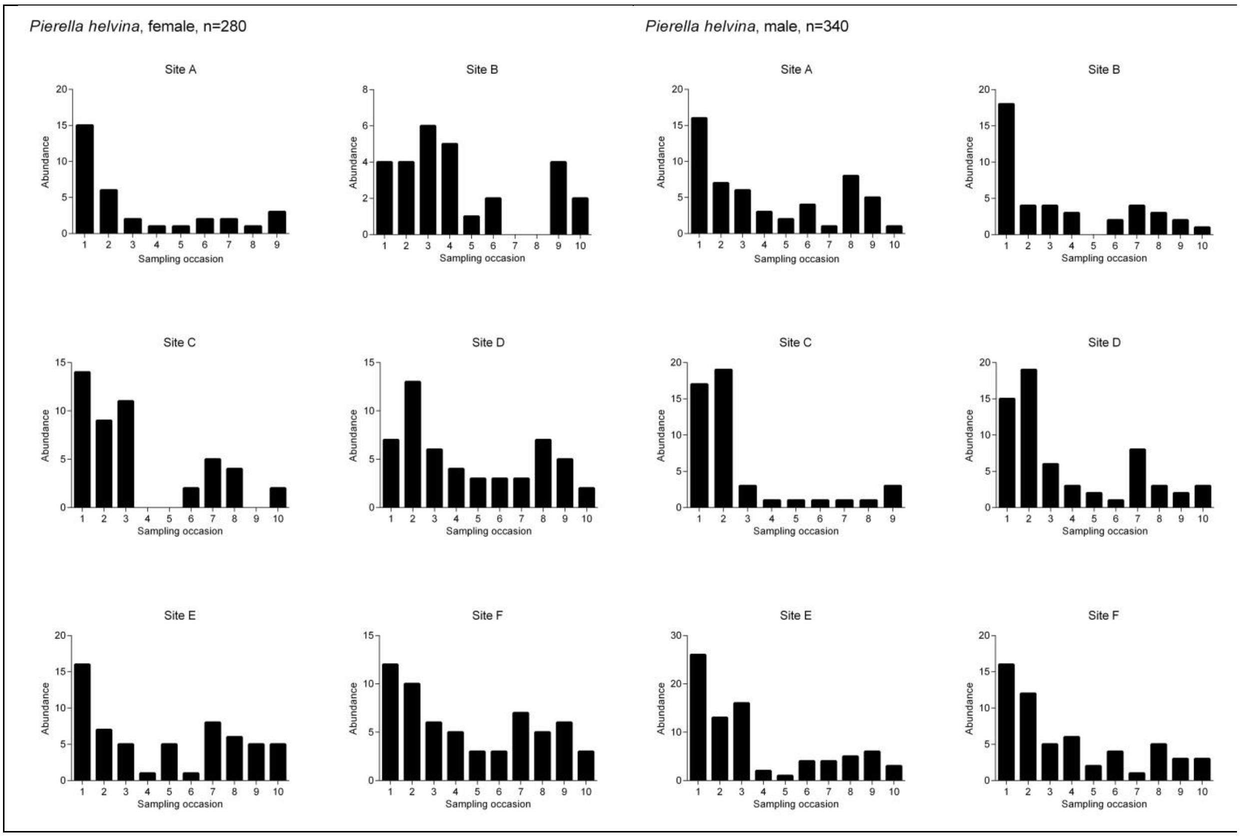

Dulcedo polita, female, n=205
Dulcedo polita, male, n=126
Site A
Site B
Site C
Site D
Site E
Site F
Abundance
Sampling occasion


Pierella helvina, female, n=280
Pierella helvina, male, n=340
Site A
Site B
Site C
Site D
Site E
Site F
Abundance
Sampling occasion

Vita

The author was born in Jacksonville, Florida. She obtained her Bachelor’s degree in English from Stetson University in 1987, and pursued a career in medical publishing. In Fall 2007, she joined the University of New Orleans graduate program to pursue a PhD in conservation biology with Dr. Phil DeVries.