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# Weather-Related Color Polymorphism of *Rothschildia lebeau* (Saturniidae)

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In 1868, Guérin-Méneville described an orange-colored male saturniid moth from the vicinity of Caracas, Venezuela, as *Rothschildia lebeau*. In 1905, Schaus described a rusty brown male Honduran *Rothschildia* as *R. aroma* and in 1921 he described a pinkish male from Guatemala as *R. morana*. In 1934, Benjamin described the south Texas portion of the *R. lebeau* population as *R. forbesi*. As is commonplace with large saturniid moths, wing color, shape, and size played a major role in the authors' decisions to view these animals as different species. On the bases of genitalic comparisons and familiarity with wing variation in the genus *Rothschildia*, Lemaire (1978) and Draudt (1929) synonymized these (and other) *Rothschildia* under *R. lebeau*; Lemaire (1978) retained several subspecific names, the bases for which were geographic range, wing shape and size, and wing color. In 1980, I did not yet know of this astute act of taxonomic lumping and was confronted with the identification of dark chocolate-colored *Rothschildia* (Fig. 1) in the lowlands of northwestern Costa Rica as *R. aroma* and sympatric rust-to orange-colored *Rothschildia* (Fig. 1) as *R. lebeau*. Hoffmann (1942) was confronted with the same problem in lowland Chiapas, Mexico, and concluded that *R. lebeau* and *R. aroma* were sympatric and different. As these two different-colored moths did not appear to differ in ecology in my study site, I set out to determine if they were the same species. The inquiry quickly evolved into an exploration of what appears to be an environmentally-controlled color polymorphism, which is of adaptive significance in that the colors track the seasonal shifts in the background against which the moth is cryptic. Here I describe this seasonal and interhabitat color variation and discuss its probable adaptive environmental significance.

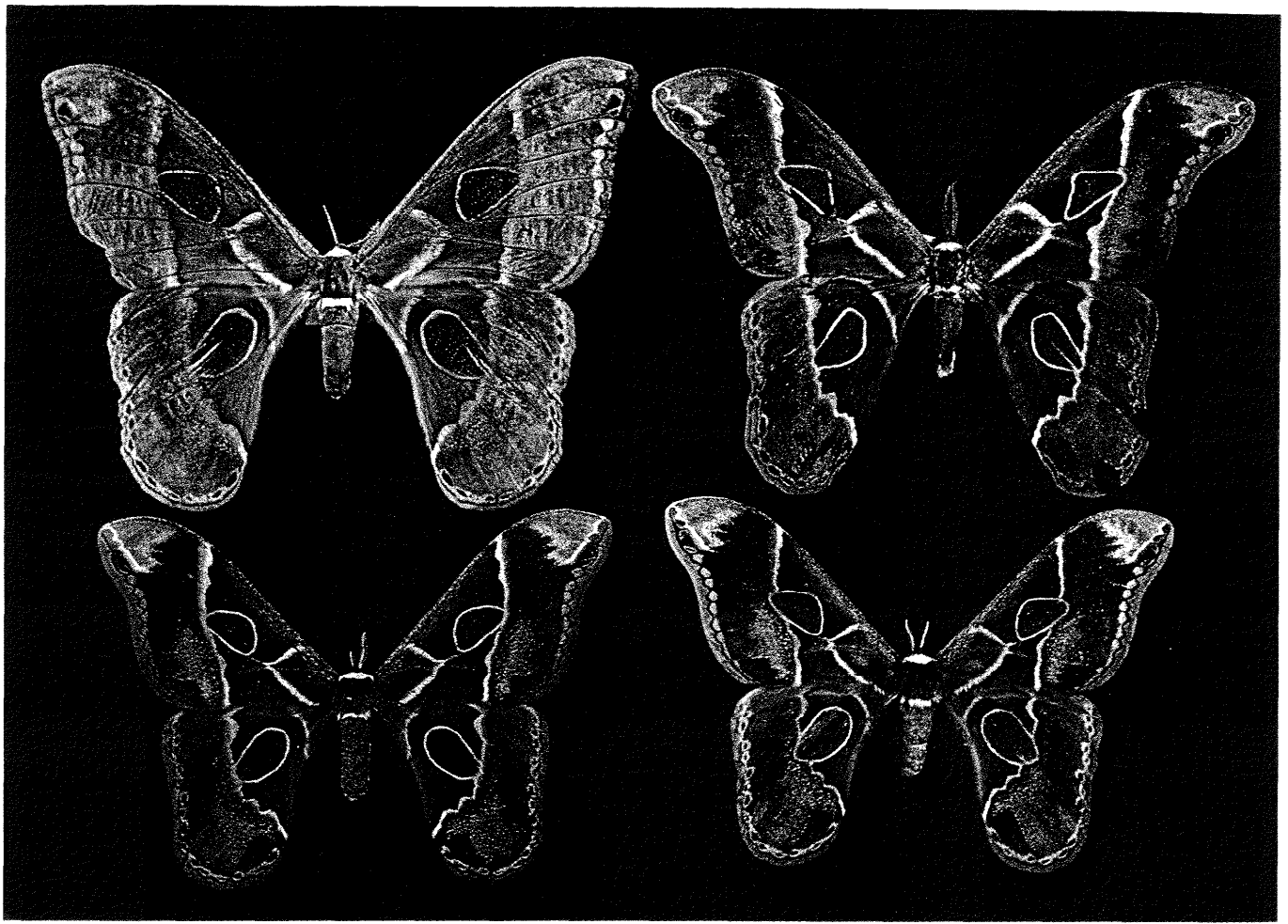
*Rothschildia lebeau* occurs from the wettest to driest lowland (0-1,200 m) forests of Costa Rica, but here I only report on that portion of the population in the deciduous and evergreen "dry" forests (and their secondary succession) of Santa Rosa National Park (Boza and Mendoza 1981, Hartshorn 1983). The 10,500-ha Park lies at 0-350 m elevation and between the Pan-American Highway and the Pacific Ocean, 25 km south of the town of La Cruz, Guanacaste Province, in northwestern Costa Rica (Fig. 2). Approximately 1 to 2 m of rain fall at this site during a 6 to 7 month rainy season (May-November) and the remaining months are windy, sunny, and largely rainfree. In the middle of the rainy season (late July-early August) there is a short and variably intense dry season (the Costa Rican veranillo). The vegetation is that type which clothed the dry Pacific coastal lowlands of Central America

and much of tropical lowland Mexico before European agriculture. Taxonomic and ecological detail on the 30-species resident saturniid fauna of Santa Rosa National Park can be found in a recent review and field guide (Janzen 1982,1984).

In 1980, I set out to see if I could rear chocolate-colored offspring from a wild-caught bright orange to rust-colored female *R. lebeau* mated with a bright rust-colored *R. lebeau* male. Such a rearing would be primary proof of the synonymy of *R. lebeau* with the various darker but otherwise similar *Rothschildia* at Santa Rosa. A wild-caught female of this color eclosed 6 days before the rains began in May 1980, attracted numerous rust-colored males, and was allowed to mate with the most bright rust-colored individual. The larvae were reared inside a large net strung on branches of *Xanthoxylum setulosum* (Rutaceae), one of four known natural host plants of *R. lebeau* at Santa Rosa (Janzen 1984). From these, 152 living pupae were divided into four groups with equal age distributions and 1:1 sex ratios. Immediately after pupation, the cocoons were hung in four screen cages: one group hung in the forest in deep shade and rain; one group hung in the sun, wind, and rain (dappled shade); one group hung under a porch roof (shade and no rain); and one group hung indoors immediately under a fully insulated translucent roof segment where daytime temperatures reached 30 to 40°C at 1300 h and the daytime air was very dry. The three outdoor groups were subjected to maximum daytime temperatures of 26 to 30°C. Nighttime temperatures were the same for all four groups, from 20 to 23°C. The experiment occurred during the first half of the rainy season; eclosion was completed by 31 August 1980, with more than 90% of the individuals eclosing in the last week of July and the first week of August.

All four sets of cocoons produced chocolate- and rust-colored moths (see the siblings from this experiment in Fig. 1) and also intermediate colors termed 'chocolate-rust' (Table 1). It is clear that the types of *R. aroma* and *R. morana* are nothing more than color morphs of *R. lebeau*, as Lemaire (1978) concluded (and as I concluded after examining the types). The moth recently discussed as *Rothschildia aroma* in El Salvador (Quezada 1967,1973, Quezada et al. 1973) is conspecific with the Santa Rosa *R. lebeau*. The light- to dark-colored *R. lebeau* and *R. aroma* that Hoffmann (1942) worried over from Veracruz to Chiapas, Mexico, were also merely color morphs of a single moth, *R. lebeau*.

However, only 11% of the females and none of the males in the group exposed to extreme heat and dryness were chocolate in color; among their siblings in the outdoors, 40%



**Fig. 1.** *R. lebeau* from Santa Rosa National Park, Costa Rica. (Upper left) Mother of the two sisters below. (Upper right) Father of the two sisters below. (Lower left) Chocolate-colored daughter. (Lower right) Rust-colored daughter.

**Fig. 2.** Santa Rosa National Park, Costa Rica. Photo taken during wet season shows mosaic of habitats.



of the males and 31% of the females were chocolate in color (Table 1). From these results, two quite different questions came to mind: (1) Are the color morphs in *R. lebeau* environmentally induced (and if so, by what cues)? (2) Is this trait explicable in the context of the adaptive significance of the moth's wing color?

In 1982, the experiment was repeated, but the cool and wet contrast with dry and hot was made more extreme by holding one-half of the cocoons in an indoor damp room (average daily maximum temperature of 26.9°C, minimum 22.0°C) and soaking them twice daily with water. Again, the same hot, dry conditions as used in 1980 produced primarily rust-colored moths and the cool wet conditions produced primarily chocolate-colored moths (Table 1). In 1983, half of 66 *R. lebeau* sibling cocoons were placed on Drierite (anhydrous CaSO<sub>4</sub>) and half in wet plastic bags, 2 to 4 days after spinning, and all maintained at a temperature of 20 to 22°C; all individuals eclosed in about 4 weeks (as usual with *R. lebeau*) and were chocolate-colored, while 51 sibling cocoons in moist plastic bags at Santa Rosa ambient tempera-

Table 1. Percentage of *R. lebeau* that were rust-(R), chocolate-rust-(CR), or chocolate-colored (CC) following treatment of the pupae with outdoor rainy season weather or hot and dry conditions (1980), or treatment of the pupae with cool and wet conditions or hot and dry conditions (1982) (see text for details)

1980															
Outdoor rainy season								Hot and dry conditions							
Males				Females				Males				Females			
R	CR	C	n	R	CR	C	n	R	CR	C	n	R	CR	C	n
60	0	40	57	36	33	31	58	100	0	0	19	61	28	11	18

1982															
Cool and wet conditions								Hot and dry conditions							
Males				Females				Males				Females			
R	CR	C	n	R	CR	C	n	R	CR	C	n	R	CR	C	n
22	22	55	22	0	25	75	8	65	29	6	17	44	56	0	9

tures (like those of the three outdoor groups in 1980) produced about one-third each of rust, chocolate-rust-, and chocolate-colored individuals. I conclude that the light color morphs of *R. lebeau* are environmentally induced or cued by high temperature, and that this color change is not influenced by humidity.

What is the pattern of appearance of these colors in nature? The proportions of rust-, chocolate-rust-, and chocolate-colored male *R. lebeau* attracted to several lights placed nightly in the forest at Santa Rosa in 1980, 1982, and 1983 are detailed in Table 2. It is evident that the first moths to eclose, those that appear just before the first heavy rains of the year, are almost invariably rust-colored. Among these individuals there is even an occasional moth that is so light-colored as to be almost orange or yellow (see fig. 1 of Janzen (1982)). As the rainy season progresses, the proportion of dark individuals rises; by the end of the rainy season, chocolate-colored males constitute as much as 75% of the males arriving at lights. However, 1983 had an exceptionally dry beginning to the rainy season and the proportion of rust-colored males remained very high during the early rainy season. Likewise, the mid-rainy season dry weather was exceptionally harsh in 1982 and the proportion of rust-colored males rose; on the other hand, the mid-rainy season dry weather was also harsh in 1983, but the proportion of rust-colored males did not rise.

At Santa Rosa, dry weather means hot days. For example, the 24 days before the first substantial rain in 1980 (on 24 May) had a mean maximum of 33.6°C (range, 30-36°C) while the 26 days following (25 May to 19 June) had a mean maximum of 30.2°C (range, 27-32°C). September 1980 was even cooler, with a mean maximum of 29.7°C (range, 26-32°C). In addition, not only do the prerains dry days have greater maximum temperatures, but objects such as cocoons have a higher chance of direct insolation because of the nearly leafless forest canopy (*R. lebeau* cocoons occur suspended from twigs 0.4-2.0 m above the ground). Of equal importance, the absence of shading leaves and cooling moist soil results in the intra-forest air-mass heating up faster, longer, and hotter during the day than it does in the rainy season under a shady canopy and over moist soil.

All of the *R. lebeau* that eclose before the rainy season begins and during the 2 to 3 weeks immediately thereafter

(Table 2, first two rows under each year) are from cocoons that were spun at the end of the previous rainy season and contained pupae that remained dormant during the 4-5 months of rain-free dry season. These pupae experienced in common the long dry season, but apparently differed in moisture microenvironment or in susceptibility to moisture cues. It is not the case that some are simultaneously programmed to eclose early and produce rust-colored wings and others to eclose late and produce chocolate-colored wings. When dormant cocoons were placed in hot (insolated), but moist plastic bags during the last month of the dry season (1981 and 1982;  $n = 103$ ), all the adults eclosed rust-colored (or lighter) within a month; alternatively, when their siblings were placed in cool, wet bags in the same calendar days, 50 to 90% of the individuals eclosed with chocolate-colored wings (1981 and 1982;  $n = 61$ ).

Dry weather at Santa Rosa means not only hotter days but also light background colors in the forest. Dry, dead leaves and tree bark are generally yellow, beige, rust, light gray, and other light pastel earthtones. Additionally, with maximum penetration of the sun into the forest understory, shadows are at their lightest. During rainy weather, dead leaf and bark surfaces darken with moisture and mold, the canopy is fully leafy and casts deep shade, and the sun rarely penetrates enough to render a large area of understory light-colored. It is against these backgrounds that a *R. lebeau* hangs suspended from twigs and branches during daylight hours, 'fervently wishing' to be overlooked by birds and monkeys. Male and female *R. lebeau* are highly edible to at least five species of birds and six species of mammals at Santa Rosa, and were rejected by no vertebrate to which one was offered. It is normal for 20 to 50% of the male *R. lebeau* attracted to virgin females to have bird beak marks on their wings. Predation by vertebrates is undoubtedly one of the major causes of the short lives of *R. lebeau* adults (1-10 days).

I interpret the seasonal color polymorphism of *R. lebeau* as an adaptation that renders the moth a better match with the different backgrounds against which it hides in dry and wet weather, than would be the case were it monomorphic. It is significant in this context that all *R. lebeau* I have encountered in the evergreen rainforested parts of Costa Rica are chocolate to dark chocolate-rust in color (46 at six sites).

In addition to matching wing colors seasonally with ambient colors, *R. lebeau* has a number of other wing traits that can be interpreted in the context of predator avoidance. The clear "windows" in the wings are unambiguously holes in the rotten leaf. The lightly crenulated surfaces of the wing membranes between the veins (exceptionally visible in the living *R. lebeau* female pictured on the cover of Janzen (1983)) are those of a drying and wrinkled leaf. The pale brown margins of the wings are not only fungal-attacked and torn-leaf margins, but even have a black fungal hypha or rhizomorph meandering along them. The prominent white lines on the central wing areas well represent the pale linear discolorations found on drying dead leaves attacked by fungi. The wings are held open in a semispreading position when at rest (again, as exemplified by the living undisturbed female on the cover of Janzen (1983)). When a resting *R. lebeau* is approached or lightly touched, it often slightly moves its wings up and down within the plane of the wings in the resting position. This movement mimics a leaf gently disturbed by the wind or by bumping a branch. It appears to be directly analogous to the gentle swaying or slow shaking behavior of a lightly disturbed phasmid walking stick (*R. S. Peigler*, personal communication).

The natural population of *R. lebeau* at Santa Rosa is usually made up of a mix of color morphs, except in the most extremely hot and dry weather before the rains begin (Table 1). This heterogeneity may be generated in part by the microclimatic heterogeneity that is experienced by the pupal population. However, it is also possible that there has been selection for variability of response to moderate mesic weather. This might occur through the adaptive significance of the moth not looking like its conspecifics if it is likely to eclose during a population peak that is sufficiently high to create species-specific directed searching by its predators (e.g., see Janzen (1984) for a discussion of this point with respect to Santa Rosa saturniids in general). *R. lebeau* commonly produces such peaks in adult density at Santa Rosa. It is relevant that the portion of the population lacking dark morphs, that portion which emerges before the rainy season, is generally of the lowest density of the year.

Owing to contour, soil type, disturbance history, and proximity to nearby volcanic foothills, Santa Rosa has a number of habitat types that each cover hundreds of hectares. The males of *R. lebeau* in these different habitats can differ in their proportions of color morphs, as indicated by males captured at traps baited with virgin females (Table 3). The traps were 2.4 to 8.1 km apart and interchange among traps ranged from 1 to 10% of the captures. The differences in proportions among habitats are as would be predicted from the seasonal differences. For example, as mentioned earlier, only about half the normal amount of rain fell during the first half of the 1983 rainy season (June-July). Site S is the habitat with the densest, darkest rainy season forest of those censused; its *R. lebeau* males were about twice as chocolate-colored and half as rust-colored as in the three other, more open habitats censused during 8 to 23 July 1983. However, as the abnormal 1983 rainy season progressed without getting wetter and the mid-rainy season small dry season become ever more intense, the proportion of site S males that were rust-colored increased to match that of two other Park habitats in late July and August (about 40%). At the same time, the proportion of rust-colored males substantially decreased at site C on the eastern boundary of the Park; this site is so close to the more rainy volcanic foothills 10 km to the east of the Park that it

Table 2. Percentage of *R. lebeau* males that were rust-, chocolate-rust-, or chocolate-colored among those to arrive at lights placed in the forest at Santa Rosa in the 1980, 1982, and 1983 rainy seasons

	1980			
	Rust	Chocolate-rust	Chocolate	n
Before rains: 6-24 May	74	24	2	46
After rains, parent generation: 25 May-19 June	46	17	37	54
Middle rainy season, first generation: 2 July-20 Aug.	31	29	41	108
Last half rainy season, second generation: 24 Aug.-28 Dec.	20	32	48	95
1982				
Before rains: 20-25 May	100	0	0	20
After rains, parent generation: 28 May-7 June	35	15	50	20
Middle rainy season, first generation: 6 July-26 Aug.	50	21	29	58
Last half rainy season, second generation: 20 Sept.-21 Oct. <sup>a</sup>	11	22	66	187 <sup>a</sup>
1983				
Before rains: 8-30 May	100	0	0	10
After rains, parent generation: 1-29 June	72	13	16	32
Middle rainy season, first generation: 6 July-14 Aug.	29	12	59	49
Last half rainy season, second generation: 21 Aug.-7 Dec.	16	10	75	219

<sup>a</sup> Based on males attracted to virgin females placed less than 1 km from the light site.

Table 3. Percentage of *R. lebeau* males that were rust-, chocolate-rust-, or chocolate-colored among those to arrive at traps baited with virgin female *R. lebeau* at 4 sites in Santa Rosa in 1983

Date	Site	Chocolate-			n
		Rust	Rust	Chocolate	
8-23 July	1	19	25	56	59
	2	50	16	34	82
	3	57	17	26	86
	4	44	21	31	105
25-31 July	1	37	26	38	104
	1-22 Aug.				
9 Sept.-27 Oct.	1	44	21	35	68
	2	43	13	45	40
	3	28	30	42	57
	4	44	25	31	32
9 Sept.-27 Oct.	1	12	12	77	323
	2	10	18	72	285
	3	7	14	79	170
	4	16	14	70	297

often rains only there in dry weather. When the second half of the rainy season came on strong (rainy and cool during 64% of the days in September and October), the proportion of rust-colored individuals fell to 7 to 16% at all sites (Table 3).

These results suggest that the *R. lebeau* population at Santa Rosa may be thought of as a multicolored sheet with its greatest color heterogeneity during dry portions of the rainy season, and greatest homogeneity just before the rains start and during the peak of the rains. The moth is seasonally tracking the background for its crypticity, just as do northern vertebrates that become white in the winter. It appears to be using an environmental cue for this tracking, just as occurs with other seasonally variable Lepidoptera (e.g., Riley 1980, Hoegh-Guldberg and Hansen 1977, Peigler 1976).

The degree to which the species can be expected to have such a polymorphism over its entire range (south Texas to tropical South America, Lemaire (1978)) will depend on the annual omnipresence and color contrast among the various seasons in which the adults are present, coupled with the predator regime to which the adults are subjected. The same color morphs common at Santa Rosa are present in the *R. lebeau* population described by Hoffmann (1942) for lowland Veracruz, Mexico, an area with a seasonal climate much like that of Santa Rosa. My dark morph is his *R. lebeau* form *lebeau* and his *R. lebeau* form *benjamini* is my rust-colored morph. Likewise, when Benjamin (1934) described *R. lebeau* in south Texas portion as *Rothschildia forbesi* (cf. Lemaire 1978, p. 14), he noted that "The new species occurs in two color phases, a dark form and a light form. These forms may represent only dimorphism or possibly represent local "wet" and "dry" forms depending upon whether the individuals bred in the humid bottoms which were once river courses or in the semi-desert areas." Cocoons from south Texas collected during winter (presumably cool) conditions produce entirely chocolate-colored morphs when the moths eclose in the spring (R. S. Peigler, personal communication).

At Santa Rosa, *R. lebeau* is not unique among saturniids in such seasonal color change; it is also displayed by *Othorene purpurascens*, *O. verana* and *Adeloneivaia isara* (Janzen 1984). And, just as with *R. lebeau*, the two *Othorene* species are found in the Costa Rican rainforest only as dark morphs.

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