

The influence of the 1997-1998 El Niño upon the Galápagos lycosid populations, and a possible role in speciation

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Abstract

El Niño is a worldwide climatological event occurring every 2 to 8.5 years. This event is associated with high sea-surface temperatures across the tropical Pacific and weak or reversing easterly trade winds. The combination of both leads to abnormally strong convective storms in the eastern Pacific and heavy rainfall in western Latin America (especially Ecuador and Peru) and in the Galápagos. The authors had the opportunity to witness the recent 1997-1998 El Niño event during their stay in the Galápagos in March and April 1998. The effect of extremely wet conditions upon the *Hogna albemarlensis* populations of the islands Santa Cruz, Santiago and Volcán Cerro Azul (Island Isabela) were observed.

Hogna albemarlensis, a coastal species, normally lives in saline habitats near lagoons and in permanent wetlands below 600m of altitude. It exhibited an extremely aggressive expansion of its distribution all over the islands and volcanoes, occurring everywhere in very high densities and even outnumbering the highland species *Hogna galapagoensis* which presumably evolved from the founder species *H. albemarlensis*. A situation was created in which both the coastal and the highland species, met each other for a certain period of time. Every El Niño event is followed by a number of extremely dry years (called La Niña) resulting in the drying out of all temporary wetlands produced during the El Niño period and once again restricting the lycosid populations to their former areas. El Niños have certainly played an important role in the speciation of the lycosid species on islands where the coastal species and highland species occur. A hypothesis is proposed.

Key words: Galápagos, Lycosidae, speciation, El Niño

INTRODUCTION

Seven different lycosid species belonging to the genus *Hogna* can be distinguished morphologically in the Galápagos archipelago. Their distributions over the islands have been studied since 1982 and are well known (Baert & Maelfait 1997).

The authors witnessed the 1997-1998 El Niño during their stay on the Galápagos from March-April 1998, the second strongest El Niño of the 20th century. One of the species, *Hogna*

albemarlensis (Banks 1902), normally confined to the coast, showed an extremely aggressive expansion of its distribution throughout the three islands visited (Santa Cruz, Santiago and Volcán Cerro Azul of Isla Isabela).

There have been five strong El Niño events on the Galápagos since 1965: 1975-76, 1982-83, 1986-87, 1992-93 and 1997-98 (Snell & Rea 1999). An El Niño event is a worldwide climatological and oceanographic phenomenon resulting in extreme drought in the western part

Table 1. Catches of two *Hogna* spp. from Isla Santa Cruz. Numbers caught: | or 2: 1 or 2 specimens, +: 3-10 specimens, ++: 10-100 specimens, +++: > 100 specimens. Collectors: P: S. Peck, R: L. Roque, A: S. Abedrabbo. Blank: not sampled that year, * sampled in November and December, ** sampled in November. Grey columns: Years of El Niños. The localities are ordered according to a South-North transect.

Annual rainfall (mm)		640	2769	63.6	277.6	1254	78.5	85.5	503.3	856.3	747	187	1655	1752			
Year		1982	1983	1985	1986	1987	1988	1989	1991	1992	1993	1996	1997	1998	1998	2000	
Collectors				P				P		P, A			R *		**		
	Alt. (m)																
<i>Hogna albertensis</i>																	
Littoral zone: Coastal lagoons	0-1		++		+				+++			+++		+++		+	++
Southern Dry arid zone	2-100		++	0	0			0	1			0		++			+
Southern Transition forest	190		+													+	+
Southern Culture zone	230-500		1		++							++		++			1
Southern <i>Miconia</i> shrub	500				0		+	1				+		1			1
Southern <i>Scalesia</i> forest	570		0	0	2		+	0				+					++
Los Gemelos pampa	570		0		0		++					++		++		+	++
Media Luna pampa	600		0	0	0		0	0	0			0		++			1
Northern Transition forest zone	300-560				0		1		+	++		0					
Northern Dry arid zone	0-300				0		0		0	0		0		1			
<i>Hogna galapagoensis</i>																	
Southern <i>Miconia</i> zone	500-620			++			1	+				+		0			0
Southern <i>Scalesia</i> forest	570		1	++	++		+++	+++				+++					
Los Gemelos pampa	570		++		1		++					++	+++	+			
Pampa zone	600-875		++		++		+++	+++	++			+++		++			+++
Northern <i>Scalesia</i> forest	650							+++									

of the Pacific Ocean and extreme heavy rainfall along the western coast of the American continent, especially in Peru, Ecuador and on the Galápagos islands.

In this paper we evaluate the possible importance that past periods of strong consecutive El Niño events might have had upon the speciation of the lycosid species of the Galápagos.

MATERIAL AND METHODS

An overview of all the sites where *Hogna albertensis* and *Hogna galapagoensis* have been caught or observed by us and other collectors since 1982 on the central island Santa Cruz is given in Table 1. The differentiation in the occurring vegetation zones is after Baert et al. (1991). Most sampling was done during the months of March, April and May. Those made in December and/or November are indicated with an asterisk. The annual rainfall (in mm) given for each year is the rainfall measured at the Charles Darwin Research Station (CDRS), a meteorological station situated on the southern coast of the island. The annual rainfall at Bellavista (at 200 m of altitude) is on average 500

mm higher than on the coast (Snell & Rea 1999). The years characterized as El Niño years are indicated with grey background. A number of sites are sampled by means of pitfall traps each time we visit the islands.

Table 2 and 3 give an overview of the sites where *Hogna* species were caught on Isla Santiago and on the Volcán Cerro Azul (Isla Isabela) respectively. Sampling was with pitfall traps or by hand catches.

RESULTS

Isla Santa Cruz

Distribution of the Hogna species in climatically normal years

In normal, climatically dry years, *Hogna albertensis* is found in all coastal salt marsh habitats around lagoons. It can also be encountered around the unique permanent water pool called 'El Chato', situated along the southern flank of the island in the Transition forest zone at an altitude of 190 m, and also around temporary pools situated at higher altitudes in the small pampa area of Los Gemelos in the *Scalesia* forest zone (Table 1). Here rainfall is more frequent so that the temporary pools do not

Table 2. Catches of two *Hogna* spp. from Volcán Cerro Azul (Isla Isabela). Ha: *Hogna albemarlensis*, Hg: *Hogna galapagoensis*, H1: *Hogna* species 1. Numbers caught cfr. Table 1. n: not present.

Cerro Azul (Isabela)	Alt. (m)	1986	1991	1998
Caleta Iguana	5		Ha(++)	
Caleta Iguana, open	5		Ha(+)	Ha(++)
Western slope	80		Ha(+)	
Western slope	150		Ha(+)	
Western slope	200		Ha(+++)	
Western slope	300		Ha(++)	
Western slope	400		Ha(++)	
Western slope	450	Ha(++)		
Western slope	530			Ha(++)
Western slope, pampa	620		Ha(+)	
Western slope, pampa	680		H1(++)	H1(++),Ha(+)
Western slope, pampa	700	Ha(++)		
Western slope, pampa	760		H1(+);Ha(+)	
Cerro Gavilan	850		H1(+);Ha(+)	
Western slope, pampa	1000		H1(+);Ha(+);Hg(l)	
Western slope, pampa	1100	H1(l);Ha(+),Hg(+)	H1(l);Hg(+)	Ha(++)
Western slope, ferns	1200	Hg(l)	n	
Western slope, xerophytic	1300	Hg(+)	n	
Top, xerophytic	1530	n	n	Ha(++)

stay dry for too long. It is never encountered above the altitude of 600 m (the temperature inversion zone situated not far below this altitude on Santa Cruz makes upward ballooning of lycosid pulli from below impossible, while the broad forest zones between the arid and the pampa zones are surely barriers) nor along the northern side of the island (except around coastal lagoons) where rainfall is extremely low (the upper borders of the vegetation zones reach higher along the northern side of the island. Arid zone: S ca. 100 m, N ca 300 m; Transition zone: S ca. 250 m, N ca. 500 m).

H. galapagoensis is a typical highland pampa species encountered at altitudes above 600 m and becoming more abundant with increasing altitude. It is very rarely found in the lower *Miconia* zone above 500 m. Both species occur in mixed populations at Los Gemelos (570 m altitude).

Situation observed during the 1997-1998 El Niño (March-April 1998)

As a result of frequent rainfall there was an abundance of permanent pools all over the island for the duration of the El Niño. The presence of *H. galapagoensis* could only be confirmed above 800m altitude and at the site of Los Gemelos (see further). *H. albemarlensis* was

found in high numbers up to the pampa zone near Media Luna (600 m altitude) where *H. galapagoensis* seemed to have disappeared (see Table 1). The same occurred at Los Gemelos where normally both species live in a mixed population. *H. galapagoensis* was found in high numbers in November 1997, in March-April 1998 there was a much higher density of *H. albemarlensis* than of *H. galapagoensis* and in November of the same year no more *H. galapagoensis* were found. This situation was unchanged in March-April 2000, while *H. galapagoensis* reappeared at Media Luna. Table 1 shows further that both species were only found along the northern side of the island (between 300 and 500 m altitude) during an El Niño year or in the year just after.

Isla Isabela – Volcán Cerro Azul

Based on observations in 1986 and 1991 (Table 2), *H. albemarlensis* occurs here from the coast up to an elevation of 1100 m (temperature inversion zone). Another *Hogna* species (H1) lives more or less between the elevations of 650 m and 1100 m. A few specimens of *H. galapagoensis* (the species found at the highest elevation of Santa Cruz) have been found between 1000 and 1300 m altitude.

During the 1997-1998 El Niño (March—

Table 3. Catches of two *Hogna* spp. from Isla Santiago, Isla Rabida and Isla Bartolomé. Ha: *Hogna albemarlensis*, Hg: *Hogna galapagoensis*, H6: *Hogna* species 6. Numbers caught: cfr table 1. P: collector S. Peck. n: not present..

	Alt. (m)	1986	1991(P)	1992(P)	1998
Isla Santiago					
Playa Espumila	2	Ha (++)			Ha(++)
Southwestern slope	300		Ha(+)		
Southwestern slope	600		Ha(++)		
Aguacate camp	650		Ha(++)	Ha(+++)	Ha(++)
3 km NE of Aguacate	740		Ha(+++)		
Los Jabboncillos	820				Ha(++)
Top of island	900	H6(+);Ha(+);Hg(+)	Ha(++)		
La Central	700	Ha (++)			Ha(++)
Isla Rabida		n	n	n	Ha(++)
Isla Bartolomé			n	n	Ha(++)

April 1998) *H. albemarlensis* had invaded the whole of the followed trajectory (only a few sites (see Table 2) were really sampled) from coastline up to the volcano rim (1530 m alt.) and occurred everywhere in high densities.

DISCUSSION

Facts

H. albemarlensis is clearly an eurytopic species. Although it lives preferentially in coastal salt marsh habitats, it is able to thrive and build high populations in other wet situations in the vicinity of fresh water pools (occurring temporarily during an El Niño year), as long as these pools subsist. As these pools dry out, their population density diminishes strongly and after a short time they disappear completely. This species displays a quick expansion of its distribution during very wet years. This might explain its wide distribution over most of the islands of the archipelago (Baert & Maelfait 1997).

During the 18 years (between 1982 and 2000) the populations of the coastal *Hogna* species (*albemarlensis*) and the highland *Hogna* species (*galapagoensis*) were monitored on the island of Santa Cruz, two 'very strong' El Niño events occurred, the first was in 1982-83 (December 1982 – July 1983), the second in 1997-98 (November 1997 – May 1998). Quin et al. (1987) stated that 'very strong' El Niño events, as the one in 1982-83, occur on average nearly every 50 years, as the previous event was in 1925-26 and before that in 1891. Enfield (1987) stated that the 1891 event most closely

resembled the 1982-83 event and therefore concluded that 'very strong' El Niños occur on average every 100 years.

It is only within the 1997-98 El Niño event (March 1998) that *H. albemarlensis* was recorded in high numbers in the pampa zone above the *Miconia* border at Media Luna (Table 1), while *H. galapagoensis* seemed to have disappeared from this locality. The situation was still the same two years later (March 2000). Both species can sometimes be found in mixed populations at Los Gemelos (alt. 570 m) (Table 1). During the 1997-98 event *H. galapagoensis* was wiped out of this small pampa area by *H. albemarlensis*. There are two facts that indicate that the 1997-98 El Niño was more prolific for *H. albemarlensis*. The difference between both 'very strong' El Niño events is that the 1982-83 event was extremely wet, but only during a short period of time (from December 1982 till July 1983), while the 1997-98 event (November 1997–May 1998) was preceded by an extremely wet 'dry season' (March – June 1997) having the effect of two consecutive El Niños.

The records made on Volcán Cerro Azul (Table 2) show that *H. albemarlensis* can reach much higher altitudes (up to the summit of the volcano situated at 1530 m, while the top of Santa Cruz is at 875 m altitude) and that this species might have reached the summit pampa zone of Santa Cruz. Unfortunately the summit of Santa Cruz could not be reached in 1998 due to the heavy rainfall. Possibly, it could not reach the summit of the island, as most of the pampa

zone nowadays is converted into a dense *Cinchona* forest, which might have been a limiting barrier for the upward progress of the species.

That the 1997-98 event was favourable to *H. albemarlensis* is corroborated by the high densities this species attained everywhere it was found, as on Isla Santiago (Table 3) and on smaller drier islands as Isla Rabida and Bartolomé where it was never encountered before.

How did *H. albemarlensis* and *H. galapagoensis* speciate?

Hypothesis of speciation

The founder species must have reached the island of Santa Cruz (it may of course have first reached one of the islands situated in the East of Santa Cruz) by way of rafts of flotsam. It is not known when and how many times colonization may have occurred. It colonized the salt marshes along the coast and during wet El Niño years could expand to higher altitudes where permanent fresh water pools were present in rather open habitats. During a period of consecutive 'very strong' El Niños (an interglacial period, see further), it could even bridge the *Scalesia* forest zone and *Miconia* shrub zone, and establish itself in the upper permanent moister pampa zone. A very long period of drought (a glacial period, see further) resulted in the separation of the two populations, one coastal salt marsh population and one highland pampa population. Due to that separation, both populations could evolve during that long period of drought into two different species. By the time a next period of 'very strong' El Niños (interglacial period) occurred, two different species met at the border of their distribution area.

This hypothesis of allopatric speciation based on a climatologically and altitudinal barrier is only plausible if the dry period between both periods of very strong El Niños is very long, i.e. long enough to permit two separated populations to evolve into two different species which only meet after substantial speciation had occurred (Maelfait & Baert 1986). There are paleoclimatological evidences that can sustain this hypothesis.

Evidence corroborating this hypothesis

Cox (1983) has estimated that the earliest Galápagos islands probably emerged 3 to 5 million years ago. Around 3.5 to 3.2 million years ago (Keigwin 1978) the Isthmus of Panama closed resulting in a complete reorganization of the oceanic palaeocirculation (Romine 1985) producing the oceanographic and atmospheric conditions necessary for intense El Niño events (Colgan 1990). Since the closure of the Panamanian seaway and the onset of the glacial cycles, the eastern Pacific has faced two different climatic states: one during glacial periods with cool waters and lowered sea-levels and the other during interglacial periods with higher sea-levels, warmer waters and El Niño events (Colgan 1990). Over the last 700,000 years, there have been seven interglacial periods, and at these times sea-level and climate were similar to those occurring at present, and should have experienced El Niños. At the moment the earth is in an interglacial period and sedimentological evidence from Peruvian coastal plains show that in the last 7,500 years a minimum of 15 'very strong' El Niño events have occurred (Wells 1987). From the early 1500s to 1982-83, 8 'very strong' El Niño events have affected the eastern Pacific (Quinn et al. 1987). The 20th century has experienced 3 'very strong' El Niños, of which two occurred within an interval of 18 years and therefore it seems highly plausible that the Galápagos archipelago could be entering one of the wettest periods in its recent history (Snell & Rea 1999).

There is evidence that during glaciation times, i.e. periods of lowered sea-level, El Niño events were absent (Colgan, 1990). The stratigraphy of El Junco Lake on San Cristóbal Island suggests that rainfall was greatly reduced between 34,000 to 10,000 years ago (Colinvaux 1984). In conclusion, we may say that Galápagos has faced large periods of drought without El Niño events (equal to glacial period) alternating with very wet periods with El Niño events (equal to interglacial period), which supports the possibility of our hypothesis.

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