

Breeding and feeding biology of the Gurney's Hawk *Geranoaetus poecilochrous* in the paramo of Antisana, Ecuador

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RESUMEN.-

La biología reproductiva y aspectos relacionados con el aporte de presas y alimentación durante la crianza de los pollos del Gavilán de Gurney, *Geranoaetus poecilochrous*, fueron estudiados durante 1991 - 1994 y 2007 - 2012 en el páramo del Antisana, Ecuador, a 3800 – 4 000 msnm. De 8 territorios bajo control, 6 (75%) lo constituyeron grupos poliandricos. La nidificación se inicia en casi todos los meses del año, pero el 74% aconteció en los primeros seis meses del año. El intervalo entre nidificaciones consecutivas de las mismas parejas o grupos poliandricos fue de 6 - 11 meses. La presa principal de la dieta de los pichones fueron conejos, *Sylvilagus brasiliensis*. La mayoría de las presas para los pichones la aportaron los machos. Los grupos poliandricos se mantuvieron estables durante los cuatro años de estudio, salvo en un territorio en el que se detectaron 3 hembras diferentes en 14 años. Los machos contribuyeron en la construcción del nido, incubación, vigilancia y en aportar presas al nido. En los grupos poliandricos un único macho copuló con la hembra, los otros machos del grupo actuaron como meros “ayudantes”. De 15 adultos, en cinco territorios, cuatro (26.7%, 3 machos, 1 hembra) fueron de la fase clara y 11 (73.3%, 4 hembras, 7 machos) de la fase oscura. Detalles de cuatro sonidos (llamadas) son presentados. Los machos ayudantes presentan plumaje subterminal con la parte dorsal rojizo quizás por su condición de subordinados al macho alpha.

PALABRAS CLAVES: Antisana, biología reproductiva, *Geranoaetus poecilochrous*, páramo, poliandria

ABSTRACT.-

The breeding and feeding of the Gurney's Hawk *Geranoaetus poecilochrous* was studied from 1991-1994 and with further detail from 2007-2012 in the paramo of Antisana, Ecuador, at 3800 - 4400 m altitude. Of a total of 8 territories at Antisana, 6 (75%) were polyandrous groups and 2 monogamous pairs. Breeding occurred in most months of the year, but 74% of the 27 clutches registered were found in the first six months of the year. Breeding periods of the same pairs or groups had intervals of 6-11 months. The main prey was rabbits (*Sylvilagus brasiliensis*). Males brought most food to the young. Polyandrous groups remained stable over the four years of study but in one territory there were three different females over a period of 14 years. Males contributed in nest building, incubation and bringing prey to the young. Only one male was observed copulating with a female, the other males in the group were “helpers at the nest”. Of the 15 adults, in five territories, four (26.7%, 3 males, 1 female) were white bellied (light morph), and 11 (73.3%, 4 females, 7 males) were dark-bellied birds (dark morph). Details of four different calls are presented.

KEY WORDS: Antisana, breeding biology, *Geranoaetus poecilochrous*, paramo, polyandry

INTRODUCTION

Little is known on the breeding biology of the Gurney's Hawk *Geranoaetus poecilochrous*. De Macedo 1964 reports on the nesting on top of the bromeliad *Puya raimondii* in the altiplano of Peru. Lehmann 1945, who seemed to have been the first to publish on the ecology of Gurney's Hawk, apparently confused *Buteo poecilochrous* with *Buteo albicaudatus* (Cabot *et al.* 2006), so clarifying also the comments of del Hoyo 1998: "Somewhat confusing situation in Colombia, where species suspected to be migrant, because no breeding reported, but populations in Bolivia and Peru reported to be resident all year around, leaving source of any migrants to Colombia as a mystery". The distribution pattern of this hawk in Colombia and Ecuador is detailed in Cabot *et al.* 2010. In northernmost Chile pellets and prey remains correspond to insects and small rodents, but studies on breeding biology are lacking (Jaksic *et al.*, 1991; Jimenez & Jaksic 1990). Recently, Cabot *et al.* 2010 have given details on the presence of the Gurney's Hawk in Chile, in the precordilleran plateau of the Atacama desert, at 2000 m altitude. Cabot, 1991 mentioned for Bolivia "in the geographic zones where *Buteo polyosoma* and *B. poecilochrous* coincide, they tend to be segregated" [and] "on the altiplano *B. polyosoma* is a solitaire winter resident and is found on flat areas. *Buteo poecilochrous* is a permanent resident, often in pairs and generally associated with rocky hills and mountains with cliffs".

We follow Amaral *et al.* 2010, using the generic name *Geranoaetus*, but when citing previous authors we continue to refer to *Buteo*.

Here we report on the feeding and breeding of the Gurney's Hawk in the paramo of Mount Antisana. With Juan Black we noticed for the first time polyandrous groups in two different territories, but no detailed observations were made at that time on the participation of the extra males (Solís & Black, 1985).

Study area.-

Antisana is a snow-capped mountain in the eastern cordillera of the Ecuadorian Andes. The

study area was located west of this mountain at an elevation of 3.800-4.400 m, in a grass paramo with bushy areas of *Loricaria*, *Chuquiraga*, *Diplostephium* as well as trees of *Gynoxis* and patches of *Polylepis* (Muñoz *et al.*, 1985; Black 1982). It is an undulated landscape with gullies, lava flows of historic times, with rocky outcrops for roosting and nesting. Free roaming cattle and sheep grazed the area. Annual rainfall is about 700 mm with precipitation being highest between February – June and October – November, and lowest between July – September. Mid-day air temperatures range from 8° C -14° C, night temperatures are -1° C in July – August. The weather from October until January is considered mild (normally not so windy). March until June is a rainy period, whereas July - September is known for its snowfall (Black 1982).

Other birds of prey in the area are the common Carunculated Caracara (*Phalacrocorax carunculatus*) and less frequently the Grey Eagle-buzzard (*Geranoaetus melanoleucus*), the Cinereus Harrier (*Circus cinereus*), the Aplomado Falcon (*Falco femoralis*), the Kestrel (*Falco sparverius*) and the owls, Great Horned Owl (*Bubo virginianus*), Short-eared Owl (*Asio flammeus*) and Barn Owl (*Tyto alba*); Condors (*Vultur gryphus*) can be seen daily (de Vries *et al.* 1983).

MATERIALS AND METHODS

For our fieldwork we were allowed to use the facilities of the headquarters of EMAP-Q (Empresa Agua Potable Quito) at 4 000 m during 1991-1994, close to the lake Micacocha. Nearby campsites were also established. Nests were observed from hide-watches located some 40 - 50 m away. Birds were observed from vantage-points with binoculars Zeiss 10x42 and Nikon 8x40, as well as a telescope Bush 20-60x. Studies of Solís and Black 1985 and Coello 1997 were undertaken close to Micacocha (La Mica) and the western flank of Mount Antisana, whereas Alarcón 2012 also concentrated his observations at the territory of La Mica, but extending the study area, including the territory at La Virgen (Figures 1, 2 and 3). Data on

biomass were based on Solís and Black 1985 and Coello 1997: rabbit 425 g, rodent 30 g, bird 390 g, fish 250 g, not identified 30 g.

Sound recordings were made with a Marantz PMD671 recorder and a directional microphone (Sennheiser ME-80).

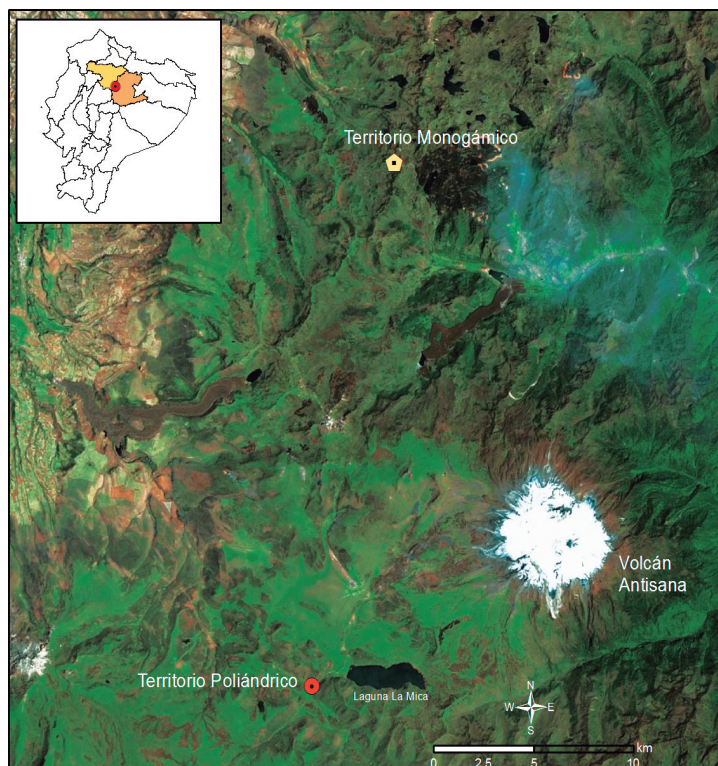


Figure 1. Territories of Micacocha (La Mica, Desaguadero) and La Virgen, around Mountain Antisana.

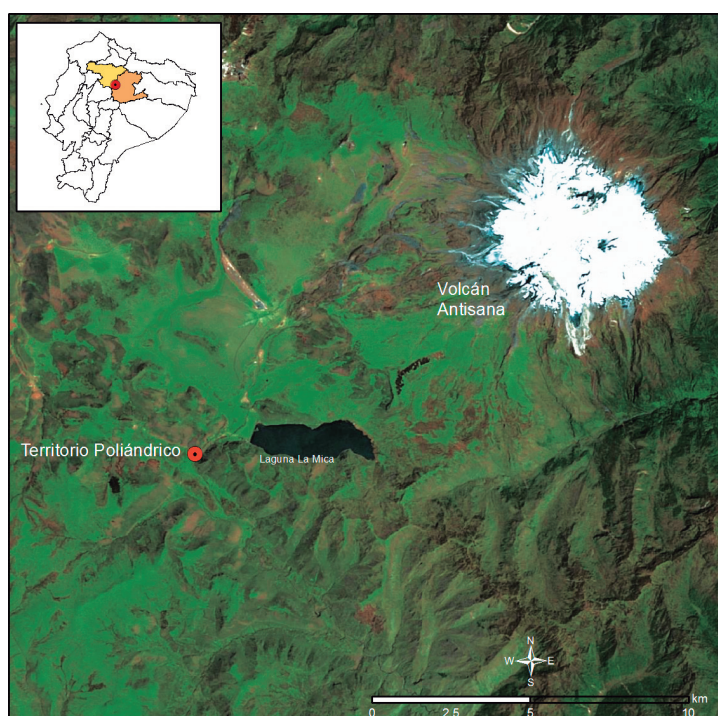


Figure 2. Territory La Mica, with the lagoon of Micacocha and the snow-capped Mountain of Antisana.

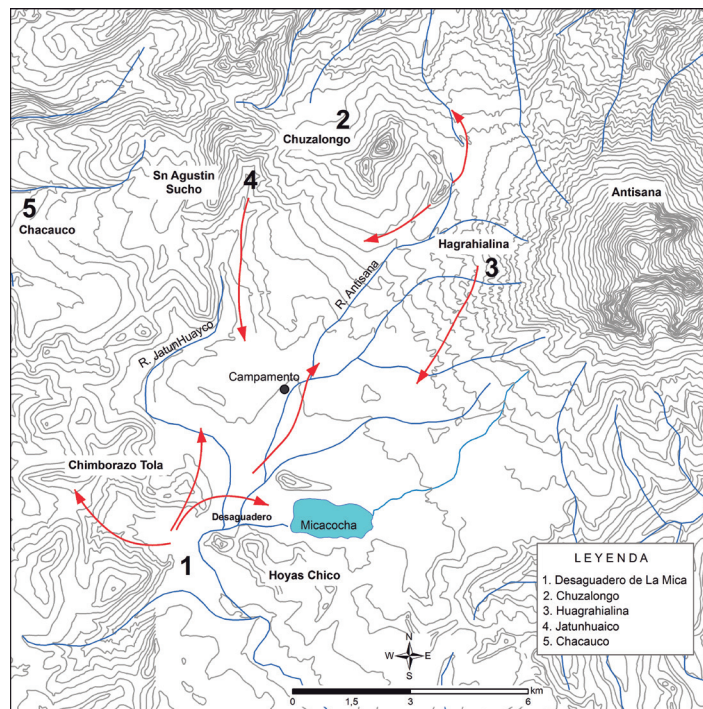


Figure 3. Territories with fly ways at western flank of Antisana.

RESULTS

Group size.-

Of a total of eight territories at Antisana, six were polyandrous groups. Three groups were observed with detail to detect composition as to morph, age and sex:

Desaguadero: a female in dark morph pre-definitive plumage; two males in dark morph pre-definitive plumage with reddish dorsal patch; and one male in light morph pre-definitive plumage.

Saraguasi: a female in dark morph definitive plumage (over six years old; according to Cabot and de Vries 2009); two males in dark morph pre-definitive plumage with reddish dorsal patch; and one male in light morph pre-definitive plumage.

Chuzalongo: a female in dark morph definitive plumage (over six years old), one male in dark morph definitive plumage; and one male in light morph definitive plumage.

A pair at Jatunhaicu was composed of a female in dark morph pre-definitive plumage and a male in dark morph definitive plumage.

Changes over time (1980-1994) were observed at Desaguadero (La Mica):

1980: female in dark morph definitive plumage (over six years old), male in dark morph pre-definitive plumage, male in dark morph definitive plumage; 1987: female in light morph definitive plumage, male in light morph pre-definitive plumage, and male in dark morph definitive plumage; and from 1991-1994: female in dark morph pre-definitive plumage, male in light morph pre-definitive plumage, and two males in dark morph definitive plumage (the different plumages are complex and related to dark or light morph, age and sex, reaching the definitive plumage when six years old; Cabot and de Vries 2009, 7 color plates with 44 photos of the different plumages; Cabot and de Vries 2010, 4 color plates with 40 photos). Some males may have been the same over more than 10 years, but 3 different females were present in 1980, 1987 and the years 1991-1994. The pair at

La Virgen appeared to remain stable over the years 2007 till 2012 as did the polyandrous group at La Mica in those years.

Breeding.-

Breeding occurred in most months of the year, but 20 of the 27 clutches were found in the first six months with peaks in March (7 clutches) and June (5 clutches). Nesting in the same territory (and assumed to be the same birds) for Sarahuasi initiated in 5 different months with intervals of 6-11 months (May and December 1991, June 1992, March 1993 and February 1993); for Desaguadero breeding occurred with intervals of 8-10 months (September 1991, June 1992, February and December 1993), whereas

for Jatunhuaycu the time was more regular (June 1991, March 1992 unsuccessful, June 1992, March 1993 unsuccessful, June 1993, and February 1994.

During the years 2007-2010 in Desaguadero breeding started in November 2007, November 2008 and October 2009 with an adult female (dark phase, over five years old), an adult male (dark phase) and a second male (light phase), as well as the presence of one juvenile of 2006 and one of 2005. Over the years 2007, 2008 and 2009, every year one juvenile was produced with the same female and the two males. Details of well-known breeding seasons are presented in Figure 4.

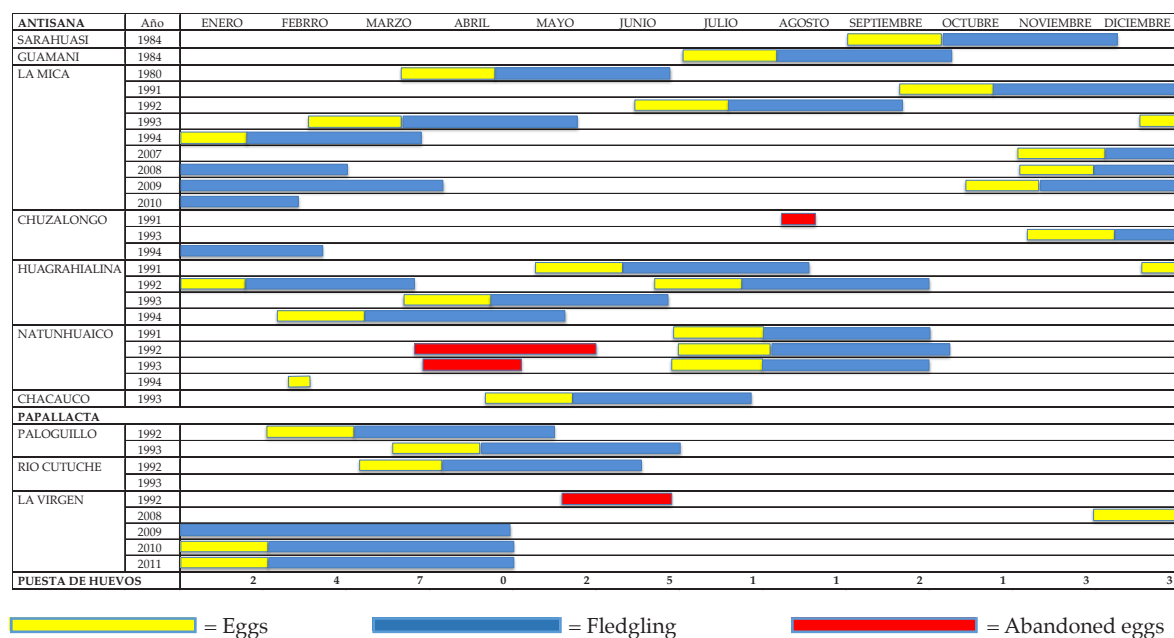


Figure 4. Breeding seasons.

During the breeding period there exists tolerance as well as aggression. An Andean Condor chased a juvenile hawk which had left the nest (Desaguadero) some 14 days earlier, but a male straight away flew to its rescue and on its turn chased the condor, which slowly glided away (23-2-1992). The same juvenile was seen again in the territory, begging for food (1-9-1992), eight months after fledging. On 3-9-1992 the female took prey from the nest (which at the time had an almost fledged young) and flew to the begging juvenile which took the prey

immediately. Again, at 13-9-1992 this juvenile flew towards the female and took prey from its talons. When the sole chick from the nest fledged (22-9-1992) both juveniles could be seen sitting together being fed. This is the first time we have seen juveniles from different breeding periods together, both being fed. At 12-1-1993, a year after fledging, this juvenile was still fed in the territory. But in other occasions, parents from Jatunhuaycu drove the juveniles away, actually attacking and chasing in the air, after six months of leaving the nest.

Nest-building and copulation.-

All 25 nests were found on rocky outcrops, 1.50-40 m above the ground, often difficult to reach. The nest was over one meter wide with an inner cup of 40 x 34 cm and 7 cm deep (n=3), made of twigs and branches of common bushes as *Chuquiraga*, *Gynoxis*, *Diplostephium*, and *Valeriana*, with dry grass and mosses for lining.

Copulations were observed, occasionally without any ceremony. We observed the female sitting in a small bush close to the nest and the male arriving and mounting immediately, lasting some 15 seconds, after which the male flew off; in this case after 35 minutes the male returned and again copulation occurred. We have no observations on multiple copulations in polyandrous groups, but two males and the female called and circled around for about 20 minutes after which the female landed in a bush and one of the males landed immediately on the female's back, copulating for 15 seconds. Seven minutes later the same male copulated again (pers. com. S. Struve). In other occasions birds may circle around with ascending and descending flights, sometimes forming an 8 in the air, the male closely following the female, and as she lands the male descends besides her and copulation follows. Copulations were observed during the whole breeding season (with eggs and young in the nest). During the courtship the male brings prey to the female. Only one male of the polyandrous group at la Mica during all three seasons (2007-2010) copulated with the female.

Incubation.-

Little information on egg-size exists. Our data of 62.2 x 47.5 (ranges 60.4-64.0 x 45.6-49.0; n=6) concur with the size 61.9 x 47.0 (n=2) given by Solís & Black, 1985.

Most incubating in the monogamous pair was undertaken by the female (84.1%; 74 hrs of observation), whereas in a polyandrous group the female brooded 38.6% of the time, and the three males, 39.1, 22.3 and 0.0 percent, respectively (17 hrs of observation). The female of the pair did 12.2% nest guarding (the male 87.8%), whereas the polyandrous female guarded 22.4% and the three males 77.6% (15.0, 9.9, and 52.7%, respectively) (details in Coello 1997).

Alarcón 2012 analyzed the activity with more detail, distinguishing six different activities: nest care, hunting, territory defense, nest guarding (vigilance), feeding and activity not known. The monogamous pair shows clearly that in all three seasons the female does most of the incubation, whereas the male does most of the hunting. Unknown activity is far more performed by the male and it refers to being away from the observation spot, close to the nest where the female almost always could be seen. The polyandrous group shows that both males incubate, but still the female takes most of the share. Both males hunt and do most of the defense of the territory and both males help in feeding the chick. The second male is more time away from the nest, out of sight (unknown activity).

Prey brought to the nest.-

Prey brought to the nest of a monogamous pair at Jatunhaico during 51 hours of observation (8 days, September 1991) amounted to 15 prey items, including rabbits, rodents and birds (Table 1) with a total of 2 785 g of biomass, 76.3% was rabbit, all brought by the female.

Table 1. Prey brought to the nest at Jatunhuaico during 51 hours (September 1991).

PREY	FEMALE		MALE		TOTAL	
	N	% Biomass	N	% Biomass	N	% Biomass
<i>Sylvilagus brasiliensis</i>	5	76.30	0		5	76.30
<i>Thomasomys</i>	0		4	4.30	4	4.30
Aves	0		1	14.00	1	14.00
<i>Salmo sp.</i>	0		0		0	
Not identified	0		5	5.40	5	5.40
TOTAL PREY	5.00		10.00		15.00	
PREY/HOUR	0.09		0.20		0.29	
BIOMASS (g)	2125.00		660.00		2785.00	
% BIOMASS	76.30		23.70		100	

At Huagrahialina during 60 hours of observation (8 days, September 1992), a polyandrous group consisting of a female with three males brought 21 prey items, with rabbits and rodents hunted by

all four adults; interestingly, the female brought also fish (trout). Here the female contributed with 29% of the biomass, the rest was brought by the three males; total biomass was 3 405 g (Table 2).

Table 2. Prey brought to the nest at Huagrahialina during 60 hours (September 1992).

PREY	FEMALE		MALE 1		MALE 2		MALE 3		TOTAL	
	N	% Biomass	N	% Biomass	N	% Biomass	N	% Biomass	N	% Biomass
<i>S. brasiliensis</i>	1	12.50	1	12.50	2	25.00	1	12.50	5	62.40
<i>Thomasomys</i>	1	0.90	2	1.80	3	2.60	5	4.40	11	9.70
Aves	0		1	11.50			0		1	11.50
<i>Salmo sp.</i>	2	11.50	0				0		2	14.70
Not identified	1	0.90	0		1	0.90	0		2	1.80
TOTAL PREY	5.00		4.00		6.00		6.00		21.00	
PREY/HOUR	0.08		0.07		0.01		0.01		0.35	
BIOMASS (g)	985.00		875.00		970.00		575.00		3405.00	
% BIOMASS	28.92		25.69		28.49		16.89		100.00	

At La Mica, also a polyandrous group with three males, one male did not bring food but rather took prey remains from the nest; however, this male later contributed with prey when the

young fledged. The other two males brought one rodent and 11 rabbits (the female contributed with six rabbits) and therefore males contributed with most of the biomass (65.5%; Table 3).

Table 3. Prey brought to the nest of Desaguadero (La Mica) during 77 hours (September 1992).

PREY	FEMALE		MALE 1		MALE 2		MALE 3		TOTAL	
	N	% Biomass	N	% Biomass	N	% Biomass	N	% Biomass	N	% Biomass
<i>S. brasiliensis</i>	6	33	4	22	7	38.50	0		17	93.40
<i>Thomasomys</i>	0		0		1	0.40	0		1	0.40
Aves	0		0		0		0		0	
<i>Salmo sp.</i>	0		0		0		0		0	
Not identified	4	1.60	5	1.90	7	2.70	0		16	6.20
TOTAL PREY	10.00		9.00		15.00		0		34.00	
PREY/HOUR	0.13		0.12		0.19				0.44	
BIOMASS (g)	2670.00		1850.00		3215.00		0		7735.00	
% BIOMASS	34.50		23.90		41.60				100.00	

The three territories combined indicate that most of the prey was brought by the males (50 of a total of 70), also in biomass the seven males contributed with 61% (versus 39% of the three females; total biomass 14 805 g; Coello 1997). Rabbits formed 83.25% of the biomass, the rest were rodents (*Thomasomys* and/or *Akodon*), birds (snipe, *Gallinago*) and fish (trout, *Salmo*).

Prey brought to chicks at the nest and preys brought to fledged juveniles (at the nest or at roosts nearby) were not different; in both cases rabbits formed the main prey. The frequency of

prey (numbers per hour) decreased however, 0.44 to 0.22, 0.35 to 0.26, and 0.29 to 0.15, respectively, for the 3 territories (Coello 1997). No clear differentiation in prey specialization, either for sex or between the males, was noted in any site.

The data obtained by Alarcón (2012) almost two decades later at La Mica, with a polyandrous group of two males at that time showed a biomass of rabbits of 94.3%. Over the three seasons studied, the female brought 11 of the 36 rabbits and contrasted with hunting only one of the 14 rodents (Table 4).

Table 4. Prey brought to the nest during 3 breeding seasons at La Mica.

PREY	MALE 1			MALE 2			FEMALE			Total prey	Total biomass	Total biomass %
	2007-2008	2008-2009	2009-2010	2007-2008	2008-2009	2009-2010	2007-2008	2008-2009	2009-2010			
<i>S. brasiliensis</i>	7	6	5	2	3	2	4	3	4	36	15300	94.30
Rodents	3	2	2	4	1	1	1	0	0	14	420	2.60
Not identified	2	3	2	3	2	1	1	1	2	17	510	3.10
TOTAL	12	11	9	9	6	4	6	4	6	67		

At La Virgen, the monogamous pair, over the three seasons (2009-2011) was almost only living of rabbits (98.2% of biomass). The female brought 10 of the 55 rabbits and four of the six rodents (Table 5).

Table 5. Prey brought to the nest during 3 breeding seasons at La Virgen.

PREY	MALE			FEMALE			Total prey	Total biomass	Total biomass %
	2009	2010	2011	2009	2010	2011			
<i>S. brasiliensis</i>	12	12	17	4	5	5	55	23375	98.20
Rodents	0	2	0	2	1	1	6	180	2.60
Not identified	2	1	2	1	1	1	8	240	1.00
TOTAL	14	15	19	7	7	7	69		

For all groups and years the grand total of prey brought to the nest is: 118 rabbits, 36 rodents, two birds, two fish and 48 unidentified items.

Reproductive costs.-

Calculated over the same period (12 hrs), polyandrous groups brought more prey biomass compared to the monogamous pair. The group with most prey (Desaguadero) raised one chick, the others (pair and group) 2 chicks each, so prey biomass does not simply relate to the output of number of chicks.

Several young were weighed when near fledging. A single chick, according to the measurements a female, weighed 1350 g, whereas the monogamous chicks had 850 g (male) and 1000 g (male), and the 2 chicks of the other group, males, 1000 g and 1050 g, at the age of fledging. The last mentioned group reared the following breeding period one female (1500 g) of a clutch of 2, one chick died when 3 weeks old. So it seems that either one female or two males can be reared.

Over four years of study (1991-1994), the monogamous pair produced 3 fledglings (2 clutches of 2 eggs failed, whereas 2 other clutches of both 2 eggs were not followed to the final stage, so this pair could have raised 4 more chicks)

from 11 eggs, while the polyandrous groups combined, on average, raised 4 fledglings (with the rather dispersed figures of 1, 4, and 7, respectively) and so totaled 12 fledglings out of 17 eggs (maximum 21, as in 4 nests eggs could not be seen and counted and may have had not one but two eggs); reproduction success for the monogamous pair was 3/11 or 0.27 (but could have been 7/11 or 0.63), while for polyandrous groups it was 12/17 or 0.70 (but could have been 12/21 or 0.57).

The polyandrous group at La Mica raised over the 3 seasons (2007-2009), every year a chick and juveniles of years before remained around. The monogamous pair at La Virgen raised also one chick every year over the 3 seasons (2009-2011), but in 2011 the juvenile died straight after fledging, falling off the cliff, breaking both legs.

Territory size.-

Territorial boundary disputes were rarely seen, but sometimes alien hawks flew in too close to the range of the nest and were chased off. It seems that groups avoid each other in a flat landscape with natural boundaries of small hills, galleys and rocky outcrops. The areas covered by the different territories fluctuated between some 10-16 km² (Figure 3).

Vocalization.-

Vocalizations in birds of prey are important messages to indicate details on behavior which may be related to the other sex, to individuals of the same species or to other predators.

Details given here on *Geranoaetus poecilochrous* are interesting as a study is underway to compare different calls of this species to its close relative *G. polyosoma*, a species living in the habitat of the bush paramo, below 3000 m and the interandean valley, as well as the subspecies *G. polyosoma peruviansis* from the coastal parts of Ecuador (Peninsula of Santa Elena) and northern Peru (Buitrón *et al.* 2010).

As the vocalizations of Buteo hawks are partly genetically fixed but influenced by differences in habitat, open grass paramo or denser bush paramo or open dry forest calls of similar behavior may be compared between the taxa. Few published data exist on the calls of the Gurney Hawk. Brown and Amadon 1968 mention "it is said to call persistently for up to five minutes at a time", for *Buteo polyosoma* they write "a continous schreeching when its nest is disturbed. A shrill yeak-yeak or kyeah kyeah". Fjeldsa and Krabbe 1990 write under the heading of voice: "a long drawn peeoh ranging from copious cry to thin whistle, hoarse

in juveniles. In display flight harsh hee hee hee" for *Buteo poecilochrous*. And for *B. polyosoma* "sometimes calls when hunting. Loud keow-kyow-kyow noted from pair near nest".

The calls of *G. poecilochrous* can be classified as rhythmic repetitives and simple, with a frequency from 1401 – 6027 kHz (Alarcón 2012). Four different calls can be distinguished, related to the following behaviors:

- Attention or warning call, a rather long "kleeeeeee". Heard when approaching the nest and also uttered by the female in absence of the male (Figure 5).
- Aggression, exciting or attack call, a very rapidly repeated staccato "ke-ke-ke-ke-ke". Heard when intruders approach or enter the territory (Figure 6).
- Begging call or submissive call, a repeated "kee", slower than the aggressive call, used by the female at the nest as well as by juveniles begging and receiving prey (Figure 7).
- Arriving or announcing call, a short "keee" made by the male when he arrives at the nest (Figure 8).

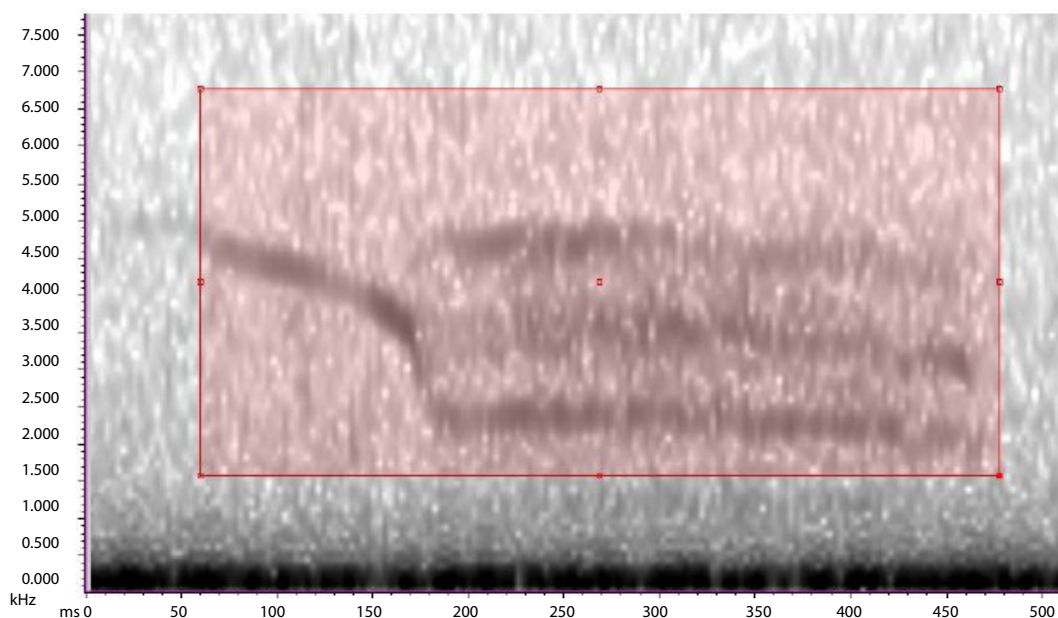


Figure 5. Attention or warning call.

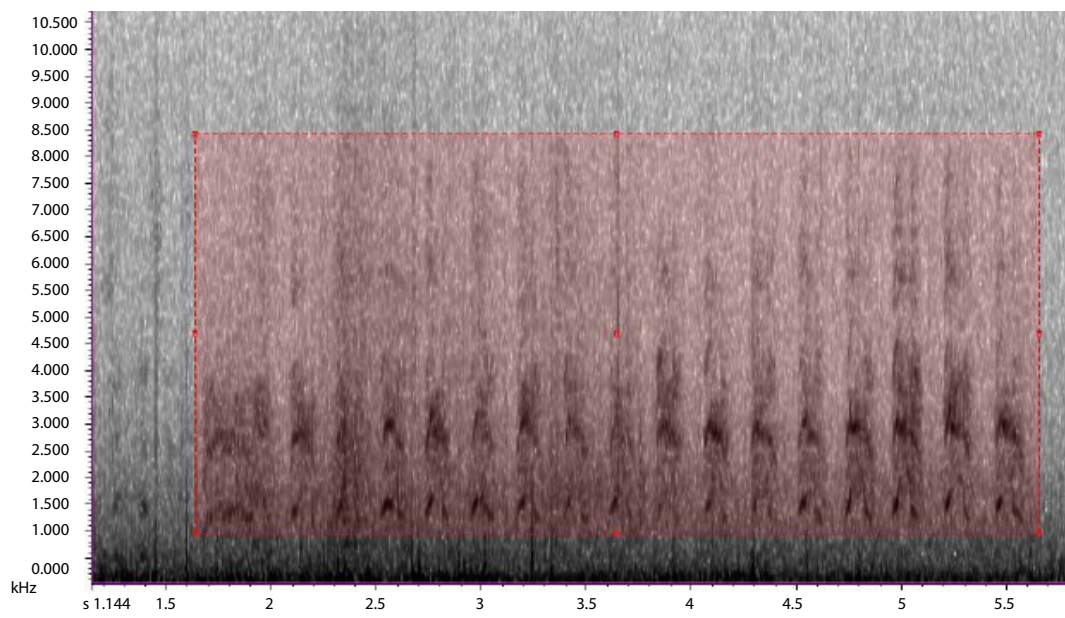


Figure 6. Aggression, exciting or attack call.

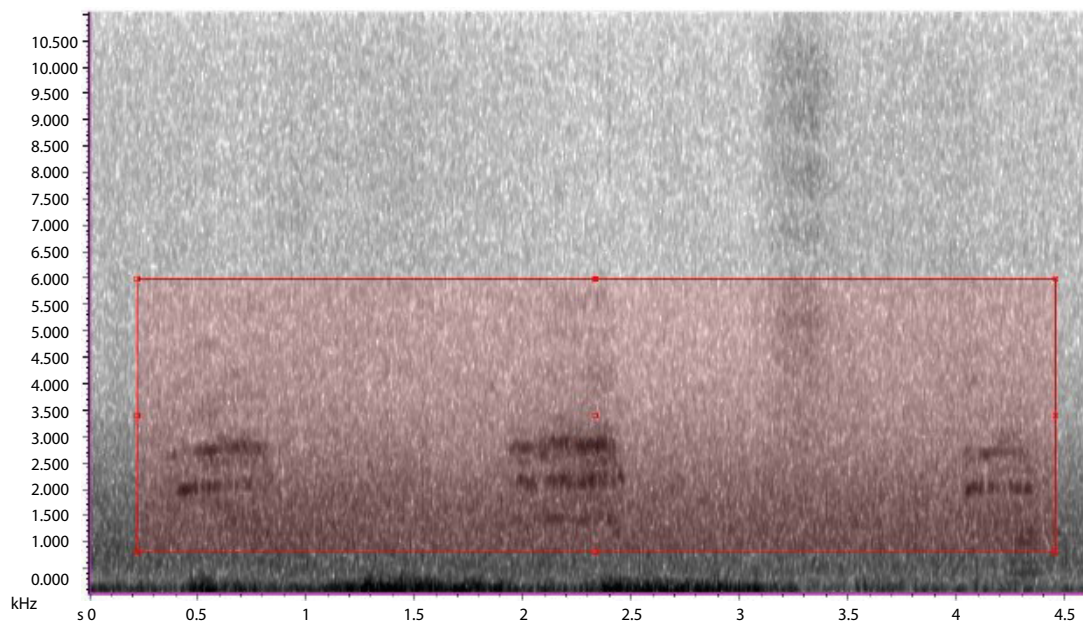


Figure 7. Begging call or submissive call.

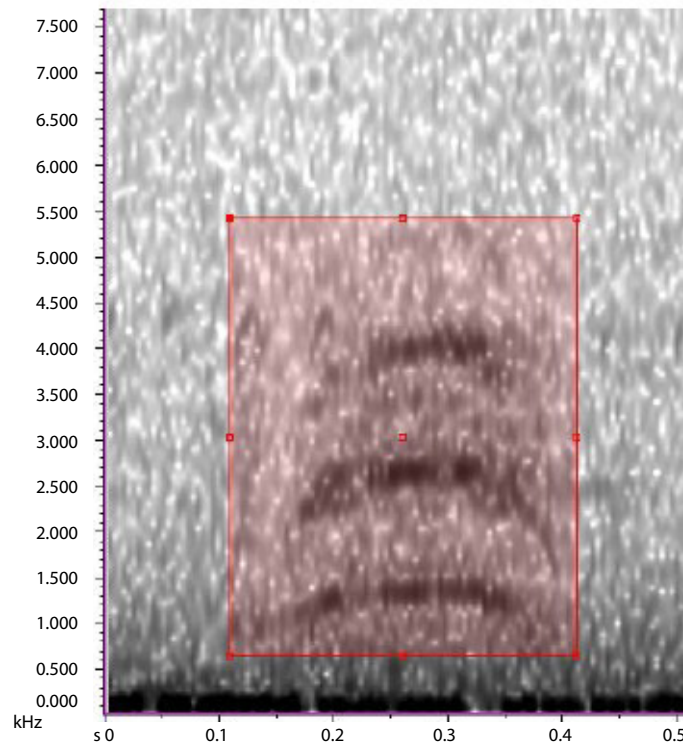


Figure 8. Arriving or announcing call.

DISCUSSION

Lehmann, 1945 confused *Buteo poecilochrous* with *B. albicaudatus* when he published on the ecology of Gurney's Hawk, as was clarified by Cabot, de Vries & Stiles, 2010, at the same time rectifying what Del Hoyo *et al.* 1998 called the "somewhat confusing situation in Colombia".

In northernmost Chile pellets and prey remains collected indicate insects and small mammals (Jaksic *et al.*, 1991; Jiménez and Jaksic 1990). Cabot, de Vries and Alvarado 2010 mention as prey *Fulica* sp, as well as *Rattus norvegicus*, found under the nests in the galley of the river Loa in the Atacama desert in Chile.

Here we demonstrate that in the breeding season at the paramo of Antisana the main prey-item are rabbits, *Sylvilagus brasiliensis*, and rodents (*Thomasomys* and/or *Akodon*) with less than 10% in biomass.

The speciation and the close relationship between *Buteo poecilochrous*, *B. polyosoma*, *B. albicaudatus* and *Geranoaetus melanoleucus* was discussed in

Cabot and de Vries 2010 and in Cabot, de Vries and Márquez 2010.

The presence and maintenance of dark and light phased birds (with the complexity of plumage patterns related to age and sex over a period of six years in *Buteo poecilochrous* and *B. polyosoma* (Cabot and de Vries 2010, 2003), is not easy to explain.

Cabot and de Vries 2010 comment "the coloration differences between sexes and ages in *B. poecilochrous* may be related to the coexistence of several individuals within a restricted area and with high food availability". Male helpers at the nest have pre-definitive plumages with a reddish dorsal patch, which may be related to being submissive to the alpha male. Females of the dark morph may breed in a pre-definitive plumage (with reddish breast band) before they reach their definitive plumage. Breeding in subadult plumage does also occur in the Galapagos Hawk when food and space (empty territories) are available, and when apparently adults are lacking (de Vries 2009).

In skuas also light and dark phases occur and Kjellén 1997 suggests that dark skuas are more efficient kleptoparasites over sea while the light phase is an advantage for hunting over the tundra, with a mosaic pattern of snow-covered areas and open areas with vegetation. At the Andean paramo dark birds may be in an advantage at certain circumstances and under certain climatic conditions with fog and cloudy weather, but light morphs are not at a complete disadvantage with clear skies and snow-covered areas at times of the year. At Antisana, with the majority of dark birds, studies in hunting behavior will have to reveal why such a variety of phases still exists.

Comparison of social groups in Gurney's and Galapagos Hawks.-

Since Brosset (1963) drew attention to the presence of three hawks at a nest-site of the Galapagos Hawk (*Buteo galapagoensis*) polyandry in this species has been studied in further detail (DeLay *et al.* 1996; Faaborg *et al.* 1995; Faaborg *et al.* 1980; Faaborg and Patterson 1980; de Vries, 1976, 1975, 1973). Faaborg and Bednarz 1990 describe the breeding behavior of two species, the Galapagos Hawk and the Harris Hawk (*Parabuteo unicinctus*), comparing the ecological factors affecting the development of group breeding, and they concluded that their social systems are widely divergent in composition, stability and function. Later, other raptors were found to be polyandrous as well and Malan *et al.*, 1997 demonstrate in the Pale Chanting Goshawk (*Melierax canorus*) polyandry to be related to habitat structure, with monogamous pairs being equally successful in other types of habitat. So ecological factors play a definite role.

With Juan Black we noticed for the first time polyandrous groups in *Buteo poecilochrous* at Antisana in two different territories, but no detailed observations were made of the participation of the extra males (Solís and Black 1985). Four territories were observed during 1991-1994, three of which were occupied by polyandrous groups (two three-male groups and one two-male group), the other being a monogamous pair. During the four years of

study the male groups (all in advanced adult plumage, with white tail and a black sub terminal band) remained stable. From 2007 till 2010 the territory at Desaguadero was again observed and over the three breeding seasons a polyandrous group of two males and the female bred every year, and in this territory it was noted that juveniles hang around in the area and are still at times being fed by the adults and so most likely start such a group bond.

In Galapagos, male groups are more numerous. Besides the arid habitat, which is the breeding ground, there is a humid region where non-breeders survive (i.e., large and high islands). So far in the Gurney's Hawk only polyandrous groups have been found at Antisana in Ecuador (i.e. mountains in the tropic) and gregarious males in the Atacama desert in Chile. Breeding of a pair has been reported in el Altiplano in Peru (de Macedo 1964).

What then makes the habitat of the paramo of Antisana different from the rest of the Andes? In Ecuador, it is the most extensive, open, undulated, swampy area, which may make conditions suitable for non-breeding birds to stay and join breeders. Forming part of members of a group within a territory would give better survival possibilities, not only as it provides hunting grounds, but prey not eaten by chicks which remains at the nest is occasionally taken. In other paramos in Ecuador (Chiles, Cayambe, Cotopaxi, Chimborazo) breeding ranges may be smaller and leaving little space for juveniles and non-breeders to be allowed to join. This situation and the possibility of breeding all year around (i.e., tropical conditions, rather than temperate, seasonal) may have led to the social system of breeding in groups and with monogamy also still not completely selected against.

The difference between the social system of the Galapagos Hawk and the Gurney's Hawk is that all males of the Galapagos Hawk copulate with the female and chicks belong to different males. The Gurney's Hawk males and subadults are "helpers at the nest" (just one male six or more years old copulates with the female) and

juveniles of different years remain in the territory and are being fed. Juveniles of the Galapagos Hawk remain up to three months within the territory and are forced out and have to survive in non-territorial areas.

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We dedicate this paper to the memory of Juan Black (1946-1996), ardent naturalist and concerned to conserve Antisana and Galapagos.

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