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THE DISTRIBUTION OF *CERCOPITHECUS (LHOESTI) SOLATUS*, AN ENDEMIC GUENON OF GABON

J.-P. GAUTIER*, F. MOYSAN**, A.T.C. FEISTNER**, J.-N. LOIREAU*, and
R.W. COOPER**

A new guenon, *Cercopithecus (lhoesti) solatus* Harrison 1988, was recently discovered in the tropical rain forest of Gabon. Its colour and coat pattern, its karyotype, and its vocal repertoire (Harrison, 1988 ; Dutrillaux *et al.*, 1988 ; Gautier, 1988a respectively), indicated that it belongs to the *lhoesti* superspecies. However, while it appears to be morphologically intermediate between *C. preussi* and *C. lhoesti* — although possibly closer to *preussi* (Harrison, 1988) — its vocal repertoire shows greater affinities with *lhoesti* (Gautier, 1988a). The three species share the same number of chromosomes ($2n = 60$), but the *solatus* karyotype differs by three chromosomal rearrangements from both *lhoesti* and *preussi*. Their relationships based on morphocline colour patterns are still debated (Harrison, 1988 ; Grubb, 1990), and the relative affinities between the three species remain unclear.

Little information is available on the ecology and behaviour on *C. solatus* : the species is semi-terrestrial and like other semi-terrestrial guenons has a very secretive and cryptic behaviour (Gautier *et al.*, 1986 ; Harrison, 1988).

The approximate distribution of *C. solatus* has been reported to be limited by the Ogooué river to the north and east, and by the Offoué river to the west. Its southern limit was supposed to be associated with the human settlements stretching along the Koulamoutou-Mimongo road (Gautier *et al.*, 1986 ; Harrison, 1988 ; Gautier, 1988b ; Fig. 1).

Following a more detailed study, results presented below describe the present day range of *C. solatus* and its ecological correlates. Present and past factors which could explain the restricted distribution of this species are briefly discussed.

METHODS

The distribution survey was carried out during 38 weeks of field study between 1985 and 1989. It was based on a series of interviews with local hunters, and on information obtained from the villagers where wild-caught living and dead

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monkeys were found. Direct observations were also carried out : however, only 2.5 h of actual contacts with *solatus* were achieved, out of 291 h of searching, due to the discrete nature of the species.

Inquiries were conducted in 102 localities (n° 1 to n° 102 ; Fig. 3) along a linear distance of 1 405 km. Three hundred and thirty people belonging to 21 different tribes were interviewed. Interviews were carried out as follows. The head of each village was asked to inform the best hunters that we were doing a primate survey. No mention of *solatus* was made at this point. Hunters were asked to give vernacular names of all the primates they knew. The reliability of their account was then tested in two ways : first by asking them to name monkeys on colour photographs ; and second by asking them to identify the animals after hearing their species-specific calls (especially those of adult males) imitated by one of us. The latter method proved to be very reliable because hunters regularly use calls to locate monkeys in the forest. Information on the relative abundance of sympatric simian species was also obtained. Scoring ranged from 9 to 7 for abundant species ; 6 to 4 for common species ; 3 to 1 for rare species ; 0 for absent species. A relative rank order was obtained by summing the results from different interviews within the same zone. To test the reliability of such estimates, we compared the relative rank order obtained from hunters with those we obtained by direct observations at one site (Maki, n° 14, Fig. 1) ; results were significantly positively correlated ($r_s = .843$, $n = 9$, $p < .01$). Additional information on habitat preference and vertical distribution of the various species was also requested. This was compared with our own observations and published literature.

All these data were recorded on check-sheets, which specified the grid reference, the name of the village, and the list of people interviewed. The information was analysed by computer. Statistical tests used were t-tests for parametric data and Mann-Whitney and Spearman rank correlation for non-parametric data.

Taking into account the fact that an average hunt lasts one day, and that the mean distance travelled in one day when hunting is about 10 km (round trip), we estimated that hunters had a fairly accurate knowledge of the fauna in a radius of about 5 km. This area was further subdivided into four areas of 25 km² each, corresponding approximately to 100 km² per interview. Ten sectors were defined (S1 to S10 ; Fig. 2) by regrouping the zones where interviews were carried out. Altogether they cover a surface area of between 12 000 and 19 000 km².

RESULTS

I. — GEOGRAPHIC DISTRIBUTION

The exact locations of 9 live wild-caught monkeys and 16 dead specimens are known (Appendix 1). Together with direct observations of wild animals at three sites, they allow us to circumscribe a 5 150 km² area within which the species is probably present (Fig. 1). Interviews were undertaken, concentrating on boundary zones, to more closely define the distributional limits of *C. solatus*.

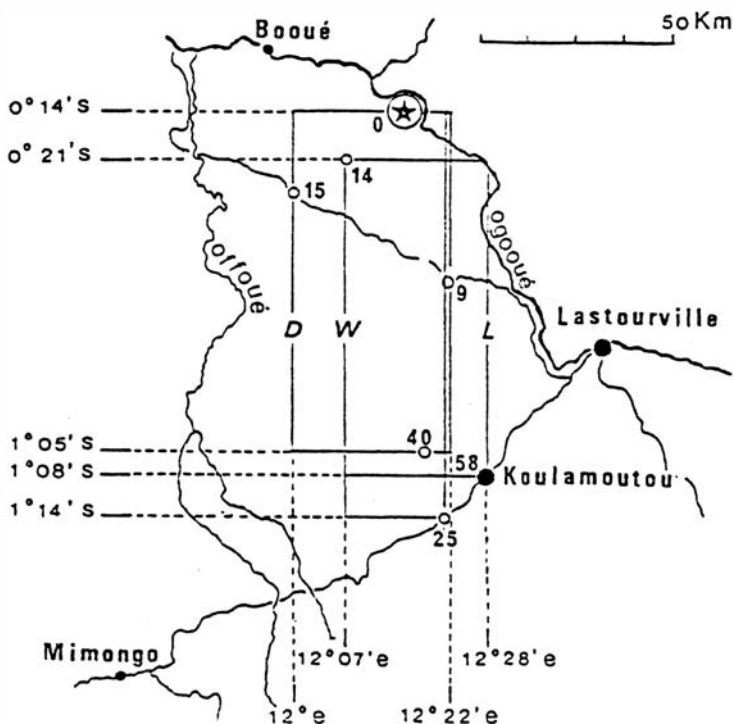


Figure 1. — First approximation of the range of *C. solatus* based on wild caught animals (L), collected dead specimens (D) and direct observations in the wild (W). Figures refer to villages. Star : Location of the first specimen collected.

1) Northern limit : the role of the Ogooué River

On the right bank of the Ogooué river, an area of 875 to 1 000 km² was investigated (northern part of S8, Figs. 2 and 3). Forty five per cent of the 22 people interviewed knew the species ; 91 % reported that it did not occur on the right bank of the river, while 9 % reported that it did so infrequently. Even if *solatus* is occasionally present there, the Ogooué river does probably constitute its northern limit.

2) Western limit : the role of the Offoué River

Investigations were undertaken on both banks of the Offoué river (S2, S3, S7, Figs. 2 and 3). Of the 73 people questionned at 19 locations (an area of about 3 400 km²), 73 % knew the species, and 97 % of them stated that it did not occur on the left bank of the Offoué.

Further north the species seems to live on both banks (S7, n° 79, Fig. 3). However, in the upper course of the Offoué, *solatus* does not even reach the right bank of the river and is not found between this river and the Onoy river. It was

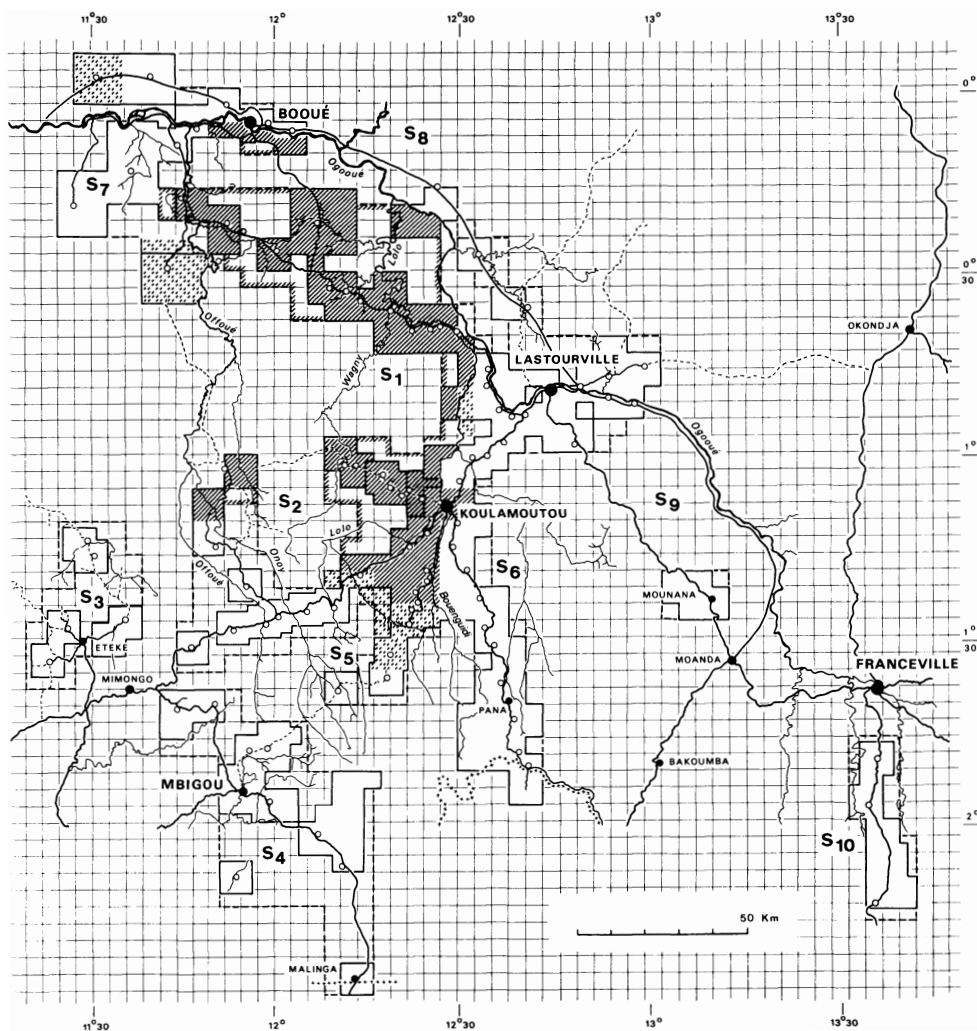


Figure 2. — Map of investigated areas showing where *C. solatus* is missing (white areas), uncertain (hatched interrupted lines), and present (hatched solid lines). Extensive and intensive areas of investigation are respectively surrounded with solid or interrupted lines. Foot tracks : interrupted lines ; roads and rivers : solid lines ; interrupted cross lines : boundary with the Congo Republic.

reported absent from a number of localities (n^{os} 29, 33, 34, 35, 36) including the hilly areas close to Mt Iboundji. Thus, its limit must lie somewhere to the east of the Onoy river.

3) Southern limit

No obvious natural barrier can account for the southern limit of the species : rivers are relatively small and their roughly south-north courses cannot constitute

real obstacles. Inquiries were carried out on both sides of the Mimongo-Koulamoutou road and along trails south of it (S3, S4, S5, S6, Fig. 3 ; an area of about 2 100 km²). On the Mimongo-Malinga road (S4), 76 % of the 25 people interviewed did not know the species. However 24 % stated that it occurred around Koulamoutou (n° 58 ; Fig. 3). Investigations in this area (S5) were carried out at ten sites (an area of about 1 000 km²). All 45 people questioned knew the species and confirmed its presence south of Koulamoutou up to Lètemba (n° 61) in an area of about 500 km². Southwards, as far as Popa (n° 66 ; an area of about 350 km²), its status remains uncertain : 45 % of the 29 people interviewed attested to its presence, but 55 % stated that it was absent. South from Popa to the border with the Congo Republic, the species is absent.

4° Eastern limit

The area around the Bouenguidi, the Lolo, and the Ogooué rivers (between 0° and 2°S) was investigated (about 3 500 km², S2, S6, S8, S10, Fig. 3). On the Koulamoutou-Pana road (S6), all the 25 people questioned confirmed that *solatus* was absent, but 64 % of them knew the species. Familiarity with the existence of *solatus* increased with increasing proximity to Koulamoutou (Fig. 3) ; 56 % of the statements indicated that the species exists only on the left bank of the Bouenguidi river.

All the 29 people interviewed to the east of the Ogooué confirmed that *solatus* does not exist on the right bank of the Ogooué up to Lastourville. Furthermore, it does not occur on the left bank in the Lastourville area. Thirty people were interviewed between Koulamoutou and Lastourville (650 km²). Of the 25 who knew the species, 92 % stated that it was absent from the right bank of the Lolo river in its upper course, up to the village of La Lolo (n° 6, Fig. 3). Downstream from this village, *solatus* is present on both banks of the river as confirmed by the thirteen people interviewed (about 900 km²) and by direct field observations.

From the above results, a map of the distribution of *C. solatus* can be drawn (Fig. 4). This distribution embraces an area of 9 500 to 10 300 km², lying between 0°03' S and 1°35' S, and between 11°41' E and 12°33' E. Its status is unclear in a further area of 700 to 1 100 km². The Ogooué river constitutes the northern limit of the species range ; the eastern limit consists of the Ogooué river, up to the village of La Lolo, the Lolo river up to Koulamoutou, and the Bouenguidi river beyond this town. The Offoué river roughly corresponds to the western limit in the lower part of its course but not higher up where *C. solatus* only occurs east of the right bank of the Onoy. Finally, the present southern limit must lie somewhere around 1°30' S. This distribution area of *C. solatus* is definitely larger than that previously described (Gautier, 1988b).

II. — ECOLOGICAL CORRELATES

1) Habitat characteristics

The distribution area of *C. solatus* is centered on the Forêt des Abeilles, an area of 400 m average altitude (Walter & Barret, 1983) characterized by large hills

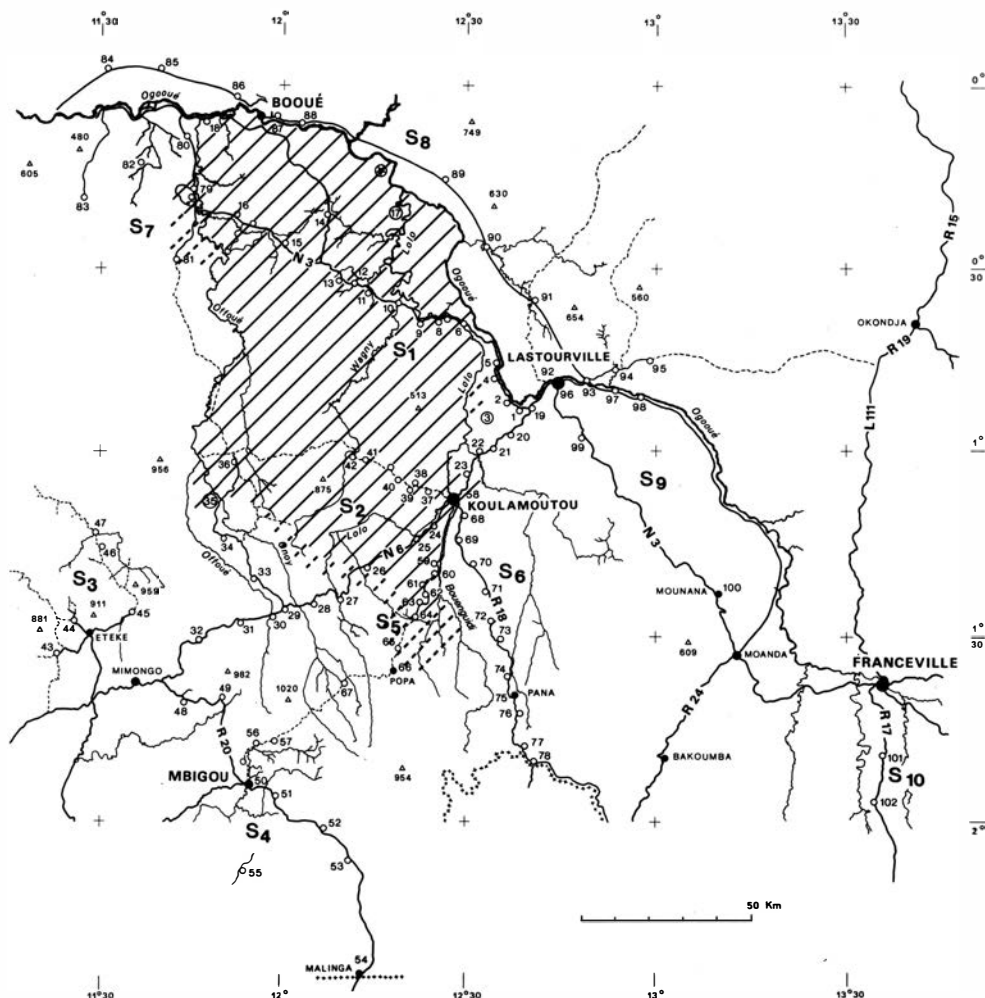


Figure 3. — Present distribution of *C. solatus* (hatched solid lines). Uncertain status of the species is indicated by interrupted lines. Circles indicate towns (black circles) and other localities (white circles) with their reference numbers (1, 2, 3...). S1, S2, etc. : sectors.

intersected by gullies and water courses. The highest elevations in this area are found at Mt Iboundji (980 m, n° 34, 35, Fig. 4) in the south-east, at Mt Petit Maboko (765 m, n° 71), and in the Popa region (from 695 m to 949 m, n°s 63, 66) in the south.

An analysis of the altitudinal range of *C. solatus* shows that the areas in which the species is present are of lower average altitude than those in which it is absent (393 m vs 521 m, $t = -4.25$, $df = 75$, $p = 0.0001$). The irregular limit of *C. solatus* in the south-east and in the south appears to result from the species avoiding highlands, as indicated by 73 % of the interviews of the local hunters.

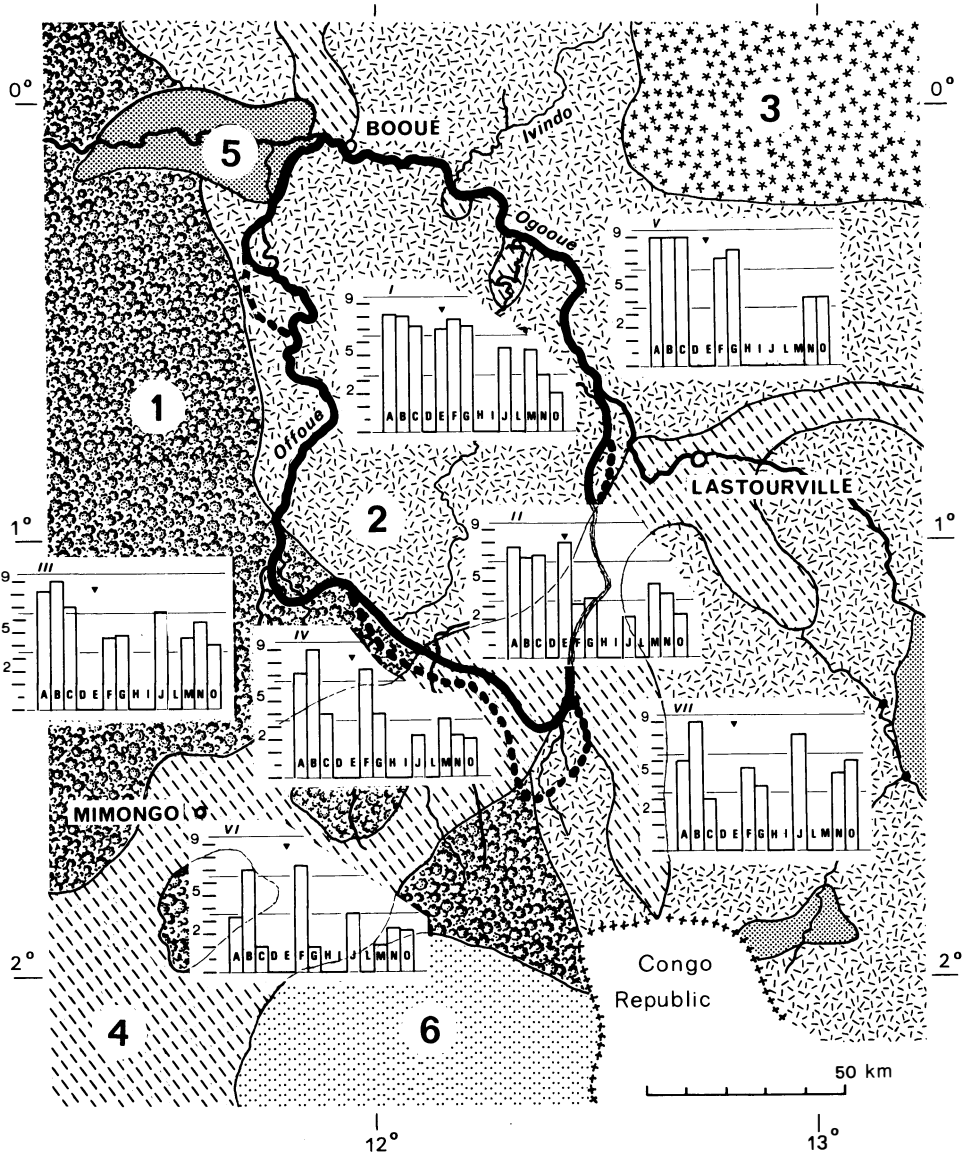


Figure 4. — Distribution area of *C. solatus* (thick solid line) and of forest types (from Caballé, 1978). 1 and 2- tropical rain forests of central Gabon ; 3- tropical rain forests of eastern Gabon ; 4- crops and secondary forests ; 5- woodland savannas ; 6- transition forest. Histograms (I, II, III...) indicate the species composition and the relative abundance of primate assemblages in seven different areas. A : *Cercopithecus nictitans* ; B : *C. cephus* ; C : *C. pogonias* ; D : *C. neglectus* ; E : *C. solatus* ; F : *C. (Miopithecus) talapoin* ; G : *Lophocebus albigena* ; H : *Cercocebus torquatus* ; I : *C. galeritus* ; J : *Mandrillus sphinx* ; L : *Colobus guereza* ; M : *C. satanas* ; N : *Pan troglodytes* ; O : *Gorilla gorilla*. Figures 2, 5, 9 on the ordinate indicate the index of abundance (see text).

As for its preferred forest type, it appears that *C. solatus* mostly occurs within the evergreen forest of central Gabon characterized by the presence of such

species as *Aucoumea klaineana*, *Paraberlinia bifoliolata*, *Scyphocephalum ochocoa*, *Pycnanthus angolensis* and *Pentaclethra eetveldeana*. The disappearance of this forest type could well determine its southwestern distribution limit. Indeed, the border between forest types 1 and 2 (Caballé, 1978 ; Fig. 4) corresponds to the western and south western limit of *solatus*. Moreover, the occurrence of woodland savanna near the confluence of the Offoué and Ogooué rivers seems to coincide with the species northwestern limit. In the south, the evergreen forest is fragmented and separated from a similar forest block by a broad band of degraded forests and crops around the human settlements ; the southern limit of *solatus* is situated in this degraded zone.

2) Community structure

Fourteen species of simian primates occur in Gabon (Harrison, 1988 ; Blom *et al.* in press) : six guenons, three mangabeys ; two colobines ; the mandrill and two apes. Four species assemblages can be recognized on the basis of their species composition within the seven investigated zones (histograms I to VII, Fig. 4), within and around the distribution area of *solatus*. Whatever the assemblage, four species are always absent (*Cercopithecus neglectus*, *Cercocebus torquatus*, *C. galeritus* and *Colobus guereza*) and seven species always present (*C. nictitans*, *C. cephus*, *C. pogonias*, *C. talapoin*, *Lophocebus albigena*, *Pan troglodytes* and *Gorilla gorilla*). The distinction between the species assemblage including *C. solatus* and the assemblages of the surrounding areas depends on three species *C. solatus*, *Colobus satanas*, and *Mandrillus sphinx*. A total of ten species characterizes the *C. solatus* assemblage. In all the surrounding simian communi-

TABLEAU I

Relative abundance of the mandrill, the chimpanzee and the gorilla, within (I, II) and outside (II, IV, V, VI, VII) the C. solatus distribution area

(average rank, standard deviation and range ;
n = number of interviews ; ** p < .005).

Community	<i>C. solatus</i>	<i>M. sphinx</i>	<i>P. troglodytes</i>	<i>G. gorilla</i>
I, II	7.7 ± 2 (4-9 ; n = 7)	3.7 ± 2.4 (1-8 ; n = 9)	3.7 ± 1.8 (1-6 ; n = 10)	2.1 ± 1 (1-4 ; n = 10)
III, IV, VI (n = 24)		3.5 ± 2.8 (0-8)	3.1 ± 2.1 (1-7)	2.5 ± 2.1 (0-7)
VII (n = 8)		7.7 ± 1.5** (5-9)	5.1 ± 2.2 (1-8)	5.7 ± 1** (4-7)
V (n = 7)			4.3 ± 3 (1-8)	4.3 ± 3 (1-8)

ties, fewer species (from 7 to 9) co-occur. This suggests both that *C. solatus* is not replaced by a vicariant species in these communities and that the region where it is found may be a centre of endemism.

The relative abundance of the three other semi-terrestrial primates (the mandrill, the chimpanzee and the gorilla) does not significantly vary between the communities where *C. solatus* is present (I, II Table I) and those where it is absent (III, IV, V, VI ; $p > .05$ for all combinations), with one exception (VII). In this last community, the mandrill and the gorilla are significantly more abundant than in the communities including *C. solatus* (I, II ; $U = 50.5$; $p < .005$ and $U = 55.5$, $p < .005$ respectively). Thus the competitive pressure from sympatric semi-terrestrial primates does not seem to have a major influence on *C. solatus* distribution.

The relative abundance of simian species seems to relate partly to the level of degradation of the habitat (Table II). The role of this factor is obvious for the four

TABLEAU II

Relative abundance of primate species according to the level of forest degradation (average rank, standard deviation and range).

Significant differences are indicated : * $p < .05$, ** $p < .005$, *** $p < .0005$.

Species	Slightly degraded habitats (I, III, V)	Moderately degraded habitats (II)	Heavily degraded habitats (IV, VI, VII)
<i>C. nictitans</i>	8.4 ± 0.6 (7-9 ; n = 16)	7.6 ± 0.5 (7-8 ; n = 5)	$5.2 \pm 3.3^{***}$ (0-8 ; n = 27)
<i>C. cephus</i>	8.5 ± 0.7 (7-9 ; n = 15)	6.8 ± 2.9 (2-9 ; n = 5)	8.0 ± 2.2 (1-9 ; n = 27)
<i>C. pogonias</i>	7.6 ± 1.3 (4-9 ; n = 14)	7.0 ± 1.2 (6-9 ; n = 5)	$2.5 \pm 2.2^{****}$ (0-7 ; n = 27)
<i>C. solatus</i>	7.0 ± 1.4 (6-8 ; n = 2)	8.0 ± 2.2 (4-9 ; n = 5)	
<i>L. albigena</i>	$6.6. \pm 2.1$ (3-9 ; n = 14)	$3.6 \pm 2.1^*$ (1-6 ; n = 5)	$2.7 \pm 2.7^{***}$ (0-7 ; n = 27)
<i>M. sphinx</i>	6.1 ± 1.6 (3-8 ; n = 9)	$2.2 \pm 1.3^{**}$ (1-4 ; n = 5)	4.4 ± 3.2 (0-9 ; n = 27)
<i>C. satanas</i>	5.0 ± 2.2 (2-9 ; n = 10)	4.8 ± 1.1 (3-6 ; n = 5)	$2.2 \pm 2.3^*$ (0-7 ; n = 19)
<i>P. troglodytes</i>	4.5 ± 2.4 (1-8 ; n = 17)	4.0 ± 1.4 (3-6 ; n = 5)	3.2 ± 2.2 (1-8 ; n = 27)
<i>G. gorilla</i>	3.5 ± 2.4 (1-8 ; n = 17)	2.4 ± 1.1 (1-4 ; n = 5)	3.2 ± 2.4 (0-7 ; n = 27)

arboreal species whose abundance regularly decreases with habitat degradations and is significantly lower in highly degraded areas (*C. nictitans* : $U = 502$; $p = .0002$; *C. pogonias* : $U = 471$; $p = .0001$; *L. albigena* : $U = 423.5$; $p = .0004$; *C. satanas* : $U = 209$; $p = .007$). A similar although not significant tendency is shown in other species, except for *C. cephus* and *C. solatus* which remain fairly abundant in secondary forests.

DISCUSSION

Semi-terrestrial forest monkeys such as *C. lhoesti*, *C. neglectus* and *C. hamlyni* present a real challenge to those studying their population densities (e.g. Thomas, 1991) because direct observation of such secretive species along transects is impracticable. The problem is even worse with species such as *C. solatus* or *C. lhoesti* which do not give loud calls which could be used to locate them (Gautier, 1988a). Under these conditions, the only practicable method is to interview local hunters, but this method has its limitations. However, the people who depend on forest resources for their livelihood have a detailed knowledge of the fauna ; if properly carried out, their interviews can provide a source of reliable data. In this study, the maximum and minimum areas of distribution of *C. solatus* differ by only 8 %, a relatively small figure indeed.

C. solatus is an endemic species which occurs exclusively in a specific vegetation type characteristic of evergreen forest in central Gabon, and which clearly avoids high ground. It occupies an ecological niche which does not seem to be filled elsewhere in Gabon since it is the only medium-sized guenon which is semi-terrestrial and inhabits primary rain forest. Other semi-terrestrial species such as *Cercocebus torquatus*, *C. galeritus*, and *Cercopithecus neglectus* are associated with riparian forests (Gautier-Hion & Gautier, 1978) while the other terrestrial primates (the mandrill and the two apes) are much larger in size.

Degraded vegetation does not seem to affect the abundance of *C. solatus*. The species is able to live close to villages and even to raid crops. Thus, although *C. solatus* can be caught in ground snares due to its terrestrial habits (Gautier *et al.*, 1986 ; Harrison, 1988), its cryptic behaviour makes it well-adapted to degraded habitats where the dense undergrowth probably contributes to its protection. This situation is similar to that of *C. cephus*, an arboreal species able to use small supports in secondary growth and to survive near villages. The ability of *C. solatus* to coexist with human population indicates that its restricted distribution and its southern limit of distribution does not result from a drastic reduction of its numbers through human influence.

C. solatus has undoubtedly one of the smallest distribution areas among African monkeys. The range of *C. lhoesti* in eastern Zaire is about 40 times larger (Colyn, 1988). The present distribution area of *C. preussi* is very patchy due to the amount of forest degradation in Cameroun (Oates, 1988 ; Larnoud, 1988) and the species is mainly found today from the north-west flank of Mt Cameroun to the Cross River ; however, *C. preussi* probably ranged in the past from the Sanaga to the Cross river (Booth, 1958), a formerly forested area about four times the size of that of *C. solatus*.

The disjoint distribution of the three « *lhoesti* » species (2 000 km separating *lhoesti* and *preussi*, 600 km *preussi* from *solatus*, and 1 600 km *solatus* from *lhoesti*) was discussed by Harrison (1988). Comparing the distribution of *C. preussi* and

C. lhoesti to those of other closely-related mammals in the highlands of Cameroun and the Kivu highlands in Zaire, Harrison (loc. cit.) referred to the work of Moreau (1966), who hypothesized a northern montane corridor linking eastern and western species during the Pleistocene episodes of forest expansion. This could explain the present distribution of these two monkeys. In the same way a southern dispersal route similar to that suggested for highland forest trees (White, 1981) might explain the present distribution of *C. solatus*.

Such hypotheses are tenable only if the *lhoesti* group species are considered as mountain forms. However, this is clearly not the case for *C. solatus*, which even avoids moderate altitude areas. Although *C. lhoesti* does occur in mountain forests, its range also spreads down from the western Rift to the right bank of the Zaire river and mostly includes lowland forests under 500 m (Colyn, 1988). Furthermore, contrary to what happens in other guenons (such as *C. mitis*, Colyn, 1991), *lhoesti* has not differentiated into sub-species adapted to altitude, and the same form colonizes both lowland and mountain areas. It cannot therefore be considered a true mountain form either.

There are two subspecies of *C. preussi*, *C. p. insularis*, which inhabits mountain areas on Bioko island (Butynski & Koster, unpubl. report), and *C. preussi preussi* which lives in both the lowland forests at Idenau (100-300 m; Gartlan & Struhsaker, 1972) and on the slopes of Mt Cameroon (up to 1 600 m, Eisentraut, 1963). As Oates (1988) pointed out, all the sites where *C. p. preussi* was recorded contained a preponderance of vegetation types other than mountain forest. Thus, there is little evidence that *C. p. preussi* is a mountain form, and its present occurrence in elevated areas could result from the gradual disappearance of lowland forests.

Recently, the importance of the major refuges usually assumed to explain the quaternary history of the biota of Central Africa (i.e. the East Central refuge, close to the Rift mountains, and the West Central refuge, close to Mount Cameroon) has been called into question (Colyn *et al.*, 1991). Instead it has been proposed that a number of primates in Central Africa radiated from lowland forest refuges located in and around the Central Zaire Basin.

Comparing the ranges of arboreal and semi-terrestrial guenon species, Gautier-Hion (1989) showed that the latter generally have more limited distributions and a lower level of speciation and sub-speciation than arboreal forms; furthermore, all occur in the Central Zaire Basin or around its borders. Since these terrestrial forms are now considered as less derived than arboreal ones (Dutrillaux *et al.*, 1988; Ruvolo, 1988), it was suggested that the guenons probably constitute a diphyletic group which exhibited different evolutionary radiations in the two lineages. A review of African forest primates by Grubb (1990) also shows that the species with a restricted distribution are mainly semi-terrestrial. The disjoint and limited distribution of the species of the *lhoesti* group is therefore probably related to differences in evolutionary radiation between the more recent arboreal guenons and the older semi-terrestrial ones. Not being able to establish for the time being the evolutionary relationships between the three *lhoesti* species on the basis of their morphological or genetic characteristics, a plausible scenario for the radiation of this species group cannot be established.

None of the three species of the *lhoesti*'s group has been adequately studied in the wild, and the ecological and behavioural data at hand cannot help to establish their phylogenetic affinities. This means that a long-term study of these

species must be undertaken as soon as possible. Unfortunately time is getting short, as all three are threatened: *C. solatus* and *C. lhoesti* are vulnerable to extinction and *C. preussi* is endangered (Lee *et al.*, 1988).

With its very restricted distribution *C. solatus* is at risk from habitat loss and hunting pressure. Part of the Forêt des Abeilles is already exploited for timber, and logging licenses have been issued for most of *C. solatus* distribution area. Proposals to protect all or a substantial part of the Forêt des Abeilles, by including it in the Lopé Okanda Reserve, have already been formulated (Gautier, 1988b; Wilks, 1990). Only an integrated plan for rational forest utilisation and conservation management in Gabon will guarantee the survival of *C. solatus*.

SUMMARY

This study of the distribution of *C. solatus* was mainly carried out by interviewing 330 local hunters at 102 locations. The species was found to occur in a 9 500-10 300 km² area. Its distribution is limited to the north and east by the Ogooué, Lolo, and Bouenguidi rivers, and to the west by the Offoué river in its lower course. In the southwest, its distribution follows the limit of a specific forest type. The southern limit seems to coincide at least in part with increased elevation. Anthropogenic factors cannot account for such a restricted distribution, as *C. solatus* is also found in the degraded vegetation of the settled areas, where its abundance is apparently similar to that found in the primary lowland forest which covers most of its range. Historical factors which may explain the radiation of the *lhoesti* superspecies are discussed. The status of mountain species commonly attributed to the *lhoesti* group is questioned.

RÉSUMÉ

Cette étude sur la distribution de *C. solatus* repose principalement sur une série d'interviews. L'aire de distribution de cette espèce endémique est particulièrement limitée (variant entre 9 500 et 10 300 km²). Au Nord, à l'Est et au N.-O., l'Ogooué ou ses affluents en constituent les limites. Par contre, au S.-O., *C. solatus* n'atteint pas la rivière mais sa limite suit celle des forêts de plaine qui couvrent l'essentiel de son aire de distribution. Au Sud, l'augmentation de l'altitude rend compte *pro parte* de sa distribution irrégulière. Les facteurs anthropiques ne peuvent rendre compte de l'aire de distribution réduite de *C. solatus*, puisque l'espèce colonise les forêts secondaires dans lesquelles elle atteint une abondance comparable à celle observée en forêt primaire. Les facteurs historiques qui ont été proposés pour expliquer la distribution disjointe des trois espèces de *lhoesti* sont discutés. Le statut d'espèces de montagne qui leur est attribué couramment est notamment débattu.

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APPENDIX I

A: LOCATIONS AND CHARACTERISTICS OF LIVE MONKEYS COLLECTED

Number (Nb) refers to the villages on Fig. 1 & 3

N°	LOCA. & (Nb)	LONGIT., LATITU.	SEX	AGE	WGHT.	COL.DATE	COLLECTOR
1	Maki (14)	12°07'E, 00°21'S	M	Juv	2660	20/12/84	Harrison
2	La Wagny (10)	12°19'E, 00°35'S	F	In2	1460	18/06/85	Moysan
3	La woubou (12)	12°11'E, 00°32'S	M	In1	677	14/06/86	Moysan/Loireau
4	Maki (14)	12°07'E, 00°21'S	F	In2	1830	19/06/86	Moysan/Loireau
5	Maki (14)	12°07'E, 00°21'S	M	Sad	4400	20/05/86	Moysan/Loireau
6	Maki (14)	12°07'E, 00°21'S	F	Juv	2600	11/04/86	Loireau
7	Koulam. (58)	12°28'E, 01°08'S	M	In1	572	18/05/86	Loir./Moys./Feist.
8	La Wagny (10)	12°19'E, 00°35'S	F	In1	650	23/02/89	Gautier
9	Koulamou. (58)	12°28'E, 01°08'S	M	In1	480	04/03/89	Gautier
10	..? ..? ..? ..? ..? ..?	..? ..? ..? ..? ..? ..?	F	In2	1790	17/02/89	Orbell

B: LOCATIONS AND CHARACTERISTICS OF DEAD MONKEYS COLLECTED AND SPECIMENS REFERENCES

BM(NH), British Museum of Natural History (London, U.K.); MNHN, Muséum National d'Histoire Naturelle (Paris, France); STBI, Biological Station of Paimpont (Rennes University, France)

N°	LOCA. & (Nb)	LONGIT., LATITU.	SEX	AGE	WGHT.	COL.DATE	SPECIMENS	COLLEC.REFER.	COLLECTOR
1	Bali riv. (00)	12°15'E, 00°14'S	M	Ad.	-	08/03/84	-	-	Harrison
2	Bali riv. (00)	12°15'E, 00°14'S	M	Ad.	-	30/03/84	Skin	BM(NH) 84.2086	Harrison
3	Mbiga (15)	12°00'E, 00°25'S	F	Ad.	-	23/12/84	Skin & Skull	BM(NH) 85.1148	Harrison
4	Mite.Mik. (09)	12°22'E, 00°38'S	M	Ad.	6675	25/01/86	Skin & Skelet.	BM(NH) 87.19	Gautier
5	Mite.Mik. (09)	12°22'E, 00°38'S	F	Ad.	4225	25/01/86	Skin & Skelet.	BM(NH) 87.20	Gautier
6	Mite.Mik. (09)	12°22'E, 00°38'S	M	Ju.	1730	25/01/86	Skin & Skelet.	BM(NH) 87.21	Gautier
7	La Woubou (12)	12°11'E, 00°32'S	F	Ad.	-	10/03/86	? ? ?	?	Loireau
8	La Woubou (12)	12°11'E, 00°32'S	M	Ad.	8700	02/04/86	? ? ?	?	Loireau
9	La Woubou (12)	12°11'E, 00°32'S	F	Ad.	3500	13/04/86	? ? ?	?	Loireau
10	La Wagny (10)	12°19'E, 00°35'S	F	Ad.	4050	28/02/89	Skin & Skelet.	MNHN 199043	Gautier
11	Mogabo I (41)	12°14'E, 01°01'S	M	Ju.	2800	04/03/89	Skin & Skelet.	MNHN 199045	Gautier
12	Moukoumou (40)	12°19'E, 01°05'S	M	Ad.	5800	06/03/89	Skin & Skelet.	MNHN 199044	Gautier
13	Moukoumou (40)	12°19'E, 01°05'S	M	Ad.	-	06/02/89	Skull	STBI Gab89 07	Gautier
14	La Wagny (10)	12°19'E, 00°35'S	M	Sad.	-	22/02/89	Skull	STBI Gab89 08	Gautier
15	La Wagny (10)	12°19'E, 00°35'S	F	Sad.	-	24/02/89	Skull	STBI Gab89 09	Gautier
16	La Wagny (10)	12°19'E, 00°35'S	M	Sad.	-	24/02/89	Skull	STBI Gab89 10	Gautier