

Biological Patterns in Owl Taxonomy, with emphasis on Bioacoustical Studies on Neotropical Pygmy (*Glaucidium*) and Screech Owls (*Otus*)

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Only a few years ago, leading ornithologists argued that the listing of bird species should be complete. But, a short time after, new species of birds were described, and the descriptions of species new to science still continue. What was the reason for this? Well, up to now taxonomy and systematics of birds were based nearly exclusively on morphology and plumage patterns. I don't want to say that these are not important, but we must keep in mind that many plumage patterns are caused by adaptation to ecological conditions. Therefore some parameters more are wanted to complete the mosaic for a realistic, more biological species concept (E. Mayr 1963; J. Haffer 1974, 1987, 1990), leading to new views in systematics. We all know the phenomenon of convergence, which in many cases has misled taxonomists. A good example of this problem is the New World Vultures, which have been placed in the Falconiformes for a long time. The results of recent studies (König 1982) on morphology and behaviour of that group led to the conclusion that the Cathartidae should be included in the Ciconiiformes, removing them from the Falconiformes. Meanwhile molecularbiological investigations on the DNA have confirmed that the New World Vultures are really storks and not related to birds of prey (Sibley & Ahlquist 1990; Wink pers. comm. 1992).

Biological patterns, such as ecology, bioacoustics, behaviour, and molecular biology may give doubtless very important parameters for a clear and reliable species concept and for a systematic arrangement of bird species as well. Biological patterns are also wanted as measures in owl taxonomy. Nearly all species of that probably polyphyletic order are active at dawn or at night. Most of them show a rather large variability of plumage patterns, so that it is quite difficult to distinguish similar forms according to these patterns. On the other hand many species show different morphs in colouration, being often called "phases", which they are not! A phase is something temporary, while a red morph of an owl will never change into a grey one! The colour-morphs in owls are kept for life.

Because of their nocturnal life, owls can afford variability of plumage patterns in the same species, as well as similarity of plumage in two or more taxa. Therefore it seems that plumage patterns are of less importance for mutual recognition of members of the same taxon than are vocalizations in these nocturnal birds. In addition to this, it is important to know that in owls the whole vocabularies are totally inherited (Scherzinger 1978, 1990; König 1991) and show little geographical variation. Real dialects, as we know in most Passeriformes, don't exist! A few species show a larger individual variation, e.g. *Aegolius funereus* (König 1968, 1969), but the scale of variability is nearly identical in the different populations within the range of their distribution.

Tengmalm's Owls from North America show the same individual variability in song-patterns as do birds from Scandinavia or Germany. Living in a more or less boreal climate, where no competing owl species of about the same size lives in sympatry with it, *Aegolius funereus* can afford individual variation of the song, which species competing with equally-sized specimens of other taxa in tropical or subtropical habitats cannot do. These show very little individual variation of vocal patterns. Knowing this, it may be assumed that vocalizations are obviously the most important mechanisms of isolation between owl species. In our example the Boreal Owl of North America is doubtless conspecific with Tengmalm's Owl of Northern Eurasia. As migratory birds the two populations may have contact with each other across the Bering Strait, as there is a similar situation in some other holarctic species, such as *Asio otus*, *Surnia ulula* and *Strix nebulosa*.

An example for the contrary is the North American Pygmy Owl, known as *Glaucidium gnoma*, which, according to the different patterns of vocalizations, should be split into two species (König 1991): *Glaucidium californicum* (Rocky Mountains, south to Arizona, perhaps northern Mexico) and *Glaucidium gnoma* (Mexico to Panama or even NW South America). While the first seems to be rather closely related to the Eurasian *Glaucidium passerinum*, the latter has to be separated as a different species, because of its totally different voice - in spite of similarity in plumage patterns! I'll come back to that example somewhat later, when I will give some more details stressing my hypothesis on the specific character of vocalizations, based on my own investigations on South American Pygmy and Screech Owls.

Several years ago I began with taxonomical studies on Neotropical *Glaucidium*. Soon I had to realize that polymorphy, individual variation of plumage patterns, and colour-morphs put up enormous difficulties in distinguishing the different taxa. So I began with ecological and bioacoustical studies in the field in South America, in order to find biological patterns as additional help. These investigations are being continued. Beyond that I kept specimens of some species in aviaries for closer observation of their behaviour.

During the research in the field I dropped into a similar problem in Screech Owls (*Otus*), living sympatrically with Pygmy Owls in several regions of tropical and subtropical South America. For the past three years I have been in cooperative contact on these items with J.W. Hardy (Florida Museum of Natural History), J.T. Marshall (National Museum of Natural History, Washington), J. Vielliard (University of Campinas, Brazil), and M. Wink (University of Heidelberg, Germany). With the latter and his staff a close cooperation has begun on the study of blood-samples of owls (PCR, DNA-sequences) in order to get more and very important biological patterns for the taxonomy and systematics of owls. The investigations in the field have been supported by the German Research Council (Deutsche Forschungsgemeinschaft, DFG).

In many owl-lists only three species of *Glaucidium* are mentioned for the whole of South America (e.g. Burton 1973; Eck & Busse 1981): *Glaucidium brasilianum*, *G. jardinii*, and *G. minutissimum*. In 1989 J. Vielliard described a new species of Pygmy Owl: *Glaucidium hardyi*. The plumage patterns of this taxon closely resemble those of *G. minutissimum*, but both species have totally different voices (Figs. 1 and 2). While real *minutissimum* utter a song of equally spaced double-notes, the Amazonian species utters a trill at intervals (Figs. 3 and 4). According to Vielliard's studies *Glaucidium minutissimum* is only distributed in Eastern Brazil, while in the Amazon region it is replaced by the new taxon (Vielliard 1989; König 1991). In this case the question arises whether the Least Pygmy Owls from Mexico to Panama are *minutissimum*, or if they represent a separate species, which might be called *G. griseiceps*. This name has been used in a subspecific sense and is the oldest name attributed to races of *G. minutissimum* (Ridgway 1873; Sharpe 1875). The Central American birds differ vocally from those of Eastern Brazil, but are very similar in plumage patterns. They utter sequences of normally 3-8 equally spaced notes repeated, alternating with a pause of a few seconds (Figure 5). Further studies, which will include molecular biology (PCR, DNA-sequences), will show if these birds are in reality specifically distinct from *minutissimum*.

Revising Andean *Glaucidium* (König 1991), I found four different types of songs of Pygmy Owls living at higher altitudes. The first may be recorded in montane forests from Venezuela to Ecuador, the second, a different one, in also rather moist cloud forests from Peru to Northern Argentina. In montane forests of the Western Cordillera of Colombia you may record yet another song differing from the two mentioned, as consisting of series of double-notes or "couplets", while in dry regions of Western Peru and SW-Ecuador, from sea-level up to about 3500 m, series of

evenly spaced notes given in a very fast sequence (about 7 notes per second) may be heard.

At first one might think of dialects or subspecific patterns. But, comparing ecological facts and studying the distribution of the birds singing in the manner mentioned, you will come to the conclusion: they must be different species! And so it is: The first is *Glaucidium jardiinii*, which has two different types or strophes in its song. The male begins its territorial song with several “stuttering” and irregular, short trills, being then followed by another strophe, an evenly spaced series of rapidly sequenced notes (about 4 per second). (Figs. 6 and 7).

The second taxon utters also two different strophes in its territorial song. It begins in general with 2-3 long (each about 1 - 1 1/2 sec. long), melodious, rather flutelike trills, followed by equally spaced notes in rather slow sequence (1 1/2 - 2 per second). With little individual variation this type of song may be recorded in montane forests on the eastern slope of the Andes from Peru to Tucumán in Argentina (Figs. 8 and 9). This owl apparently is not *jardiinii*, but a new species, to be separated from the latter, which lives north of the Marañón-depression. The new species is *Glaucidium bolivianum*, described in 1991 (König 1991). Also, according to PCR-studies of the DNA, this taxon has to be treated as a valid species, as it is beyond that ecologically, bioacoustically and biometrically distinct from *G. brasilianum*, as well as it is apart from *G. jardiinii* (König 1991). (Figs. 10 and 11).

The third taxon, of Western Colombia, utters long series with double-notes or “couplets”. Like the now separated *G. bolivianum*, this species had been merged with *G. jardiinii*. But comparing song patterns, the similarity with the Central American *G. gnoma* is striking (Figure 12). I am rather sure that these birds belong to *gnoma*, as well as the Pygmy Owls of the mountains of Costa Rica (*costaricanum*) which now should be considered a race of *G. gnoma* and not of *G. jardiinii*, which is distributed in South America only.

The last taxon lives in arid regions, bushy country and rather dry, open forests from sea-level up to about 3500 m on the western slope of the Andes (W-Ecuador to SW-Peru, and probably NW-Chile, north of the Atacama desert), reaching eastwards into the region of the valley of Río Pampas in Central Peru. Specimens of this taxon have been erroneously determined in museum collections as either *Glaucidium brasilianum* or *G. jardiinii*. In reality they represent a new species: *Glaucidium peruanum* (König 1991). The song consists of long sequences of equally spaced notes in very rapid succession (about 6-7 notes per second) (Figure 13). Meanwhile I know by DNA-evidence, studied by M. Wink and his staff, that *peruanum* is apart from both the similar in outward appearance *brasilianum*, as well as *bolivianum*, and has to be treated as a valid species.

Of the West-Colombian taxon we could not yet obtain DNA-material, but we hope to get it quite soon, so that we will be able to prove the affinity with *gnoma*.

The splitting into different species is, of course, not only based on voice and ecological circumstances, but also on biometric characteristics and plumage patterns. But the vocalizations as biological patterns, being apparently the most important mechanisms of isolation between owl species, gave the deciding impetus for intensive research for more parameters. The DNA-evidence is under study, and the first results stress the hypothesis, that vocal evidence is a specific pattern in owls.

As I expressed in the introductory part, *Glaucidium gnoma* should be split into two species. If songs are compared of birds from the Rockies with those of southern Mexico, it will be found that there are enormous differences, while the song of *californicum* (of the Rocky Mountains) shows great affinities with the Eurasian *G. passerinum*. The territorial songs of both are single notes uttered at intervals of several seconds (Figs. 14 and 15). Both species may have allospecific rank within a “superspecies” called *Glaucidium passerinum*. *Glaucidium gnoma*, ranging from Mexico to NW-South America, should be separated specifically from the North American form (*G. californicum*) (Amadon and Bull 1988; Hardy *et al.* 1990; König 1991). Its song consists of sequences of double-notes or “couplets”, sometimes in an irregular rhythm (Figure 12).

Glaucidium brasilianum is a polymorphic species. But the vocalizations show rather few individual variations. So the distribution of this rather common species reaches from Texas to central Argentina and Uruguay. It is widely distributed in tropical and subtropical South America, avoiding higher mountains and montane forests, as well as the dry western slopes of the Peruvian and Ecuadorian Andes, where it is replaced by other taxa. Its song consists of sequences of single notes at medium speed (about 3 notes per second). (Figure 16).

By patterns of the barring in the tail, which is not very variable in the Austral Pygmy Owl

(*Glaucidium nanum*) of Patagonia, this taxon has been separated from *G. brasilianum* by some authors (Figs. 17 and 18). Many gave it subspecific rank; others assumed that it might be only a morph. Comparing the vocalizations and studying its ecology, differences between *brasilianum* and *nanum* are rather clear, so that it seems more appropriate to give *nanum* specific rank, as an allospecies within the superspecies *G. brasilianum*. Its song is similar to that of *brasilianum*, but with a more rapid succession (about 4-5 notes per second) and more “staccato” patterns. In other vocalizations the differences are much clearer, as in the “chirrup” being uttered by both species (Figs. 19 and 20). Now the results of DNA-studies of birds from Santa Cruz in Argentine Patagonia prove the hypothesis of *nanum* being specifically distinct from *brasilianum*.

If we arrange the different taxa of Pygmy Owls according to ecological factors and bioacoustical patterns, it seems appropriate to build up species-groups, maybe sometimes superspecies with allo- or paraspecies. The plumage patterns and morphological facts don't speak against that. So the actual taxonomical situation might appear as follows:

- Group 1: *Glaucidium passerinum* - superspecies, with allospecies *G. passerinum* (Eurasia) and *G. californicum* (Western North America, south to Arizona).
- Group 2: *Glaucidium minutissimum*, *G. griseiceps*, *G. gnoma*. *G. griseiceps* and *minutissimum* might build a superspecies *G. minutissimum*.
- Group 3: *Glaucidium jardinii*, *G. bolivianum*, *G. hardyi*. *G. jardinii* and *G. bolivianum* eventually represent allospecies within the superspecies *G. jardinii*.
- Group 4: *Glaucidium brasilianum*, *G. nanum*, *G. peruanum*. All three species might be allospecies within the superspecies *G. brasilianum*, according to DNA-evidence (König, Heidrich & Wink, in prep.).

Glaucidium siju from Cuba might - according to bioacoustical evidence - perhaps belong to the *passerinum*-group. DNA-evidence is urgently needed.

On the map (Figure 21) the distribution of the Neotropical taxa of *Glaucidium* - according above all to vocal evidence - is indicated.

The situation of the different Neotropical taxa united in the genus *Otus* is even more complicated (Hekstra 1982). So I want to show only one example dealing with four species of southern South America: Morphologically all are very similar, one being slightly larger. All have grey, brown and reddish morphs. Three have yellow, one has mainly brown eyes. In each species males and females utter two different types of songs, which we call “A-song” (territorial song) and “B-song” (songs between mates at close range, maybe sometimes also uttered as response to playback) (Marshall, Behrstock & König 1991).

Otus choliba, the Tropical Screech Owl, has a wide distribution in tropical and subtropical South America. The bird has yellow eyes and a “herring-bone”-like plumage pattern on its underside. The two song-types are much more diagnostic for this species than are plumage patterns. The A-song is a short trill followed by 1-3 loud striking notes. The B-song is a low bubbling, resembling the song of *Aegolius funereus* (Figs. 22 and 23).

The two following species may live sympatrically with *Otus choliba* in certain regions of Southern Brazil, Eastern Paraguay and Northeastern Argentina (Misiones): *Otus atricapillus* is a bird of rather dense rainforest at lower altitudes. It normally has brown eyes, but morphs with yellow eyes occur, and not such a regular, herring-bone-like pattern on the underside. Its two songs are very distinctive. The A-song is a long (8 up to about 20 seconds) rapid trill with normally 14 notes per second. In the B-song a “bouncing-ball” character is diagnostic (rhythm like that of a table-tennis ball dropping onto hard ground). (Figs. 24 and 25). The B-song of the female is similar.

Otus sanctaecatarinae is somewhat larger and stouter than the previous species and has yellow, sometimes hazel-brown eyes. The plumage patterns are similar to *atricapillus*, but the ear-tufts are longer. The bird lives generally at higher altitudes in more open forests, even in groups

of trees within human populations (Belton 1984). The vocalizations are very diagnostic. The A-song is a rather long trill (about 8-10 seconds), while the B-song has a "reverse bouncing-ball" character (the sound-sequence begins rather fast and gets gradually slower towards the end). Female B-song consists of sequences of very harsh, rather barking sounds, differing from vocalizations of female *Otus atricapillus* (Figs. 26 - 28).

Otus hoyi has been recently described as new species (König & Straneck 1989). It has yellow eyes, short ear-tufts and resembles in plumage patterns a small *Otus sanctaecatarinae*. The song is similar to that of *Otus atricapillus*, but the sequence of sounds is slower (about 11 notes per second), and the B-song has no "bouncing-ball" character. Also the B-song of the female is different from both *atricapillus* and *sanctaecatarinae* (Figs. 29 - 32). According to DNA-evidence *Otus hoyi* is not too closely related to *atricapillus*, but it obviously builds a superspecies together with the latter and *sanctaecatarinae*. The bird lives in montane forests on the eastern slope of the Andes of Northern Argentina and Southern Bolivia. Its distribution is separated from the occurrence of *atricapillus* and *sanctaecatarinae* by the thorny Chaco (about 700 - 800 km), in which the only screech owl seems to be *Otus choliba*. At rather close range in Bolivia, but at much lower altitudes, lives another similar species with also yellow eyes and an A-song very similar to *Otus atricapillus*: *Otus guatemalae*, which is distributed from Cochabamba in Bolivia northwards through Peru to Mexico. This species seems to have some relationship with *Otus atricapillus*.

According to our actual knowledge, the taxa *atricapillus*, *guatemalae*, *hoyi*, and *sanctaecatarinae* are best understood as allo-, resp. parasppecies in a superspecies: *Otus atricapillus*, while the similar *Otus choliba* has to be set apart, as being not related to them, as the DNA-evidence shows (Wink, pers. comm.). (Figure 33).

As in *Glaucidium* so in *Otus* too, the different taxa within every presumed species-group may have evolved from a common ancestral species. Populations of the latter probably got separated from each other for thousands of years during the Pleistocene, when the distribution of forests had been changing several times due to climate conditions.

These mentioned species of *Otus* are only one example for the difficulties in distinguishing the different taxa of this difficult genus. It was J.T. Marshall (1967) who first pointed out the high importance of vocalizations for taxonomy in this group of owls. In this sense, and using some more biological patterns, we try to get through the "taxonomic jungle" still existing in some groups of owls. The DNA-studies of M. Wink and P. Heidrich in Heidelberg will be an essential and decisive contribution to the mentioned investigations. So Wink and myself intend to establish a new systematics of the Strigiformes, based on a more biological species concept, in which bioacoustics and molecular biology will play an important role. Regarding the results of the mentioned investigations on Neotropical *Glaucidium* and *Otus*, such a revision seems quite urgent. So it may be mentioned that the genus *Glaucidium* should perhaps be split into the "true" *Glaucidium* and other groups of species, among them above all some African and Asian taxa.

Also the taxonomy of the African *Otus leucotis* should be discussed, for example, as the "subspecies" *granti* has a voice quite different from typical *leucotis*. Maybe there is a similar situation as in Eastern (*Otus asio*) and Western Screech Owl (*O. kennicotti*) in North America. Also *Strix* needs a worldwide revision, as well as the *Tytonidae* and some more.

The taxonomic and systematic studies on owls of the world can only be managed by team-work. Therefore we ask our colleagues for cooperation in order to provide us material from museum specimens preserved in alcohol, of which we only need a small tissue of breast-muscle. Zoological gardens and similar institutions who keep live owls might give an important contribution to scientific research if they could provide us with 2-3 small drops of blood of some species in question. The blood can be taken without harming the birds in any way, and can be preserved in a special buffer. Beyond that we are interested in recordings of owl-vocalizations, especially when the exact determination and locality are known. Also every observation of lesser known owls is of great interest. Taxonomy is no longer "grandfather's zoology" dealing only with series of stuffed museum specimens, but a modern and exciting field of research, not only for science but also for the conservation of species. If we want to protect a certain taxon, we must know its specific taxonomic patterns, in order to study and arrange the ecological requirements as well as the habitat of the doubtless right species we wish to preserve. Therefore taxonomy has to play an important role within the research of the World Working Group on Birds of Prey and Owls. In this field quite a lot will have to be done in the near future.

Figure 1. *Glaucidium minutissimum* from Eastern Brazil. Photo: R. Harling.

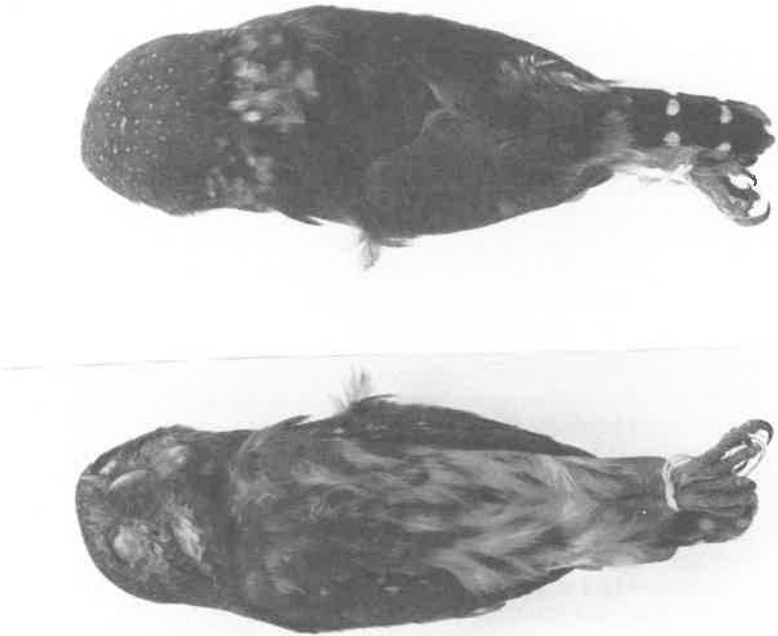


Figure 2. *Glaucidium hardyi* from Eastern Peru. Photo: H. Lumpe.

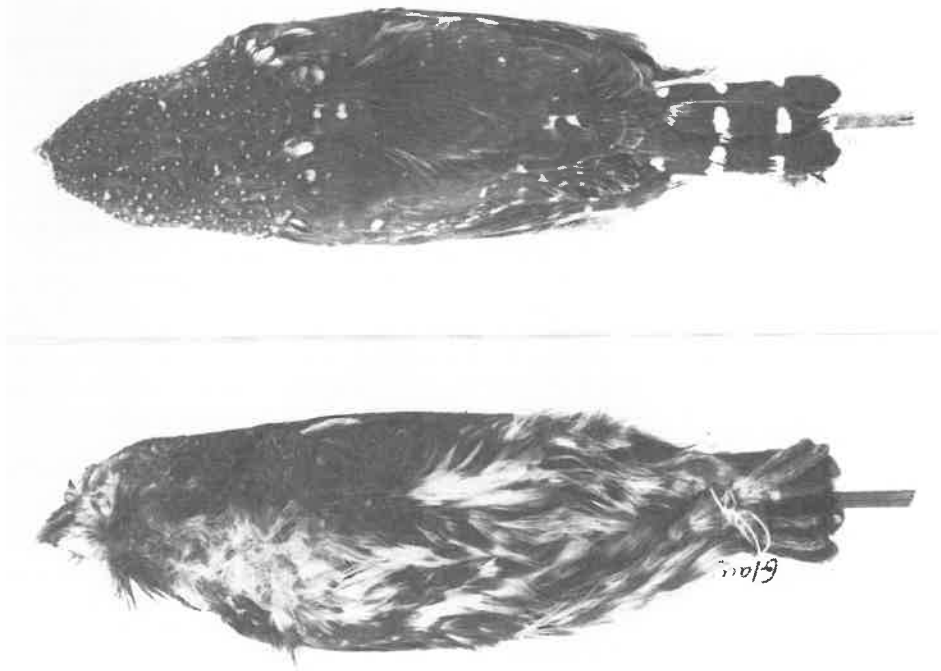


Figure 3. Strophe of song of *Glaucidium minutissimum*. Boissucanga, S. Paulo, Brazil. Rec. J. Vielliard (ARA-Records, Gainesville, FL).
All Sonagrams on KAY Elemetrics Sona-Graph, Model 5500. Upper row: waveform display; lower row: spectrographic display. If nothing different is mentioned, the frequency range of the machine is put at 4 kHz and the time axis on 2 sec.

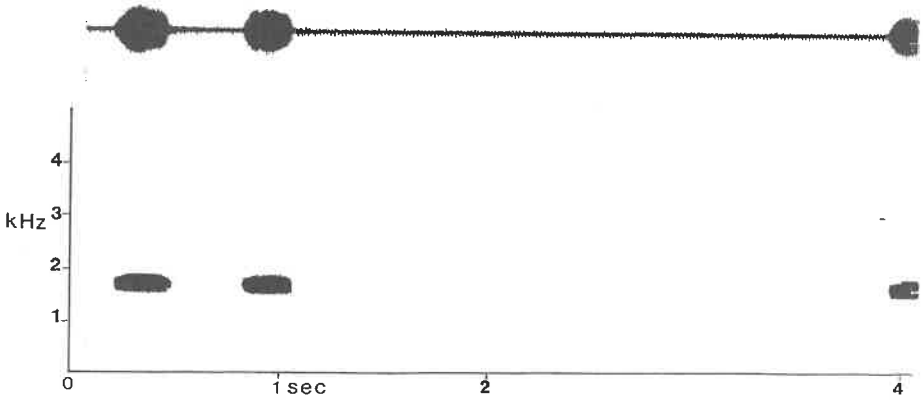


Figure 4. Strophe of song of *Glaucidium hardyi*. Rondônia, Brazil. Rec. J. Vielliard (ARA-Records, Gainesville, FL).

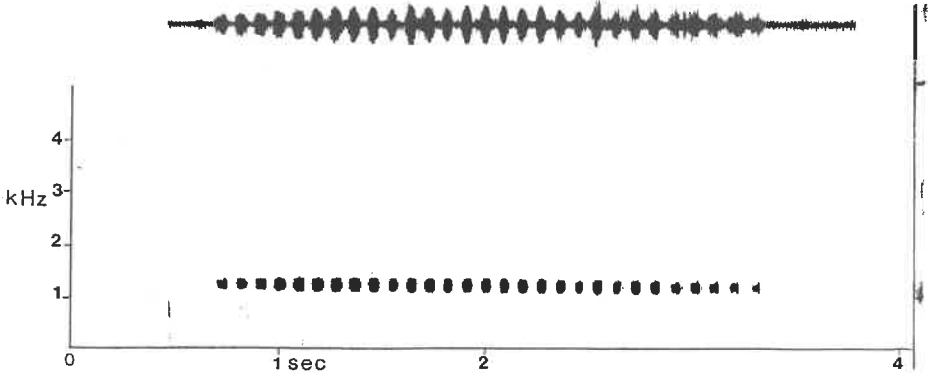


Figure 5. Strophe of Song of *Glaucidium "griseiceps"*. San Luis Potosi, Mexico. Rec. BBC (ARA-Records, Gainesville, FL).

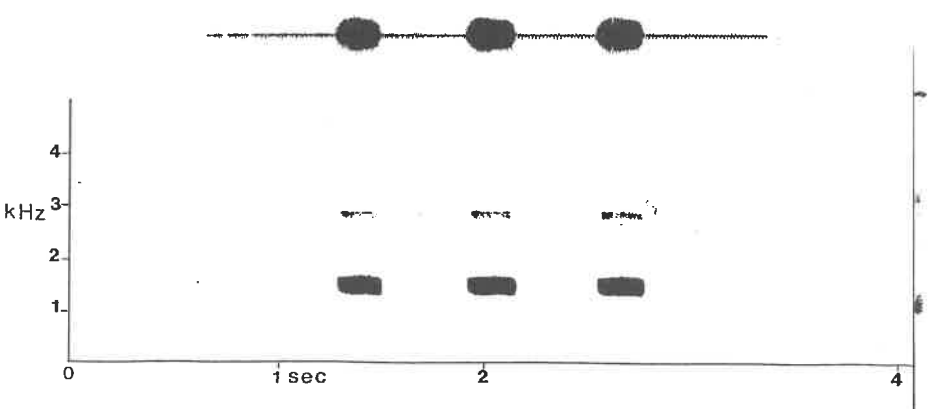


Figure 6. Several strophes of one of the song-types (introductory part) of *Glaucidium jardinii*. Páramo Zumbador, Táchira, Venezuela. Rec. P. Schwartz (ARA-Records, Gainesville, FL).

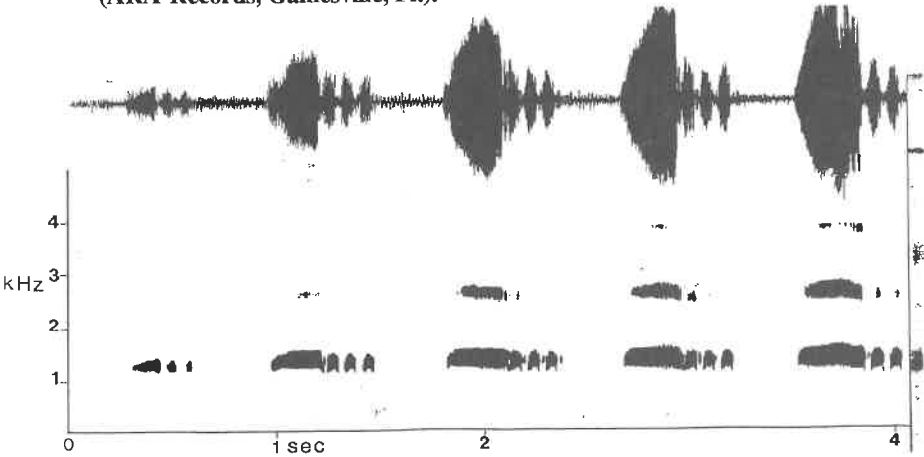


Figure 7. Sequence of the other type of song of *Glaucidium jardinii*. Same individual. Same dates.

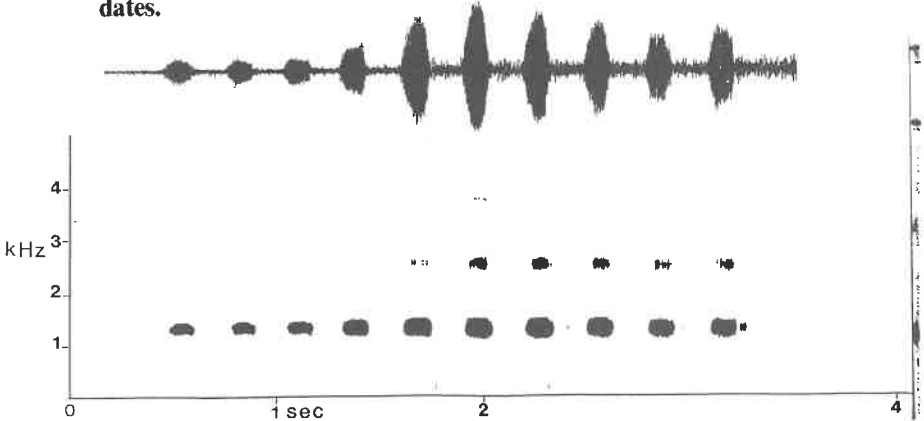


Figure 8. Part of one of the two song-types (introductory part) of *Glaucidium bolivianum*. Salta, Argentina. Rec. C. König.

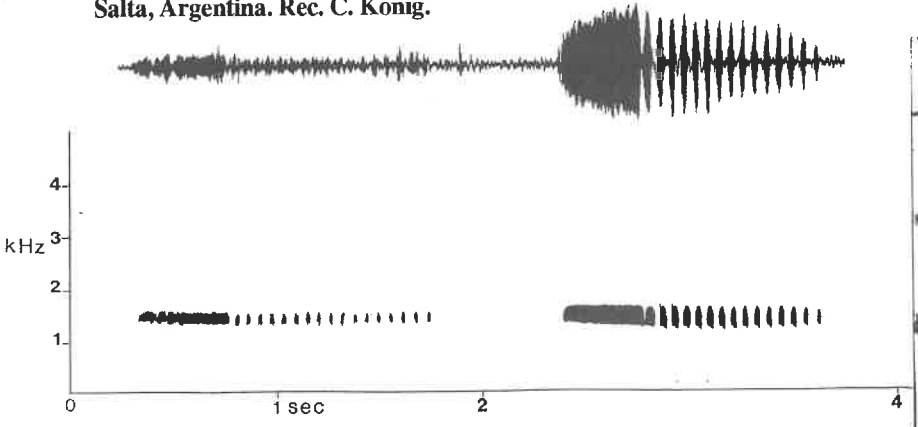


Figure 9. Part of the other song (most common type) of *Glaucidium bolivianum*. Same individual. Same dates.

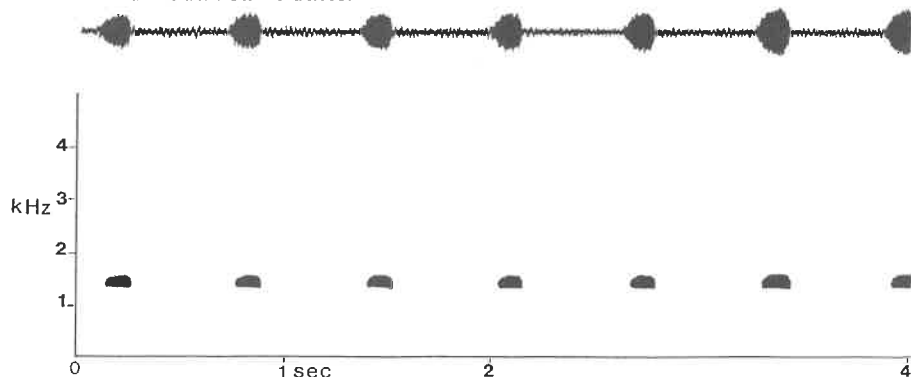


Figure 10. Skin of *Glaucidium bolivianum* from Lambate, La Paz, Bolivia (brown morph). Photo: H. Lumpe.

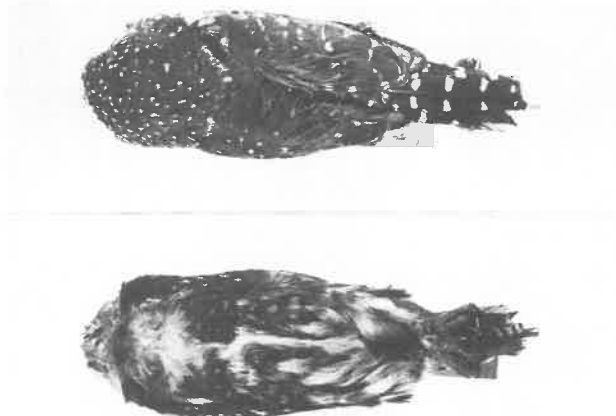


Figure 11. Skins of (from left to right): *Glaucidium bolivianum* (holotype, grey morph) from Salta, Argentina; *Glaucidium brasilianum tucumanum* (grey morph) from Anta, Salta, Argentina; *Glaucidium brasilianum tucumanum* (brownish morph) from Ledesma, Jujuy, Argentina. Photo: M. Harling.

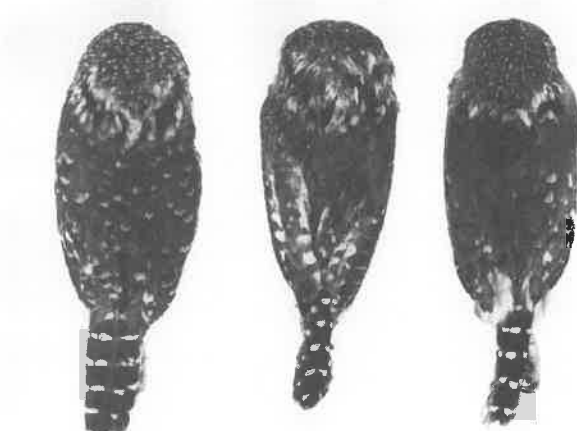


Figure 12. Part of song of *Glaucidium gnoma*. Coahuila, Mexico. Rec. J.T. Marshall (ARA-Records, Gainesville, Fl.).

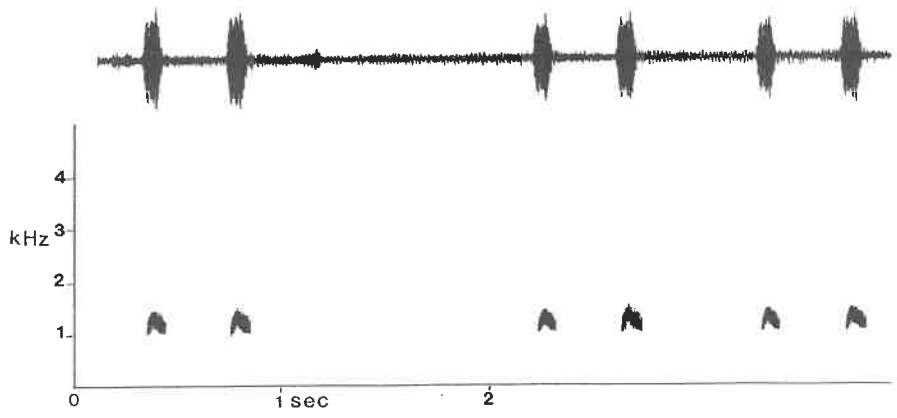


Figure 13. Part of song of *Glaucidium peruanum*. Ancash, Perú. Rec. T. Parker (ARA-Records, Gainesville, Fl.).

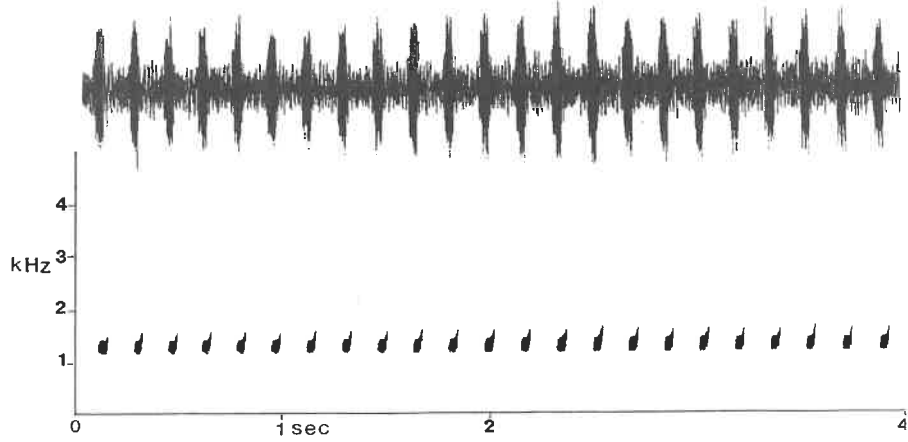


Figure 14. Part of song of *Glaucidium californicum*. California, U.S.A. Rec. J.T. Marshall (ARA-Records, Gainesville, Fl.).

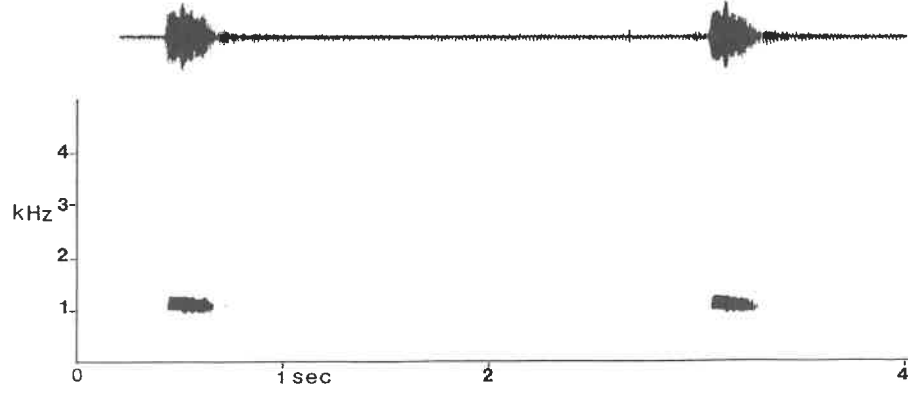


Figure 15. Part of song of *Glaucidium passerinum*. Schwarzwald, Germany. Rec. C. König.

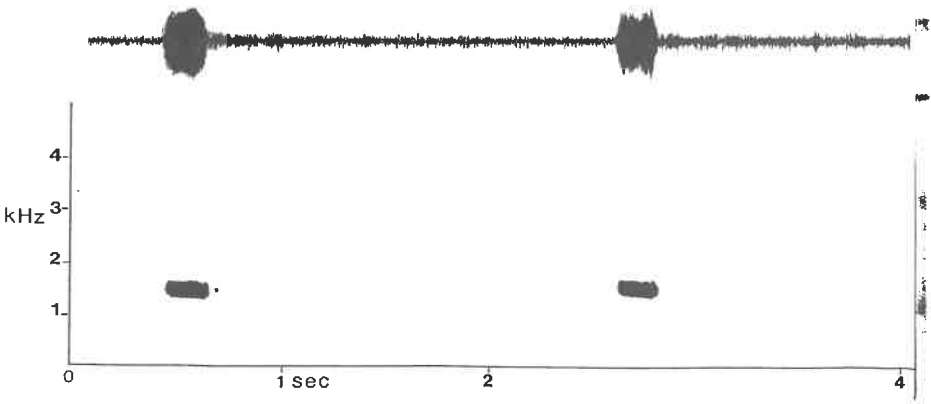


Figure 16. Part of song of *Glaucidium brasilianum*. Montecarlo, Misiones, Argentina. Rec. C. König.

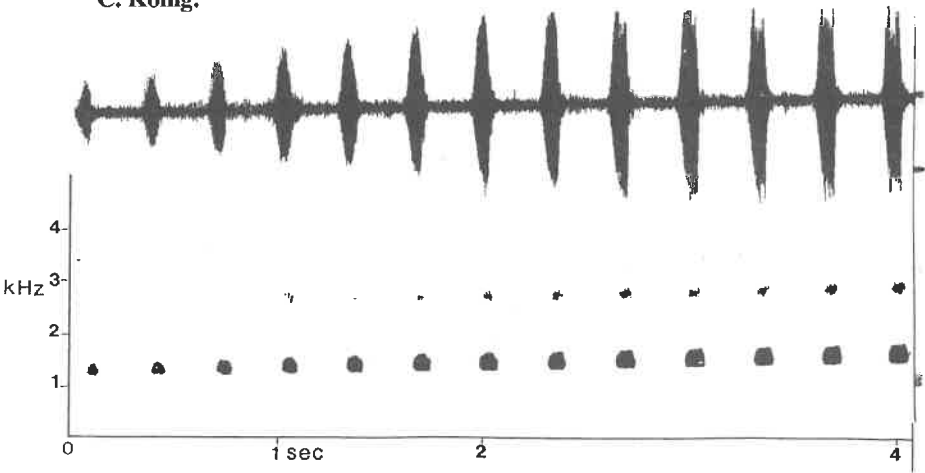


Figure 17. Tail patterns of (from left to right): *Glaucidium nanum*, *Glaucidium brasilianum* (red morph), *Glaucidium brasilianum* (grey morph). Photo: C. König.

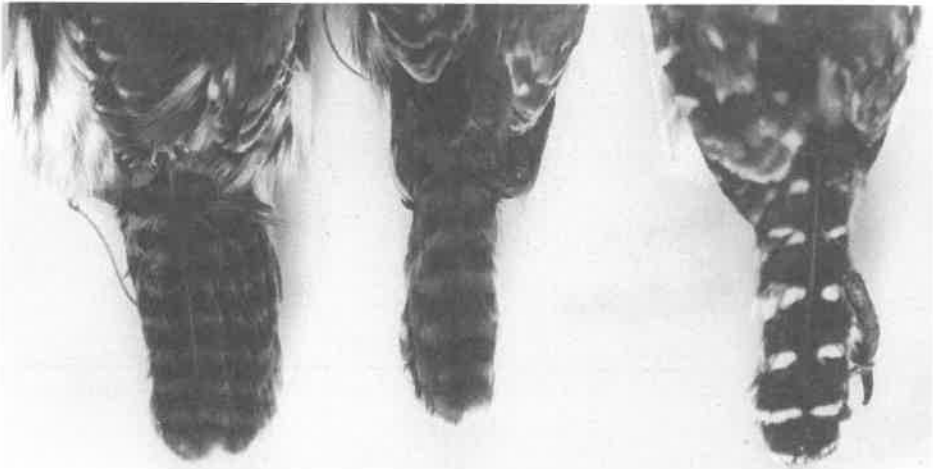


Figure 18. Male of *Glaucidium nanum* at song-perch. Lago Argentino, Santa Cruz, Argentina. Photo: C. König.



Figure 19. “Chirrup” (excited calls) of *Glaucidium nanum*. Lago Roca, Santa Cruz, Argentina. Rec. C. König. This recording and that on Figure 20 are displayed on the Sona-Graph at a frequency range of 8 kHz and a time axis of 1 sec.

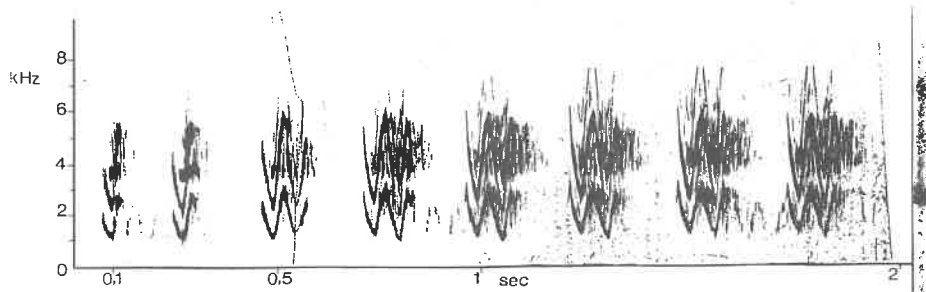


Figure 20. “Chirrup”(excited calls) of *Glaucidium brasilianum*. Salta, Argentina. Rec. C. König. Frequency range and time axis as in Figure 19.

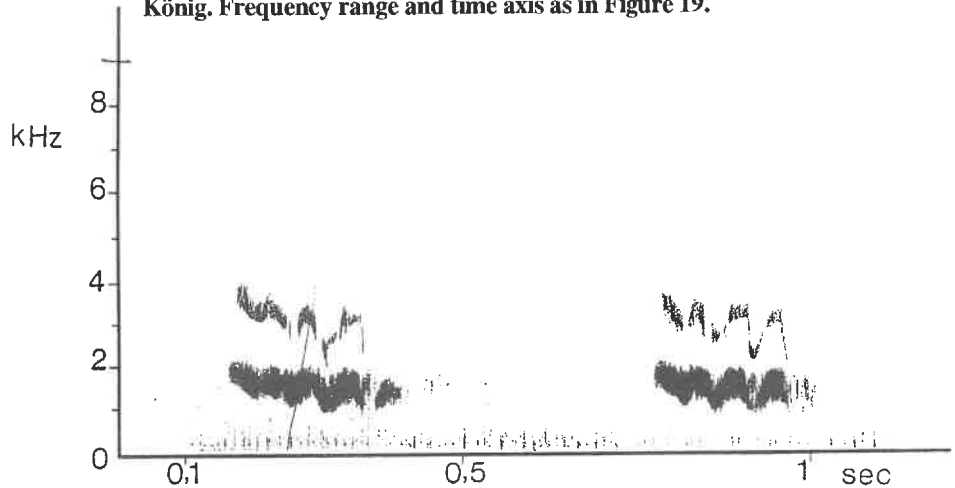


Figure 21. Distribution-map of *Glaucidium*-species (according above all to vocal evidence): A = *Glaucidium jardinii*; B = *Glaucidium bolivianum*; C = *Glaucidium "griseiceps"*; G = *Glaucidium gnoma*; H = *Glaucidium hardyi*; M = *Glaucidium minutissimum*; N = *Glaucidium nanum*; O = *Glaucidium peruanum*; ? = large, brown *Glaucidium* of uncertain status; hatched area = *Glaucidium brasilianum*; black (Cuba) = *Glaucidium siju*.
 The North American *Glaucidium californicum* is distributed in coniferous forests of the Rocky Mountains from northern North America to southern Arizona. It seems to be closely related with the Eurasian *Glaucidium passerinum*.



Figure 22. Strophe of A-song of male *Otus choliba*. Iquitos, Perú. Rec. BBC (ARA-Records, Gainesville, FL.).
 This and the following recordings of *Otus* spp. are displayed at a frequency range of 2 kHz and a time axis of 2 sec. on the machine.

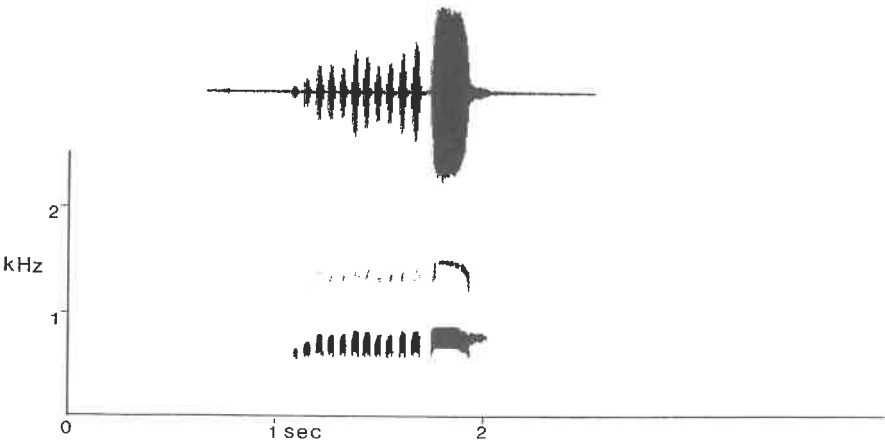


Figure 23. Strophe of B-song of male *Otus choliba*. Same individual, same data.

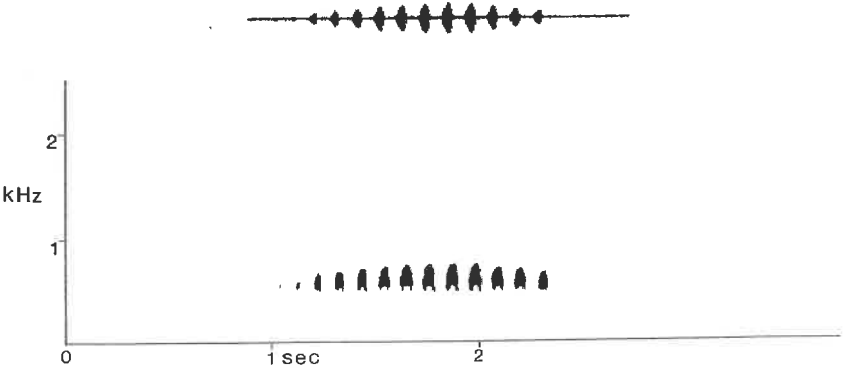


Figure 24. Part of A-song of male *Otus atricapillus*. Iguazú, Misiones, Argentina. Rec. C. König.

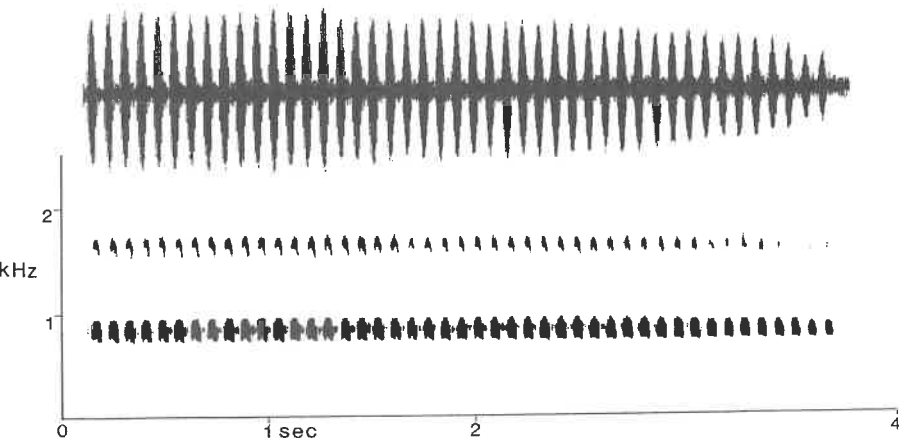


Figure 25. Strophe of B-song (“bouncing ball”) of male *Otus atricapillus*. Iguazú, Misiones, Argentina. Rec. M. Castelino.

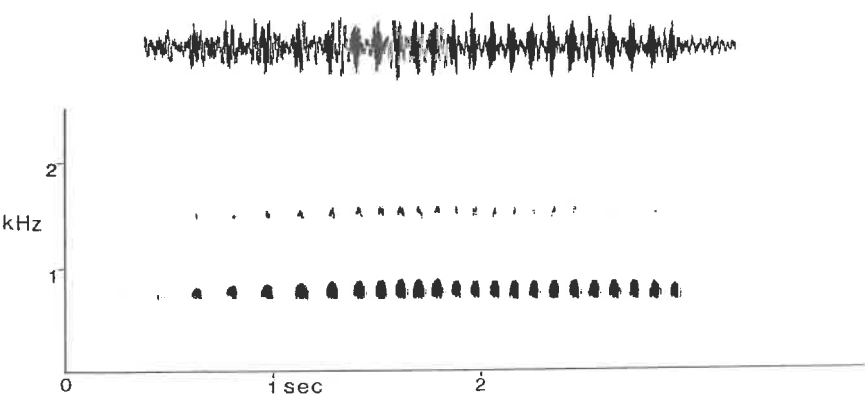


Figure 26. Part of A-song of male *Otus sanctaecatarinae*. Urugua-i Provincial Park, Misiones, Argentina. Rec. C. König.

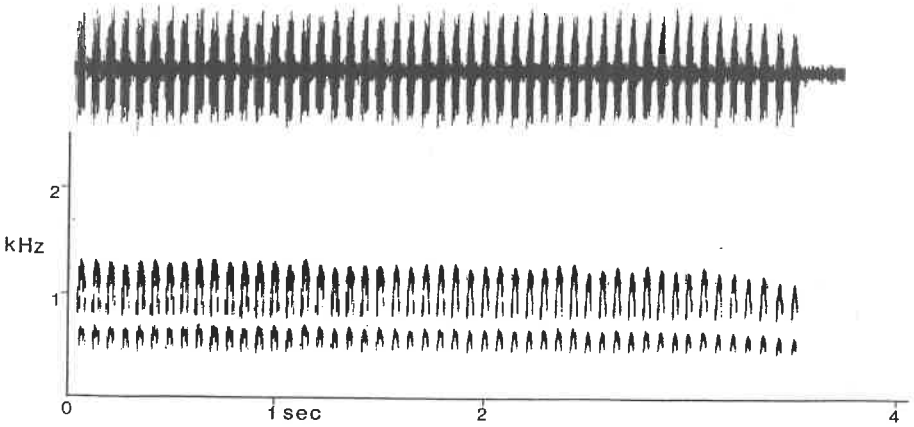


Figure 27. Strophe of B-song (“reverse bouncing ball”) of male *Otus sanctaecatarinae*. Rio Grande do Sul, Brazil. Rec. T. Parker.

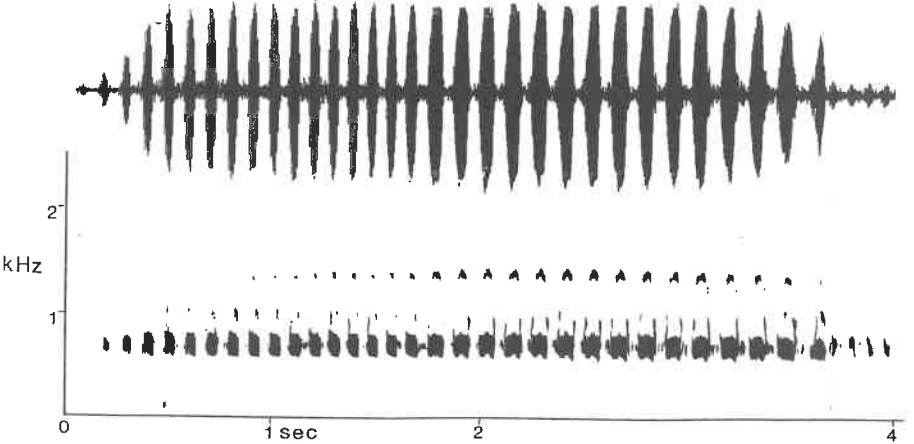


Figure 28. Strophe of B-song of female *Otus sanctaecatarinae*. Rio Grande do Sul. Rec. W. Belton (ARA-Records, Gainesville, FL.)

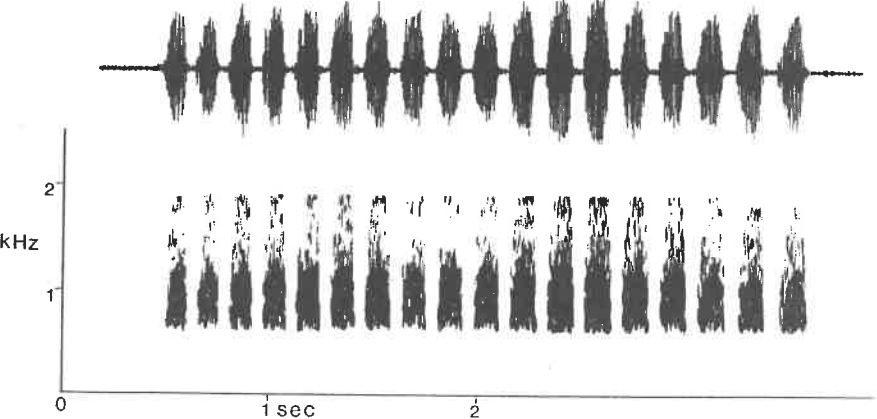


Figure 29. Part of A-song of male *Otus hoyi*. Salta, Argentina. Rec. C. König.

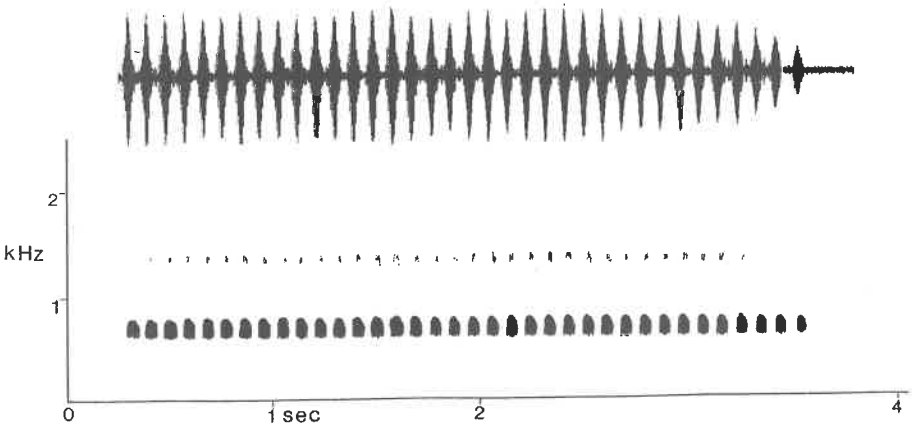


Figure 30. Strophe of B-song of male *Otus hoyi*. Salta, Argentina. Rec. C. König.

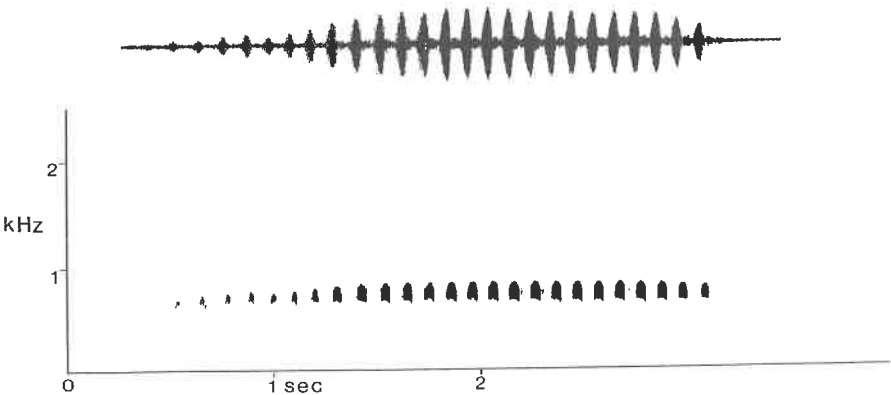


Figure 31. Part of A-song of female *Otus hoyi*. Salta, Argentina. Rec. C. König.

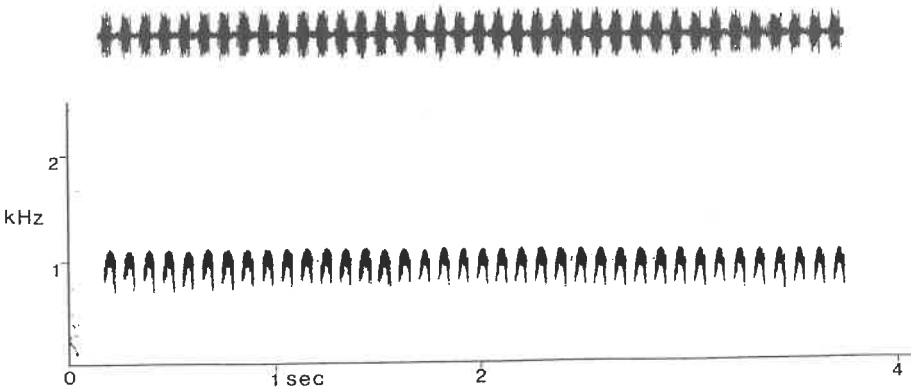


Figure 32. Strophe of B-song of female *Otus hoyi*. Same data.

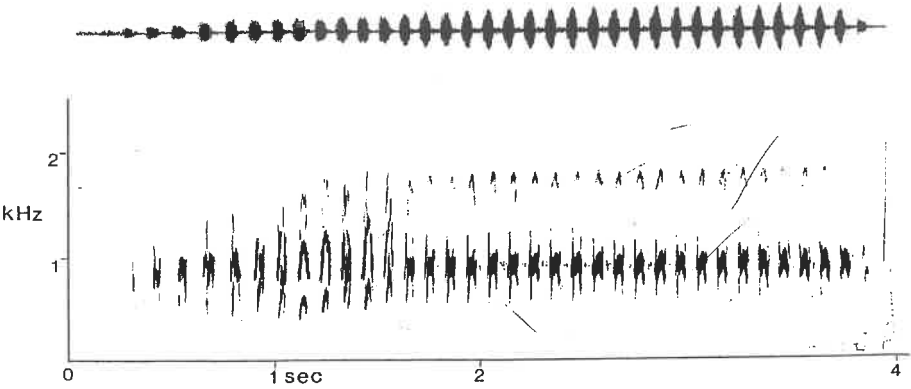
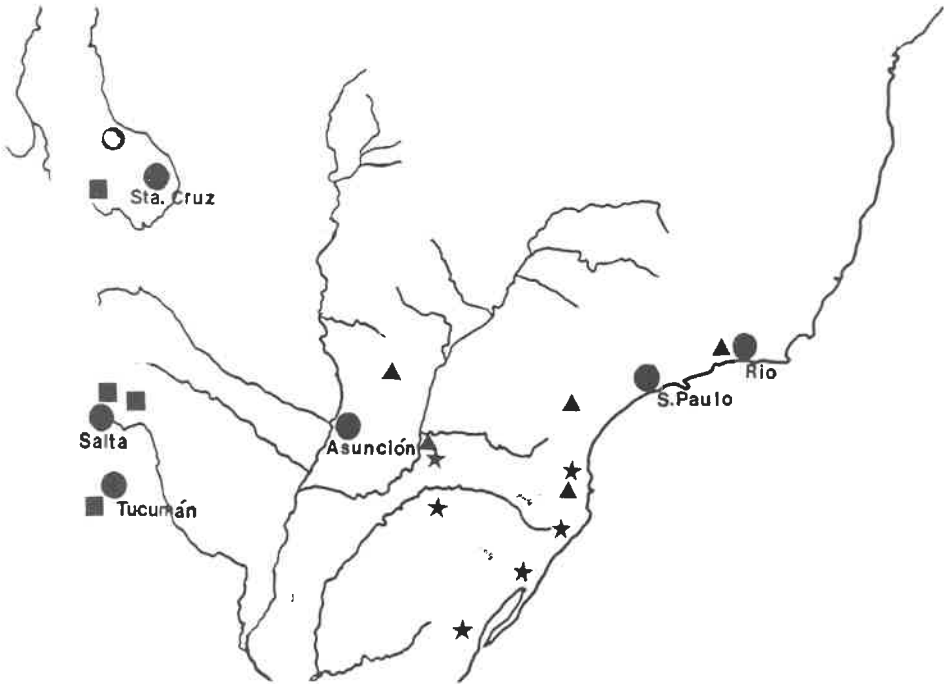


Figure 33. Distribution of
▲ = *Otus atricapillus*,
★ = *Otus sanctaecatarinae*
■ = *Otus hoyi*
○ = *Otus guatemalae*



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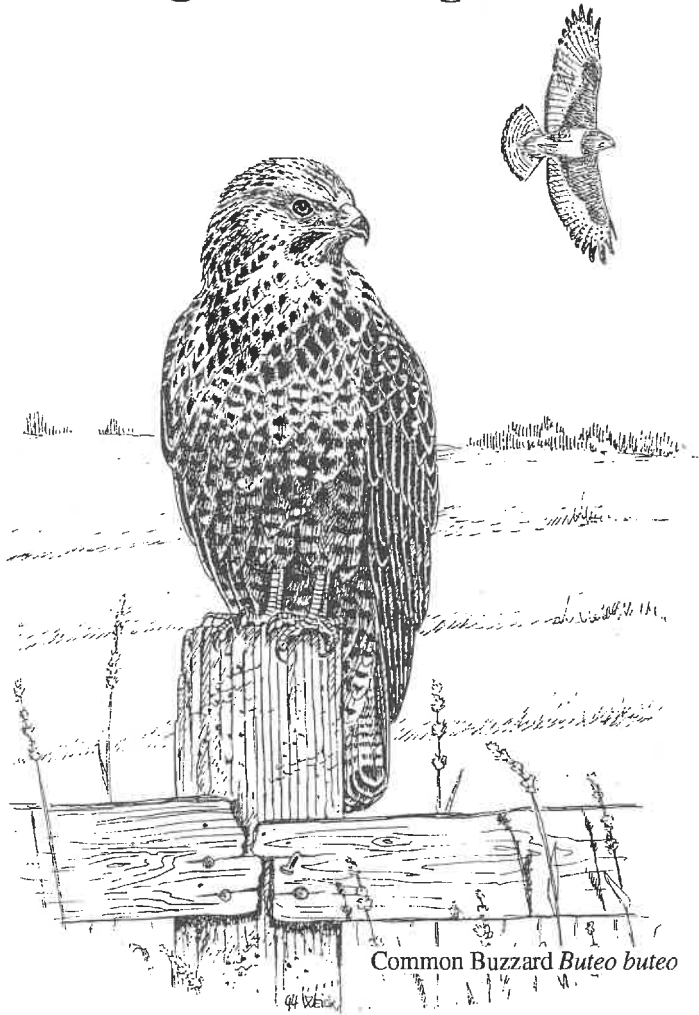
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Part 1

Population Studies: Aspects of Long-term Changes



Conveners:

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