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Species boundaries in non-tropical Northern Hemisphere Owls

K.H. Voous
Institute of Taxonomic Zoology, University of Amsterdam, P.O. Box 4766, 1009 AT Amsterdam, The Netherlands

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Abstract

A survey is presented of the status of species boundaries in non-tropical Northern Hemisphere owls in order to investigate the reality of the biological and geographical species concept applied to these owls in current handbooks. At the same time the practicability of evolutionary systematics as opposed to phylogenetic synthesis is elaborated on.

Résumé

On passe en revue la situation des limites entre espèces chez les Hiboux non-tropicaux du hémisphere Nord, afin d'examiner la réalité du concept biologique et géographique de l'espèce appliqué à ces oiseaux dans les traités en circulation courante. D'autre part, on insiste sur la praticabilité de la systématique évolutive, en tant qu'approche opposée à la synthèse phylogénétique.

1. Introduction

Accepting that according to the biological and geographical species concept reproductive behaviour and geographical variation are the keystones of species formation processes in terrestrial animals (Mayr, 1953: 19), it seems worthwhile to investigate the status of species boundaries in selected taxonomic groups on which enough knowledge on behaviour and distribution is available. In fact, it means the survey of the applicability in nature of a still important theory. Years ago I have tried to do this in relation to Northern Hemisphere ducks, geese and swans (Voous, 1964); at present another attempt will be made based on non-tropical Northern Hemisphere owls on which a comprehensive book has been published recently (Voous, 1988). The survey will be restricted to a discussion of stages in the evolution of owl-species without making special reference to expressions of doubt which in recent years have been raised against the objectivity of the concept of the geographically polytypic species.

2. Monotypic genera

Nyctea scandiaca	– Snowy Owl – circumpolar arctic tundra
Surnia ulula	– Northern Hawk Owl – circumglobal boreal forest
Micrathene whitneyi	– Elf Owl – Sonoran Saguaro desert
"Speotyto" cunicularia	– Burrowing Owl – American grasslands and semi-deserts

The taxonomic limits of species allocated to monotypic genera offer no problems. In addition to the differential nature of their morphological characters, their specificity is supported by their life styles which are directly related to their relatively uncomplicated geographical and ecological distribution. The Snowy Owl is an arctic descendant of the Eagle Owls *Bubo*; the Northern Hawk Owl is a somewhat aberrant ecotype of either *Glaucidium* or *Ninox* or of both, and the Elf Owl is a minor deviation of Pygmy Owl *Glaucidium*.

The Burrowing Owl is a case by itself. Traditionally placed in the monotypic genus *Speotyto* with an

exclusively American distribution, there has been a recent tendency of incorporating this species in the Old World genus *Athene* (see Voous, 1988: 199). DNA-analysis seems to indicate, however, that Burrowing Owls have no known close relatives (C.G. Sibley, pers. comm.). Thus, providing biochemical similarity is the ultimate indicator of relationship, the Burrowing Owl should be considered to represent a monotypic genus. If placed in the genus *Athene*, in which it is the ultimate terrestrial representative, the application of the biological and geographical species concept remains equally clear and unchallenged.

3. Monotypic species

Ketupa flavipes – Tawny Fish Owl – Sino-Himalayan submontane mountain streams
Strix butleri – Hume's Owl – Wadis in Middle East stone-deserts

As in the monotypic genera the eco-geographical distributions of these morphologically well-defined species are of a restricted nature and the species limits are unchallenged. Digging deeper into the history of these species, the Tawny Fish Owl could be an ecoform of the early Asian fish owls *Ketupa*, and more specifically of the Malay Fish Owl *Ketupa ketupu*, whereas Hume's Owl most probably is a desert derivative of early palaearctic Tawny Owls *Strix aluco*.

4. Holarctic distributions

(a) Holarctic species with wide global distributions

Tyto alba – Barn Owl – near-cosmopolitan
Asio flammeus – Short-eared Owl – semi-cosmopolitan

The Barn Owl is among the bird species with the widest global ranges. Some 35–40 geographical races are currently recognized. Apart from a gliding variation in darkness of the plumage and spotting of the underparts, body size is the most obvious geographically varying character. One may wonder whether a tiny bird of the race inhabiting Curaçao in the South Caribbean (*T. a. bargei*, body length 29 cm) would have a chance to survive when confronted with a Barn Owl from the USA (*T. a. pratincola*, body length 46 cm) of more than 1½ times its size. This situation is realized in the island of Hispaniola, where a small indigenous form (*T. a. glaucops*) seems to be forced to pair up with, or succomb under an alien giant recently arrived on its own from the Bahama Islands or the USA (*T. a. pratincola*) with a wing length almost 1½ times that of the indigenous Barn Owl. In this case one could wonder indeed whether these Barn Owls will manage to act as independently reproducing populations, that is, as two separate species. This view has been advocated by Olson (1978). It is more likely, however, that in the long run one of the Barn Owl types will oust the other (not necessarily the smaller one) and that only one survives, best adapted to the local conditions of habitat and food supply, eliminating the local species problem in the process. Another similar situation occurs on Lord Howe Island, halfway between Australia and New Zealand, where large Barn Owls from California (*T. a. pratincola*) and smaller ones from Australia (*T. a. delicatula*, body length about 72% of the North American owls) have been introduced for rodent control, allegedly without interbreeding (see Voous, 1988: 12). This, then, would be a case of a first attempt to species duplication in an insular occurrence of the Barn Owl.

Indeed, it is rumbling within the Barn Owl complex of forms. The North American Barn Owl is at least 20% larger in size than the corresponding European form (*T. a. alba*). A reason for it has been recently explained. Mammal prey supply in North America includes larger species than in Europe. In Europe no resident owl species in between the size of the Barn Owl and the Long-eared Owl *Asio otus* exists, whereas in North America the parapatric Western and Eastern Screech Owls *Otus kennicottii* and *O. asio* of intermediate size are preying on virtually the same types of prey as the Barn Owl, pressing the Barn Owl to take on the average larger prey and growing to larger size in the process. Thus, the body weights, and therefore the predation forces, of the Barn Owl and the Long-eared Owl in Europe relate to each other as slightly more than 1:1, as against almost 2:1 in North America. Would this situation permit or obstruct a mutual reproductive behaviour of Old World and New World Barn Owls

in case these populations would ever meet? As it is unlikely that this will happen, the problem is more academic than real.

Another interesting point is the fact that different groups of parasitic feather lice *Strigiphilus* (Mallophaga) occur on American, Australian and south Asian Barn Owls on the one hand and on African, Middle East and European Barn Owls on the other hand (Clay, 1966). This would indicate that the geographical separation of these populations is of old date. However, one could hardly visualize where and when Old and New World Barn Owls have been in contact with each other. Is this, then, finally, a reason to split the Barn Owl into more than one species? I think not. But the conspecificity of the groups cannot be proved either. Instead, one should realize that in more than one place the Barn Owl seems to be on the verge of bursting out of its species limits.

In the Short-eared Owl no geographical differences have been apparent between population groups inhabiting the wide expanse of cold and temperate Eurasia and North America. Even the Short-eared Owls nesting in similar climates in South American mountains and plains, as well as those in the tropical Galapagos islands, differ only very slightly in their plumage characters from those inhabiting the Northern Hemisphere. As in addition zoogeographical evidence exists in favour of the theory of a post-Tertiary range extension of the Short-eared Owl from North America into the South American continent, there is no reason to challenge the generally accepted species limits in this owl.

(b) Holarctic species traditionally treated as one species

Surnia ulula – Northern Hawk Owl – boreal forests
Strix nebulosa – Great Grey Owl – boreal forests
Asio otus – Long-eared Owl – south boreal and temperate forests
Aegolius funereus – Tengmalm's Owl – boreal forests

In these species Old World and New World races have been traditionally recognized. In *Surnia ulula* and *Aegolius funereus* the differences are trivial. In *Strix nebulosa* and *Asio otus* there is a parallel tendency of the New World owls to be more clearly barred underneath rather than longitudinally striped (Eck, 1968). As there is biogeographical evidence that boreal forests have been continuous over the Bering Sea area during one or more periods of glacial extension in the Pleistocene, connecting the northern parts of Asia and America, the conspecificity of present boreal forest owls is understandable (Voous, 1958). No behavioural differences are known to doubt this conclusion (see also Voous, 1988a on *Asio otus*).

(c) Holarctic species or species groups of doubtful taxonomic status

Otus scops/flammeolus – Scops Owls – warm-temperate and mountain forests
Glaucidium passerinum/gnoma – Pygmy Owls – boreal and mountain forests
Strix uralensis/varia – Ural and Barred Owls – boreal and temperate forests

Though being a member of the mainly Old World type of "scops owl" rather than of the New World "screech owls" (Van der Weijden, 1975; Hekstra, 1982), the Flammulated Owl has so many morphological, structural, behavioural and vocal characteristics of its own that its status as a North American endemic species is at present widely accepted (Marshall, 1966: 240; Voous, 1988: 53–58).

Though Old World and New World Northern Pygmy Owls differ in but few structural feather characteristics, their feeding ecology is different. The North American Pygmy Owl is semi-insectivorous, whereas the Old World Pygmy Owl probably hardly if ever catches insects or other arthropods. This adds a distinct ecological asset to the taxonomy of these owls which was lacking formerly. In contrast to earlier views according to which Old and New World Pygmy Owls were conspecific (Voous, 1960), the New World Northern Pygmy Owl is now treated as a separate species *G. gnoma*, whereas the Old World Pygmy Owl *G. passerinum* is considered the most advanced northern member of this otherwise mainly tropical group and the most exclusively carnivorous species of the genus at that.

On account of a superficial resemblance of Ural Owls from east Asia in particular and Barred Owls from eastern North America, Otto Kleinschmidt

(1934), originator of the concept of *Artenkreise* or superspecies, united these owls into one of his illustrated "geograms", whereas his admirer Siegfried Eck (1968) followed track by recognizing them as the geographical members of one species. This would indicate the theory of a former geographical connection or even an eco-geographical continuity. Though a connection may have existed at some time in the early Pleistocene, the presence of a third wood owl species, the Spotted Owl *Strix occidentalis* in mixed conifer forests in the Pacific Northwest of North America, disturbs the simplicity of Kleinschmidt's and Eck's views. The vocal qualities of the Spotted Owl seem to resemble those of the Ural Owl more than do these of the Barred Owl. Evidently it is premature if not unrealistic to consider one or the other of the North American wood owls as the American representative of the Eurasian Ural Owl.

(d) Holarctic species group traditionally treated as two species

Bubo bubo/B. virginianus – Eurasian Eagle Owl / Great Horned Owl – all types of densely and sparsely forested regions

The Eurasian Eagle Owl and the Great Horned Owl are each others taxonomic and ecological counterparts. Body size and more strongly barred *versus* longitudinally streaked or marmorated underparts are considered sufficient evidence for the recognition of distinct New World and Old World species. The vocal performances of these owls seem to be the same. Geographical variation in the virtually continuous range of the Great Horned Owl from Canada in the north to Tierra del Fuego in the south is considerable (differences in body size of up to 20–30%), but does not provide a basis for specific separations. Apparently tradition, rather than anything else, is the main reason for treating the Great Horned Owl and the Eurasian Eagle Owl as distinct species, unlike the situation in the Great Grey and Long-eared Owls. There is nothing to say against these different taxonomic decisions, as long as the reasons are recognized and considered practicable. Evidently the Great Horned and Eurasian Eagle Owls represent a border-line case in the sense of evolutionary systematics.

To summarize this paragraph: species limits in northern owls with holarctic distributions have been traced easily on the basis of morphology, vocalizations, habitat choice, food and geographical history. At the same time intermediate stages in the process of species formation have been strongly in evidence. Could it have been expected otherwise?

5. Complicated taxonomic situations in Old World Owls

**Tyto capensis/longimembris*
– Grass Owl – one or two species?
****Otus sunia/brucei/scops/senegalensis*
– Scops Owls – how many species?
***Bubo bubo/bengalensis/ascalaphus*
– Eagle Owls – one or more species?
***Athene noctua/brama*
– Little Owl and Spotted Owlet – conspecifics?
**Strix aluco/nivicola*
– Tawny Owl – one or two species?
**Strix uralensis/davidi*
– Ural Owl – one or two species?
**Asio otus/abyssinicus*
– Long-eared Owl – one or two species?

In the cases indicated by (*), strict geographical vicariance in basically similar habitats has been considered by some authors as convincing proof of conspecificity. Others have used plumage differences and geographic separation, supposedly of long duration, as a basis for the recognition of two species. In the species marked (**), shared geographical history on the one hand and insufficient knowledge on marginal geographical overlap have led these species to be treated usually as one (Eagle Owls *Bubo*) or as two species (Owlets *Athene*), but opinions among authors differ. Future field work more than anything else will have to decide in these border-line cases.

The Scops Owls (***) are a problem by themselves. The ranges of the Oriental Scops Owl *Otus sunia* and the European Scops Owl *Otus scops* seem to overlap in Afghanistan and western Mongolia at least, though the birds occur in different habitats. Their songs are slightly different in rhythm, but not in quality. They have been treated as one, but are

now mostly considered as two species. The Striated or Pallid Scops Owl *Otus brucei* seems to differ from the sympatric European Scops Owl *Otus scops* in both habitat (open arid *versus* forested regions) and vocalization and there is at present sufficient positive evidence to treat these owls as separate species. The European and African (*O. senegalensis*) Scops Owls differ hardly in characters of plumage and structure, but decidedly in voice (Van der Weijden, 1973). The geographically intermediate Arabian Scops Owl *Otus* (*scops*) *pamelae* seems to resemble the Eurasian and the African Scops Owls to an equal degree, but its vocalizations are a performance of its own, being halfway between the stuttering song of African Scops Owls and the *purr* of Oriental Scops Owls from Thailand (Marshall, 1978: 8; Voous, 1988: 38). Evidently the two options, either one Afro-European species or two allopatric species, have equal rights. The whole species complex is in a state of decomposition rather than of geographic radiation.

In summary: the geographical species concept is practicable, but should be treated in close combination with ecological and behavioural data, hence with caution, care and reason.

6. Complicated taxonomic situations in New World Owls

***Tyto alba/glaucops/punctatissima*
– Barn Owl – one or more species?
****Otus kennicottii/asio*
– Screech Owls – conspecifics?
***Otus guatemalae*
–Vermiculated Screech Owl – conspecific relations?
***Glaucidium gnoma/minutissimum/brasilianum*
– Pygmy Owls – how many species?
**Strix varia/fulvescens*
– Barred and Fulvous Owls – conspecifics?
**Asio otus/stygius*
– Long-eared and Stygian Owls – conspecifics?

Different opinions on the significance of strict allopatry have led to the recognition of either one or two species in the species pairs indicated with (*). None of these decisions seems to be more reasonable than the other.

The New World Barn Owl (**) has been discussed earlier; see section 4 (a).

The recognition of a Western and Eastern species of Screech Owl (***) on account of different vocalizations and an only marginal overlap in Colorado and along the Rio Grande on the Texas-Mexican border (Marshall, 1967) may have been accepted recently, but the strength of the arguments is weak. In addition, the taxonomic and behavioural nature of the relation with Central and South American congenerics, including the Vermiculated Screech Owl (**) is uncertain. All over the world the Screech Owls seem to be in a stage of hyperactive geographic speciation. Similar questions as in the American Screech Owls can be asked with reference to the Pygmy Owls (**): which of the subtropical and tropical Pygmy Owls is the Northern Pygmy Owl's nearest relative, either as a root or a descendant (Voous, 1988: 157–160). The answer depends on comparative life-history studies of these owls and the reconstruction of their distributional history.

7. Island distributions

Problems on the taxonomic status of island populations are scarce in Northern Hemisphere owls. Those involved are the marginal and extra-limital ranges of Scops Owls *Otus* in the Philippines and Indonesia and elsewhere in adjacent parts of the Indian and Pacific Oceans. More particularly, they relate to the Mountain Scops Owl *Otus spilocephalus*, Oriental Scops Owl *Otus sunia*, Collared Scops Owl *Otus bakkamoena* and the south Asian Cuckoo Owlet *Glaucidium cuculoides*. There is a tendency in ornithological literature to treat well-marked insular races as separate species, but in most cases neither proof nor doubt can be raised as to the possibility of unlimited interbreeding with other insular or continental populations as required by the biological and geographical species concept. Most decisions therefore remain subjective, but in the case of the Scops Owls some have been based on similarity of vocalizations (Marshall, 1978).

8. Vocalizations

It has become almost a fashion to use vocalizations for setting taxonomic problems. More and more one seems to forget that voice is as much subjected

to geographic variation as is any other variable character in organic beings and occurring not unfrequently in birds at that. Thus, only those differences that have been proved to represent an unsurmountable barrier in reproduction behaviour can be considered as species-specific. Differences that can stand this test are fewer than often supposed. There is therefore no need to split up the Collared Scops Owl into an Indian Scops Owl *Otus bakkamoena* and a Collared Scops Owl *Otus lempiji* on reasons of geographic voice differences as advocated by Roberts & King (1986). Similar geographic variations have been noticed in the Oriental Scops Owl *Otus sunia* in eastern Asia (see Voous, 1988: 35) and in the Western North American Screech Owl *Otus kennicottii* (Marshall, 1967). Mixed pairs of Western and Eastern Screech Owls have been described from the area of geographic contact of these owls on the Rio Grande border between Mexico and the USA (Marshall, 1967), suggesting that song differences are not unsurmountable in reproductive behaviour. On the other hand, voice rather than outward appearance is the communication method most frequently employed by nocturnal animals, including owls. Therefore a comparison of territorial songs in insular populations of Scops Owls in the Philippines and Indonesia has been used with apparent success to unravel problems of taxonomy and relationship (Marshall, 1978). The remarkably deep song of the Flammulated Owl *Otus flammeolus* from western North America is so strongly different from the song types of Old World Scops Owls that the once proposed conspecificity between these owls is now almost forgotten.

9. Species variation in time: owl fossils

With the almost explosive increase of discoveries of avian fossils, the knowledge on extinct owls has improved in a surprising way. In the present context the following selection of sub-Recent and Pleistocene owls can be made.

Tyto alba – Barn Owl, S. Europe, Israel, Mediterranean islands, North America, Mexico, West Indies, Brazil, New Zealand, etc. (see Voous, 1988: 12)

Bubo bubo – Eagle Owl, S. France (Mourer-Chauviré, 1975), Azerbaijan (Caucasus)

Bubo virginianus – Great Horned Owl, North America (Brodkorb & Mourer-Chauviré, 1984)

Nyctea scandiaca – Snowy Owl, S. France (Mourer-Chauviré, 1975)

Athene noctua – Little Owl, S. France (Mourer-Chauviré, 1975)

Strix uralensis/aluco – Ural and Tawny Owls, *Strix intermedia*: central and S. Europe (Janossy, 1972; Mourer-Chauviré, 1975)

Asio otus – Long-eared Owl, North America (see Voous 1988: 261)

Virtually all of these owls are larger in size than the respective species from to-day and most of them can be considered as chronological- or palaeo-subspecies or variations in time. Most probably the impoverished mammalian prey fauna and the general diminution of the size of mammals are responsible for the decrease in body size in Recent owl species (e.g. *Bubo*; see Voous, 1988: 86). This situation is also indicative of the fact that size alone need not be a species-specific character, though it might have been in cases of sympatry such as in the probably synchronic *Tyto robusta* and *T. gigantea*, the latter larger even than the present-day Eagle Owl *Bubo bubo*, from Upper Miocene deposits in Italy (Ballmann, 1973, 1976) and in the wood owls during and after the process of species differentiation of the Ural and Tawny Owls in Europe during the Middle Pleistocene (see Voous, 1988: 238).

Of special interest is the presence of an extremely long-legged and probably flightless Little Owl *Athene cretensis*, not unlike an American Burrowing Owl, from Pleistocene cave deposits on Crete which may have lived alongside a Little Owl of recent proportions (Weesie, 1982, 1987). This development seems to have started at a time that the mammalian fauna was more diverse and richer than today. The situation ended when the ecological condition on the island of Crete grew less varied along with a gradual decrease in size of the island.

On the whole, present data on fossil owls are not in conflict with the concept of a geographical species changing in time and place.

10. Hybrid owls

Hybrids have been raised in captivity between among other species:
(a) a female Eagle Owl *Bubo bubo* × male Great Horned Owl *B. virginianus* (Dudley Zoo, England, Risdon, 1951)
(b) a female Tawny Owl *Strix aluco* × male Ural Owl *Strix uralensis* (Scherzinger, 1983).

The hybrid progeny has proved fertile with parent species, confirming the close relationship between these species as suggested in the previous paragraphs.

Most remarkable is a case of hybridization between a female Striped Owl *Asio clamator* × male Barn Owl *Tyto alba* in the St. Louis Zoo, Missouri, USA (Flieg, 1971). This suprageneric if not suprafamilial mesalliance ended with the death of two embryos at the 15th day of incubation. The extraordinary event illustrates that genetical structures are overruled in nature by the effects of acting species boundaries.

11. Conclusion

Even in a group like owls of which, in comparison with other birds, relatively incomplete details on structure, distribution, habitat, and life style are available, the biological and geographical species concept has fully retained its value and applicability. As is to be expected in variable species, almost any border-line case is represented: it is, by analyzing these species, as if one could observe the species in the process of changing in place and time. As a matter of fact this does not include an insight in the mechanism, nor in the direction of species formation processes and specializations. Having needed and included more than solely quantifiable morphological data, the biological and geographical species concept contains more assets, and in a more realistic way at that, than can be provided by any species concept based on cladistic theories. There is no apparent need to elaborate on sister-groups, nor on such subjective concepts as apomorph and plesiomorph characters for arriving at a synthetic view on the dynamic nature of the owl-species discussed.

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