

INTEGRATING THE FOSSIL RECORD IN THE STUDY OF INSULAR BODY SIZE EVOLUTION: EXAMPLE OF OWLS (AVES, STRIGIFORMES)

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Resum

Les òlibes i els mussols (Aves, Strigiformes) constitueixen un dels millors elements per fer estudis sobre la mida corporal i diferents característiques al·lomètriques, que contemplin espècies vivents i fòssils d'ocells insulars, incloses algunes espècies recentment extingides. Al present estudi s'inclou, com a registre d'espècies vivents, devers 150 taxa insulars, distribuïts sobre 230 illes o arxipèlags. S'inclouen devers 350 taxa continentals com a comparació. El registre de taxa extingits està constituït per 35 òlibes o mussols endèmics, un terç dels quals s'inclouen dintre del gènere *Tyto*. A l'anàlisi del registre actual es consideren diferents variables, incloent-hi característiques físiques i biològiques insulars. Per als taxa vivents i extingits s'han registrat variables amb característiques intrínseques de qualsevol taxon insular. Aquestes són l'evolució de la talla corporal, la classe de talla corporal, l'evolució d'al·lometries, el rang taxonòmic i l'hàbitat. Els resultats revelen alguns patrons d'evolució insular. Aquests patrons difereixen considerablement quan es considera només el registre actual o el registre fòssil. Entre d'altres, el registre actual tendeix a estar empobrit en taxa insulars grans, degut a impactes antropogènics selectius. A més, la via més freqüent d'evolució insular deduïda a partir de l'anàlisi del registre actual sembla ser una suau tendència a la minva de mida, mentre que la tendència oposada es pot deduir a partir del registre fòssil, amb alguns casos extrems únics. Una altra volta aquestes diferències es deuen a extincions selectives. Quan s'integren conjuntament, els dos registres no indiquen cap tendència a l'evolució de la talla corporal d'òlibes i mussols a les illes.

No hi ha cap "lleï insular" per a aquest grup. Aquestes dues observacions es poden estendre a ocells en general, però fa falta un estudi integrat de gran abast. S'observen tendències al·lomètriques a les cames i a les ales, que són les mateixes que es poden observar al conjunt dels ocells. També s'observa una tendència cap a peus i urpes més grans al les òlibes insulars. Els mecanismes que afecten els exemples típicament insulars d'evolució de la talla corporal i d'evolució al·lomètrica constitueixen un altre tòpic complex i difícil. No obstant, s'assenyalen alguns factors i algunes perspectives per a investigar. Es mostra en quina via l'evolució de les òlibes/mussols a Còrsega és original. Els impactes antròpics són els factors principals per explicar les diferències entre el registre vivent i el fòssil. S'han extingit preferentment els taxa més grans, i els taxa endèmics que són resultat d'una evolució extrema. Te poc sentit considerar només el registre fòssil, talment com considerar només les faunes actuals. Com se sap pel que fa la diversitat taxonòmica i la riquesa específica, les faunes insulars vivents estan molt esbiaixades considerant la talla corporal a una comunitat. Les dades sobre els registres vivents i fòssils es complementen en molts d'aspectes. Es recomana una integració dels dos registres, quan sigui possible, abans d'emetre interpretacions. S'indiquen alguns suggeriments per al reconeixement de tipus biològics d'illes, els quals també requereixen tenir en compte l'extens registre fòssil.

Paraules clau: al·lometria, extincions antròpiques, ocells, mida corporal, illes, Strigiformes.

Abstract

Owls (Aves, Strigiformes) constitute one of the best samples for studies including both living and fossil insular bird taxa, including recently extinct, focusing on body size and some allometrical characteristics. For the extant record, around 150 endemic insular taxa, distributed on 230 islands or archipelagoes, were included in the present analysis. Around 350 continental taxa were included for comparisons. The record of extinct taxa is constituted of 35 insular endemic owls, with one third in the genus *Tyto*. Several variables were considered for the extant record, including physical and biological insular characteristics. Variables for characteristics intrinsic to every insular taxon were recorded for extant and extinct records. These are the evolution of body size, body size class, evolution of allometries, taxonomic rank, and habitat. The results provide some patterns of insular evolution. These patterns differ considerably when one considers only the extant or the extinct record. Among others, the extant record tends to be impoverished in larger insular taxa, this being due to selective anthropogenic impacts. In addition, the most frequent way of insular body size evolution seems to be slightly in favour of decreases in the extant record, while the extinct record shows the opposite trend, with some unique extreme cases. Again, these differences are due to the selective extinctions. When integrated together, the two records indicate no general trend for owls in the evolution of size on islands.

There is no 'island rule' either for this group. These two observations might be extended to birds in general, but a comprehensive, integrated study is needed. Allometrical trends are observed on legs and wings that are the same as in birds as a whole. A trend toward larger feet and claws in insular owls is observed as well. The mechanisms underlying the typically insular cases of body size evolution and allometrical evolution are another, complex and difficult topic. However, some factors, and some perspectives for investigations, are emphasized. It is shown in what way the evolution of owls in Corsica is original. Anthropogenic impacts are the main factors to account for the differences between the extant and the extinct record. They made extinct preferentially the larger taxa, and the endemic taxa resulting from evolutions of extreme amplitude. It is meaningless to consider only the fossil record, as well as to trust only the extant record. As was known for the richness and taxonomic diversity, extant insular avifaunas are also heavily biased considering body size in a community. Data on living and fossil records are complementary on many grounds. A quantitative integration of these records is recommended, whenever it is possible, before interpretations. Some suggestions for the recognition of biological types of islands are drawn, which also necessitate taking into account the extensive recent fossil record.

Keywords: allometry, anthropogenic extinctions, birds, body size, islands, Strigiformes.

INTRODUCTION

What is the insular trend for body size in birds, if there is any: increase, decrease, or a more complex trend? The answer is unclear, as it is for other Tetrapods. Frequently, the examples cited deal with gigantism associated with a reduction or loss of flight ability. The studies were rare or restricted to certain groups until recently. Mayr & Vaurie (1948, in Grant, 1965b) and Amadon (1953, in Grant, 1965b) were the first to detect in some groups today or on some islands a trend to an increase in size, considered from then to be rather general. Grant (1965b) reported individual studies showing the opposite trend, always on living groups, and at low taxonomic levels of divergence (generally subspecies). Grant (1965a) noticed that the living Passeriformes on the Tres Marias Islands (Mexico) show a clear trend to a decrease in weight. Again these are low taxonomic levels divergences, and of low amplitude. Then a growing consensus emerged that there is no simple general insular body size trend (increase or decrease) for birds (Grant, 1968, Carlquist, 1974; Case, 1978; Gaston & Blackburn, 1995; Blondel, 2000; and some restricted surveys cited by these authors). Blondel (2000) recalled the cases of gigantism in vegetarian species (e.g. *Aepyornis*, *Dinornis*, *Sylviornis*, *Pezophaps*, *Raphus*...), and of dwarfism in many Passeriformes. The cases of gigantism are numerous, often linked to a reduced or loss of flight ability. Others seem clearly linked to the size of preys (e.g. *Harpagornis moorei*; see Alcover & McMinn, 1994). Actually, the diversity and complexity of examples are great. Some examples of dwarfism exist in diverse groups, of various sizes: many Rallidae (e.g. Ryan *et al.*, 1989); two species of emus (genus *Dromaius*, Casuariiformes – Australian islands up to the recent Holocene; Parker, 1984); a cassowary (*Casuarius lydekkeri*, Casuariiformes – New Guinea; Rich *et al.*, 1988). Conversely, gigantism is reported in extinct Passeriformes (e.g. *Emberiza alcoveri* – Canary Islands; Rando *et al.*, 1999), or a Caprimulgiformes (genus *Megaeothales* – New Zealand; Rich & Scarlett, 1977). The latter cases are associated with strong reductions in flight ability (and tarsus lengthening for *E. alcoveri*). Thus, there is no evidence for a general trend toward either an increase or a decrease in size in insular birds, which seems confirmed by two recent studies (Clegg & Owens, 2002; Cassey & Blackburn, 2004).

Recently a study proposed evidence for the 'island rule' in birds (Clegg & Owens, 2002), but some remarks may be opposed to this view. The 'island rule' was established for mammals where large species tend to decrease and small ones to increase in size on islands (e.g. van Valen, 1973; Lomolino, 1985; see Meiri *et al.*, 2004 for some exceptions). The sample analyzed by Clegg & Owens (2002) was small and suffered from several important biases, some of the most problematical being the absence of data from the recent fossil record (dating from before the anthropogenic extinctions and extirpations on islands) and the exclusion of all the flightless taxa. The island/mainland differences observed in this extant sample were generally small and rarely reached the 5 % minimal value proposed by Lomolino (1985). Then, the trends observed were of very low magnitude

(essentially less than 1 or 2 % in body weight on average), and cannot compare with the well marked island rule in mammals (with up to 50% differences in some groups). This will not be developed here, yet it is better at present to consider as unknown whether the 'island rule' applies to birds or not.

To summarize, there are only more or less striking individual examples of insular dwarfism or gigantism in birds, but yet no trend appears, either with extant or with extinct forms. A necessary step is now to start integrating both records. As suggested by Case (1978), given the great disparity of patterns seen in birds, both living and extinct, it may be useful to examine bird orders separately for example, and to integrate both living and recently extinct taxa. Most of these recent extinctions or local extirpations on islands were due to anthropogenic impacts. In most cases, these impacts were Holocene in age, repeated, and indirect, such as introduction of diseases, continental predators or competitors, modification of landscape, but sometimes also direct over-hunting by humans (Olson & James, 1982; James & Olson, 1991; Olson & James, 1991; Milberg & Tyrberg, 1993; Steadman, 1995; Mourer-Chauviré *et al.*, 1999; Sadler, 1999; Duncan *et al.*, 2002; Blackburn *et al.*, 2004). The absence of such taxa in the avifaunas of today is therefore unnatural, and the only way to approximate the natural communities and complete taxon lists is to integrate both the living impoverished faunas and the recently extinct taxa. Hitherto very few analyses based on such an integrated insular record for birds have been made, a recent example being the study of an integrated Holocene bird record of New Zealand (Cassey & Blackburn, 2004). The objective of the present work is to present preliminary conclusions arising from analyses made on an integrated native insular record of the Strigiformes (owls) of the world.

The order Strigiformes is particularly well-adapted for this study, because (1) extant insular owls are widespread and frequently exhibit size and allometrical modifications; (2) recently extinct owls are well represented in the fossil record of islands, they also often exhibit these kinds of modifications - and they are relatively easy to identify osteologically. Their intermediate flight abilities can explain this. They are sedentary enough to undergo insular evolution, without too much gene flow from the continent (or other islands). Meanwhile, they sometimes cross important distances over the sea, which allows them to colonize islands up to 3500 km apart from any other land.

A study of body size and allometrical evolutions in both the recent fossil and extant records of insular owls was carried out. Some preliminary results will be exposed, as well as conclusions about the method, and perspectives to improve the pertinence of such analyses.

METHODS

The body size is expressed as a semi-quantitative variable, given the necessary approximations from the literature on extant taxa, as well as from the data on extinct forms. The allometries studied here are the relati-

ve size of the beak, the wings, the legs, the pedal digits and claws. These data are also expressed as semi-quantitative variables.

A very recurrent problem is to avoid apparently insular taxa, which actually have a relictual distribution, for anthropogenic or natural reasons, the island(s) having played the role of a refugium. Therefore, some apparently insular characteristics can well be not insular at all. The Laughing Owl *Sceloglaux albifacies* (G.R. Gray), probably extinct, was known only in New Zealand, but there are some doubts arising from the possibility of a recent wider distribution (e.g. König *et al.*, 1999). A similar case could be that of the Papuan Hawk Owl *Uroglaux dimorpha* (Salvadori), which presents today a disjunct insular distribution (Holt *et al.*, 1999; König *et al.*, 1999). According to Case (1978), many insular giant reptiles actually display a relictual distribution compared with recent Pleistocene times, like the giant monitor lizard of Komodo.

An even more widespread problem is the identification, as precise as possible, of the direct ancestor of an insular form (on the continent or on adjacent islands). It is the only way to evaluate the direction and amplitude of the insular modifications. The living Giant Scops Owl *Mimizuku gurneyi* (Tweeddale), of the Philippine Islands, was until recently often considered a dwarf eagle owl (close to the genus *Bubo*). However, recent DNA analyses by Miranda *et al.* (1997) demonstrated that it is closer to the smaller scops owls of the genus *Otus*, therefore making it a giant insular owl. This is an extreme case, with the inversion of the interpretation of body size evolution, but smaller uncertainties exist for many other taxa.

In all the cases where these kinds of doubt exist, the taxon implied was not included in the list of in situ evolved insular owls. For example, the extinct *Tyto balearica* as a species, of Western Mediterranean Islands, was not included because its closest continental relative is not known, and it is not clear at which taxonomic level it can be considered an insular owl (Louchart, 2002). *Sceloglaux albifacies*, despite typical insular-looking characteristics (long legs, short wings, terrestrial habits), is not included in the body size analyses because of its possibly relictual distribution, and its unknown ancestry (König *et al.*, 1999).

All the non-indigenous owls on islands (introduced by man) were excluded from all the analyses.

A nomenclatural, but important issue is that of the terms « dwarf » and « giant », which imply that strong modifications are involved. Actually, it is obvious at a first glance that most of the insular size modifications are slight. Proportionate dwarfism and proportionate giantism were defined as heterochronies with isometrical conservation of proportions (Gould, 1977), but no limit was quantified to define dwarfism or giantism as opposed to slight decrease or increase in size. Other categories of heterochronies imply allometrical modifications joined to the dwarfism or giantism. Many cases of heterochrony with allometries are known in flightless insular birds (e.g. Livezey, 1989; 1990; 1993; 1995), but in most cases with Strigiformes, it remains to be tested whether the allometries implied are correlated with a trend in body size modification. With this in mind, the data on

size and allometries are considered separately here. The modifications were arbitrarily considered here as slight (moderate) between 5 % and 10-15 % of change in mass, and important (strong) over this value. In the latter case, the terms dwarfism and giantism are also used.

The minimal value of 5 % of difference in mean weight (or an equivalent cubed linear measurement) between an insular taxon and its mainland counterpart to record it as a size modification follows Lomolino (1985) who defined this value as the minimum statistically reliable and applied it to mammals.

Throughout the text unless the context indicates otherwise, the term "island" refers to either an island or an archipelago.

BODY SIZE - EXTANT STRIGIFORMES

The data

A database was constituted with two main tables. In the first one, the individuals are the endemic insular taxa. In the second one, the individuals are the islands.

The variables were defined as follows.

Intrinsic variables: variables relative to the endemic insular taxa

The individuals are the endemic insular taxa (n=148) on the world: from the sub-species to the genus.

Description of the variables:

• In situ body size evolution of the taxon

The insular taxonomic unit can display the following states for this variable:

-2: important decrease (dwarfism)

-1: slight decrease

0: no change

1: slight increase

2: important increase (giantism)

?: unknown

The cases where insular endemic subspecies show invariance in size compared with the closest continental subspecies were taken into account for all the subspecies in the genus *Tyto*. For five species of Strigidae (three of *Otus* and two of *Ninox*), all the subspecies invariant in size or allometry between themselves were considered a unique insular (endemic or not) subspecific taxon called « other subspecies » for the intrinsic variables (in each of the five cases). This choice is justified by the slight differentiation observed on other characters, and because they would have disequibrated the information too much with poorly differentiated taxa, the focus of the study being on the evolutionary changes. These choices will always be taken in consideration when the data are compared and interpreted: the cases of invariance will not be quantitatively interpreted. On the other hand, these subspecies have of course been taken into account for the variables relative to the insular communities of owls associated with every studied taxon (see below).

• Taxonomic rank of insular in situ differentiation

The insular endemic taxon was considered as a taxonomic category, ranging from the subspecies to the genus. If a polytypic species is insular, it was taken into

account as such, and its different subspecies as well. Other example: if a monotypic species is insular at the genus level, it was taken in account once at the genus level. The states for this variable are:

- 1: subspecies
 - 2: species
 - 3: group of close species, superspecies, or genus
- Size class (category of weight) of the insular taxon

Five categories are defined:

- 1: < or = 150 g
- 2: 151 – 250 g
- 3: 251 – 500 g
- 4: 501 – 1000 g
- 5: > 1000 g

In the cases where the weight is not known, and no allometrical difference is reported, the weight was inferred from other measurements, and using close taxa for which these and the weight were both known.

N.B.: The taxa having undergone a size modification were classified in the category corresponding to their present size, *i.e.* after the size evolution. This choice is justified by uncertainties as regards a « precise » estimation of the weight of the ancestral taxon. In addition, it appears that a taxon would generally be only very rarely classified in a different size class if considered before rather than after size evolution. The consequences of the possible bias, minimized by the use of rather wide size classes, will be taken into account in the section Results (see below).

- The type of vegetation frequented by the insular taxon

Six categories are defined:

- 1: forested
 - 2: semi-forested
 - 3: forested to semi-open
 - 4: semi-open
 - 5: open to semi-open
 - 6: open
- i: indifferent (as regards the characteristics of density and height of vegetal cover considered here)

Extrinsic variables: variables relative to the island context

The individuals are the islands ($n=230$).

Description of the variables:

Physical extrinsic variables

- The latitude

The variable is the latitude of the island (for an archipelago, the mean of the latitudes of the different islands), distributed in three classes:

- 1: 0° - 19°
- 2: 20° - 39°
- 3: 40° - 59°

There is no case at higher latitudes.

The values combine northern and southern latitudes together in the same categories.

- The surface

The variable corresponds to the surface of the island (for an archipelago, the sum of all the surfaces of the individual islands) in km²; the surfaces are classified in five categories:

- 1: 1 – 100 km²
- 2: 101 – 1000 km²

- 3: 1001 – 10 000 km²
- 4: 10 001 – 100 000 km²
- 5: 100 000 km² – 1 000 000 km²

The four largest islands included here are by decreasing order of surface: Madagascar (787 000 km²), New Guinea (771 900 km²), Borneo (730 000 km²), and Sumatra (473 606 km²).

- The distance

This is the distance from the island (for an archipelago, the smallest one) to the closest continent or larger island where the parent-taxon lived most probably. It is classified in four categories:

- 1: 10 – 50 km
- 2: 51 – 500 km
- 3: 501 – 1000 km
- 4: 1001 – 2000 km

? : case where the area of distribution of the parent-taxon is unknown

- The situation of the island relative to the continental plateau deep of less than 200 m

Categories:

- 0: beyond the limits of the continental plateau
- 1: within the limits of the continental plateau (relative to the geographical unit from which the distance was measured)

Extrinsic variables related to the community of owls present on the island

Some characteristics of the communities of Strigiformes were recorded for every island. These characteristics are only approximately pertinent because some recent changes in distributions can affect the community which was originally contemporaneous with the evolutionary changes on the insular taxa. These changes are generally unknown. As far as possible, only sympatric taxa were considered in every community.

- The total number of taxa on the island having undergone an evolution in size in situ

All the different taxa were taken in account (insular as well as non-endemic insular), avoiding any redundancy (only the taxa considered at the lowest taxonomic rank being recorded).

The value taken by the variable is the number of taxa for each island.

The following five variables represent the total number of taxa on an island included in every of the size classes:

- Number in size class 1 (< or = 150 g)
- Number in size class 2 (151 – 250 g)
- Number in size class 3 (251 – 500 g)
- Number in size class 4 (501 – 1000 g)
- Number in size class 5 (> 1000 g)

Similarly, the following five variables represent the proportions of taxa in the different size categories relative to the total number of taxa on the island:

- Proportion in size class 1 (< or = 150 g)
- Proportion in size class 2 (151 – 250 g)
- Proportion in size class 3 (251 – 500 g)
- Proportion in size class 4 (501 – 1000 g)
- Proportion in size class 5 (> 1000 g)

Remaining variables:

- The number of endemic insular taxa on the island

- The total number of taxa of Strigiformes on the island

- The proportion of taxa having undergone an evolution in size relative to the total number of taxa on the island

This ratio is expressed in the following categories:

1: 0.01 – 0.20

2: 0.21 – 0.40

3: 0.41 – 0.60

4: 0.61 – 0.80

5: 0.81 – 1

?: unknown

- The proportion of endemic insular taxa relative to the total number of taxa on the island

This ratio is expressed in the following categories:

1: 0.01 – 0.20

2: 0.21 – 0.40

3: 0.41 – 0.60

4: 0.61 – 0.80

5: 0.81 – 1

?: unknown

- The total number of different genera on the island

- The proportion of genera relative to the total number of taxa on the island

This ratio is expressed in the following categories:

1: 0 – 0.20

2: 0.21 – 0.40

3: 0.41 – 0.60

4: 0.61 – 0.80

5: 0.81 – 1

?: unknown

- The total number of taxa divided by the decimal logarithm of the surface of the island

This value is expressed in the following categories:

1: 0 – 0.33

2: 0.34 – 0.67

3: 0.68 – 1

4: 1.01 – 1.33

5: 1.34 – 1.67

6: 1.68 – 2

7: 2.01 – 2.33

?: indeterminate

The two tables –insular taxa table and islands table– are linked by the co-occurrences, *i.e.* every occurrence of a different taxon on a different island.

The sources used to establish this database (with Access™) are (in chronological order):

Olson (1978, 1995); Bunn *et al.* (1982); Talbot Kelly (1982); Pyle & Engbring (1985); Buden (1987); Fry *et al.* (1988); Louette (1988); Langrand (1990); Burton (1992); Sargeant (1992); Dunning (1993); Taylor (1994); Castro & Phillips (1996); Cramp (1998); Del Hoyo *et al.* (1999); Bruce (1999); Holt *et al.* (1999); Marks *et al.* (1999); Doughty *et al.* (1999); and different geographical atlases for the physical characteristics of islands.

A total of 343 taxa were considered, among which 148 are endemic insular.

230 islands were included in the analysis. They are islands of more than 1 km².

The map on Fig. 1 indicates the location of these islands.

N.B.: The analyses and interpretations were processed considering the Strigiformes as a whole, independen-

tly of the taxonomy, because this group is judged ecologically and morphologically rather homogeneous. Qualitatively, the trends appear well shared between the Tytonidae and the Strigidae.

Bivariate analyses

Some analyses using the Kendall's coefficient of rank correlation were processed (using *Statistica*™). The variables are semi-quantitative (discrete categories established from quantitative data, discrete or continuous) and ordered. Therefore this type of analysis is particularly well suited. The degree of correlation obtained between the variables two by two is Kendall's tau (τ). It was calculated by the formula (Kendall, 1938, in Sprent, 1992):

$$\tau = (n_c - n_d) / (1/2 n (n - 1))$$

with n_c the number of pairs of concordant observations and n_d the number of discordant observations between variables two by two; n is the total number of observations. The analyzed data can be summarized in a series of tables of contingency, expressing the cross numbers between all the states of the variables two by two. The fact that several variables were frequently affected by a question mark is considered carefully for the interpretations. All the bivariate tests were processed, and those indicating correlations at least significant ($p < 0.05$) were retained. The value of $t = \tau \sqrt{n}$ indicates the degree of correlation ($0 < \tau^2 < 1$), and can be expressed in %.

For the correlations among extrinsic variables, the individuals are the 220 islands. For the correlations among intrinsic and extrinsic variables considered altogether, the individuals are the 148 endemic insular taxa (from the subspecies to the genera).

Results

It is difficult to interpret correlations for two isolated variables, because it is not clear whether and how the causal relations are distributed. Nevertheless, the following observations are noteworthy.

Correlations among extrinsic variables

Many variables are very significantly correlated positively ($p < 0.01$). Many of these correlations just reflect some obvious common components of the variables (like number of insular taxa – their proportion to the total, etc.) but have no insular meaning. The remaining ones, when showing values of $t = \tau \sqrt{n}$ greater than 10%, are shown in the Table 1. These correlation values remain of low magnitude, however: only two exceed 26%.

It seems that the more endemic the community is, the more frequent is the phenomenon of size evolution (proportion of cases): 51.9% correlation. Under conditions of endemism, it seems that owls « frequently » undergo size modifications.

The proportion of different genera relatively to the total number of taxa tends to be higher when the richness in endemic insular taxa is lower (40.4% correlation). A possible explanation is that an island with a low specific richness is likely to have a relatively high number of different genera. A corollary is that many different gene-

ra can reach an island, even small or remote, probably in a short time geologically. Then, a relatively lower competition is likely to occur between different genera than between species of the same genus, all other things being equal, allowing preferentially different genera to cohabit longer together. This is well known generally in animals.

Incidentally, the distance to a continent (or a larger island), is negatively correlated with the presence of a continental platform, but only rather slightly (23.8% correlation). Actually, the correlations show that the presence or absence of the platform seems at least as important as the distance regarding the insular characteristics of the communities. For typically sedentary birds like many owls, a continental bridge during low sea level periods was certainly necessary for some of the colonizations, at least for the weaker flyers.

Correlations among intrinsic and extrinsic variables considered altogether

The correlations are generally of far lower magnitude than in the case of the extrinsic variables alone. Even if highly significant, few exceed a value of 5%. Only four exceed a value of 10%, with a maximum of 26.5%, all but one being without insular signification (see above). There is only a weak trend (12.3% correlation) for larger insular endemic taxa to frequent more open habitats. This may however apply to mainland taxa as well. A future study including all continental owls will provide some clues to answer this question.

The absence of correlation between the surface of the island and any other variable is noticeable. The latitude is correlated, positively and weakly, only with the vegetation type frequented by taxa. Apparently, forested habitats are more frequented on lower latitude islands. This could be simply due to the predominance of such habitats on tropical islands. The distance is therefore the only geographical characteristic affecting communities and size evolution in this analysis. It is possible that this

is affected by anthropogenic selective extinctions and extirpations, which will be developed in the section Discussion.

Finally, a negative correlation, significant but of very low magnitude ($\tau^2 = 2.59\%$) appears between the direction of the evolution of size and size class of the taxa. It is apparent on Fig. 7. The smaller taxa would tend very slightly to increase in size, the larger to decrease, but this is no more apparent when fossils are integrated (Fig. 8; and see below).

Remark

A co-occurrence today in real sympatry (and in the same environments) of two species of one genus on one island is not rare (e.g. several islands of Indonesia for the genus *Tyto*). Even three species of *Tyto* occur together in SE New Guinea: *T. alba meeki*, *T. longimembris* and *T. tenebricosa*, but the latter lives in cloudy rain forest, whereas the two others occur in open habitats (König *et al.*, 1999). Generally, the two sympatric species are of different size in *Tyto*. However, at least in two cases (Timor and Solomon Islands), the two species are of the same size: here *T. alba delicatula* and *T. longimembris*; they also live in the same habitats (König *et al.*, 1999). This is partly in contradiction with a widespread idea (see Grant, 1965b) that two species of the same genus rarely co-exist on an island, due to interspecific competition. It appears that some traits – probably behavioural – other than size alone, can allow such a sympatry within one genus. In the fossil record, at least three species of the genus *Tyto* certainly co-existed in the Mio-Pliocene of the palaeo-« island » of Gargano (Ballmann, 1973, 1976; Pavia, pers. com.). Two species of *Tyto* lived together during part of the Pleistocene in Corsica (Louchart, 2002), and three in the Pleistocene of Cuba (*T. alba*, *T. noeli*, *T. riveroi*; Arredondo, 1982). In each of these fossil examples, however, the co-existing species were of different body size (Table 2).

	Distance	Continental plateau	Number of insular endemic taxa	Proportion of different genera genera to the total number of taxa
Continental plateau	<i>23.8</i>			
Proportion of different genera to the total number of taxa			40.4	
Number of taxa showing size evolution			51.9	
Number of taxa in the size class 1		11.4		
Number of taxa in the size class 2				17.2
Number of taxa in the size class 5		12.1		
Ratio richness / surface		10.1		26.0

Table 1. Correlation values τ^2 higher than 10%, between extrinsic insular variables, after Kendall's rank correlation test. All these values are expressed in %, and correspond to highly significant correlations ($p < 0.01$). In normal police: positive correlations. In italics: negative correlations. Here are shown only the correlations with a signification for insularity (see the text).

Taula 1. τ^2 valors de correlació superiors al 10%, entre variables insulars extríniques, segons el test de correlació re rangs de Kendall. Tots aquests valors s'expressen en % i corresponen a correlacions altament significatives ($p < 0.01$). En lletres rodones, correlacions positives. En cursives, correlacions negatives. Es mostren només les correlacions amb un significat per a l'anàlisi de la insularitat (veure text).

Species	Island/Archipelago	Known age	Putative ancestor	Size evolution	Allometrical evolution of tarsus	Allometrical evolution of wing	Size class	Taxonomic rank of divergence
<i>Tyto balearica cyrneichnusae</i>	Corsica, Sardinia	Middle Pleistocene	<i>Tyto</i> sp.	?	?	0	4	1
<i>Tyto cavatica</i>	Puerto Rico	Pleistocene	<i>Tyto glaucops/ insularis/ bargei</i>	0			3	2
<i>Tyto gigantea</i>	Gargano	Mio-Pliocene	<i>Tyto</i> sp.	2	L?		5	2
<i>Tyto neddi</i>	Barbade (Lesser Antillean Is.)	Quaternary	<i>Tyto</i> sp.	1			4	2
<i>Tyto noeli</i>	Cuba	Pleistocene	<i>Tyto alba</i>	1			4	2
<i>Tyto ostologa</i>	Hispaniola	Pleistocene	<i>Tyto alba</i>	1			4	2
<i>Tyto pollens</i>	Great Exuma, New Providence (Bahamas)	Pleistocene	<i>Tyto alba</i>	1	-L		5	2
<i>Tyto riveroi</i>	Cuba	Pleistocene	<i>Tyto alba</i>	2			5	2
<i>Tyto robusta</i>	Gargano	Mio-Pliocene	<i>Tyto</i> sp.	2	LL		4	2
<i>Tyto</i> nov. sp.	Sicily	Middle Pleistocene	<i>Tyto</i> sp.	1 or 2			4	2
<i>Tyto</i> sp.	Gargano	Mio-Pliocene	<i>Tyto</i> sp.	?			4	
<i>Tyto</i> sp.	Madeira	Pleistocene	<i>Tyto</i> sp.	-1?			2 or 3	2?
<i>Tyto? letocarti</i>	N.-Caledonia	Holocene	?	?			3	
<i>Mascarenotus grucheti</i>	Réunion	Holocene	<i>Otus</i> sp.	2(?)	LL	-1	3	3
<i>Mascarenotus murivorus</i>	Rodrigue	Holocene	<i>Mascarenotus</i> sp.	0			3	2
<i>Mascarenotus sauzieri</i>	Mauritius	Holocene	<i>Mascarenotus</i> sp.	0			3	2
aff. <i>Otus scops</i>	Madeira	Quaternary	<i>Otus</i> sp.	?			1	
<i>Gymnoglaux</i> sp.	Cuba	Pleistocene	?	0			1	2
<i>Bubo (Strix?) perpasta</i>	Gargano	Mio-Pliocene	<i>Bubo</i> sp. (?)	-1?			4	?
<i>Bubo insularis</i>	Corsica, Sardinia	Pleistocene	<i>Bubo (bubo)</i>	-2(?)	L(?)	-1	4	2
<i>Bubo osvaldoi</i>	Cuba	Pleistocene	<i>Bubo</i> sp.	1?		-1	5	2
<i>Grallistrix auceps</i>	Kauai (Hawaii)	Holocene	<i>Grallistrix</i> sp.	0			3	2
<i>Grallistrix erdmani</i>	Maui (Hawaii)	Holocene	<i>Grallistrix</i> sp.	-1?			3	2
<i>Grallistrix geleches</i>	Molokai (Hawaii)	Holocene	<i>Strix</i>	?	LL	-1	3	3
<i>Grallistrix orion</i>	Oahu (Hawaii)	Holocene	<i>Grallistrix</i> sp.	-1?			3	2
<i>Ornimegalonyx oteroi</i>	Cuba	Pleistocene	<i>Strix/Ciccaba</i>	2	L	-2	6 (=5)	3
<i>Ornimegalonyx</i> sp. 2	Cuba	Pleistocene	<i>Strix/Ciccaba?</i>	?	?	?	?	?
<i>Athene angelis</i>	Corsica	Pleistocene	<i>Athene noctua</i>	2	-L	-1	3	2
<i>Athene cretensis</i>	Crete, Armathia	Pleistocene	<i>Athene noctua</i>	1	L		3	2
<i>Athene</i> sp.	Eubea	Holocene?	<i>Athene noctua</i>	1			2	2
<i>Athene trinacriae</i>	Sicily	Middle Pleistocene	<i>Athene noctua</i>	0	L		2	2
<i>Athene</i> nov. sp.	Puerto Rico	Pleistocene	<i>Athene (cunicularia)</i>	-1?			2	2
<i>Athene</i> sp.	Cova na Reia - Eivissa (Balearic Is.)	Pliocene	<i>Athene</i> sp.	-1??			2	2
<i>Athene (cunicularia)</i>	New Providence (Bahamas)	Pleistocene	<i>Athene (cunicularia)</i>	-1			2	1?
<i>Pulstarix arredondoii</i>	Cuba	Pleistocene	<i>Pulsatrix perspicillata</i>	1	-L		4	2

Table 2. Extinct endemic insular Strigiformes in the world. The four species of *Grallistrix* are very homogeneous in terms of size and allometries, as well as the three species of *Mascarenotus*. For each of these genera, only one of the species is chosen for the size and allometrical modifications, the other species being considered as showing little change inside the genus. In *Grallistrix*, the type species *G. geleches* of Molokai, is arbitrarily considered here as representative of the basal level of evolution of the genus. In *Mascarenotus*, the species of the largest island (Réunion) *M. grucheti* is similarly considered as such. In the genus *Ornimegalonyx*, four species have been described, but it is now considered most likely that only two are valid (W. Suarez and O. Jiménez, pers. com.). *Ornimegalonyx oteroi* – the type species – and *Ornimegalonyx* sp. 2 are retained here. The references used are cited in the text.

Taula 2. Strigiformes endèmics insulars extingits del món. Les quatre espècies de *Grallistrix* són molt homogènies en termes de mida i al·lometries, igual que ho són les tres espècies de *Mascarenotus*. Per a cadascun d'aquests gèneres només s'ha triat una espècie per analitzar les modificacions de talla i al·lométriques, considerant-se que hi hauria pocs canvis dintre del gènere. A *Grallistrix*, es considera *G. geleches*, l'espècie tipus de Molokai, com a representativa del nivell basal d'evolució del gènere. A *Mascarenotus*, es considera com a tal l'espècie de l'illa més gran (*La Réunion*), *M. grucheti*. Al gènere *Ornimegalonyx* s'han descrit quatre espècies, però actualment sembla que el més probable es que només n'hi hagi dues de vàlides (W. Suarez and O. Jiménez, pers. com.). Es retenen aquí *Ornimegalonyx oteroi* – l'espècie tipus – i *Ornimegalonyx* sp. 2. Les referències emprades es citen al text.

INTEGRATION OF THE RECORD OF EXTINCT INSULAR STRIGIFORMES

The intrinsic characteristics of the 35 extinct insular endemic Strigiformes recorded here were evaluated (Table 2). 13 taxa belong to the genus *Tyto*, and 22 are Strigidae. They are distributed over the world (Fig. 1). The body size class was recorded for each extinct taxon using the relationships established for predatorial birds by Campbell & Marcus (1992) between the least circumference of the femur and tibiotarsus and the body weight.

The islands which have a most significant fossil record of Quaternary owls are generally not the same as those where live today the largest numbers of endemic owls (with the noticeable exception of the Greater Antilles). This is a geographical effect of the extinctions discussed in this paper. The two records are thus complementary geographically.

The sources used to establish the synthetic Table 2 are (in chronological order):

Wetmore (1920, 1937); Brodkorb (1959, 1969); Ballmann (1973); Arredondo (1972, 1975, 1976, 1982); Olson (1978, 1984, 1985); Olson & Hilgartner (1982); Rich & van Tets (1982); Weesie (1982, 1988); Pieper (1985); Mourer-Chauviré & Weesie (1986); Steadman (1986); Balouet & Olson (1989); Mourer-Chauviré & Sanchez Marco (1988); Olson & James (1991); Alcover *et al.* (1992); Burton (1992); Cheneval & Adrover (1993); Alcover & McMinn (1994); Arredondo & Olson (1994); Mourer-Chauviré *et al.* (1994, pers. com.); Mourer-Chauviré *et al.* (1997); Mourer-Chauviré *et al.* (2001); Mlikovsky (1998a; 1998b); Tyrberg (1998); Pieper *vide* Jaume *et al.* (1993, in Tyrberg, 1998); Steadman & Hilgartner (1999); Pavia (2000); Lou-

chart (2001; 2002); Pavia & Mourer-Chauviré (2002), O. Jiménez (pers. com.), M. Pavia (pers. com.), W. Suárez (pers. com.).

Extrinsic variables are often not well documented for the extinct taxa. Therefore, only intrinsic variables give semi-quantified results for the extinct record.

Size: observations and interpretations

The data allow a qualitative comparison between extinct and extant insular taxa, as regards the univariate trends shown by the analysis of the intrinsic variables. Every of the following intrinsic variable was considered separately: direction and amplitude of size evolution, size class, taxonomic rank of divergence. The vegetation type of the habitat being unknown for most of the extinct taxa, this variable was not included in this comparison.

Any bias toward an under-representation of the smaller taxa in the fossil record can be excluded, because the fossils of owls are easily identifiable, and the smallest owls are still « small to medium sized » birds, very unlikely to be overlooked by avian palaeontologists. This confidently allows the following interpretations.

Trends in the evolution of size in situ (Figs. 2- 4)

The indeterminate cases (« ? ») were excluded from this analysis.

The extant taxa showing insular evolution of size display a trend to decreases in size: there are almost twice as many decreases as increases in size (Fig. 2). Among the cases of important size modifications, six are decreases (dwarfisms), while only one is an increase (giantism: *Mimizuku (Otus) gurneyi* (Tweeddale), of the Philippine Islands).

The extinct taxa, on the other hand, show other trends (Fig. 3). Their disparities in comparison with the

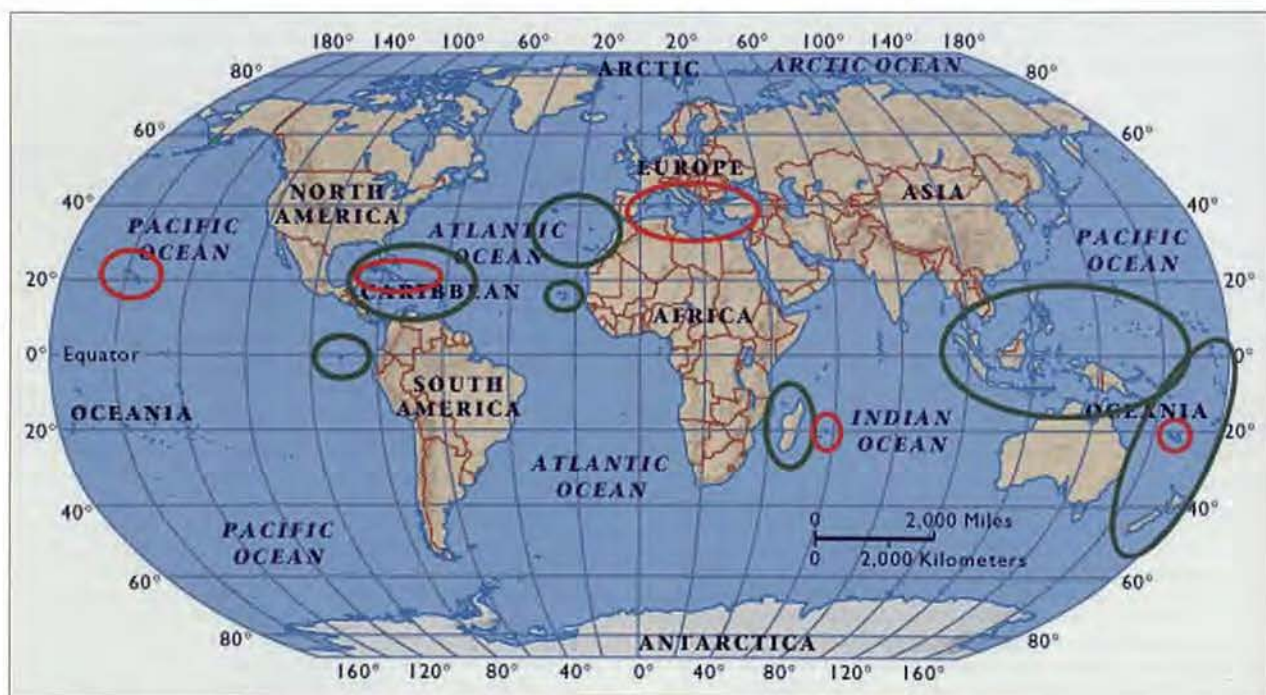


Fig. 1. Map showing the distribution of the principal islands or archipelagos where endemic extinct (in red) and living (in green) Strigiformes are recorded.

Fig.1. Mapa que mostra la distribució de les illes principals on s'han documentat Strigiformes endèmics extingits (en vermell) i vivents (en verd).

extant record are in that:

- they include a larger proportion of moderate increases in size;
- they include a considerably larger proportion of important increases in size;
- the fossil record concentrates almost all the cases of gigantism;
- dwarfism is very rare: only the case of *Bubo insularis* (Pleistocene-Holocene of Corsica and Sardinia) is well supported (Louchart, 2002).

Most of the decreases in size are uncertain. There is a need for a more precise account of the evolutionary relationships.

The deficit in cases of gigantism in living owls is clearly the effect of differential extinctions and extirpations, for the same reasons as with the size classes. This will be developed in the section Discussion. When the extant and extinct taxa are considered altogether, there is no remaining trend in the evolution of size: there are symmetrically almost as many increases as decreases (Fig. 4). In the extant record, island by island, there is no exclusion between the cases of decreases and those of increases in size: the higher the number of all cases of size modification on an island, the higher the number in both the directions. Therefore even at the scale of individual islands there is no insular trend in the evolution of size.

Size classes (Fig. 5)

The extant taxa in the two classes of smallest size (less than 250 g) are not well represented among the taxa that are present both on islands and on the continents. These size classes are better represented among insular endemic taxa. This is probably due to the higher proportion of allopatric species in certain genera in these size classes (e.g. *Otus*, *Ninox*), compared with classes of larger body size. In both these extant records the intermediate size class (3) is the best represented as is the case in most systematic groups of animals.

In extinct insular taxa, the large sizes (more than 500 g) are relatively better represented than in extant ones, endemic as well as non-endemic. A special size class (n° 6) may even be created for the extinct Pleistocene *Orni-megalyonyx oteroi*, the giant owl of Cuba, which measured around one meter high; however it is retained in the size class 5. The amplitude of the evolution of size in situ for this genus is unknown, because its continental ancestor is not identified, but it is provisionally placed in the category « +2 ». Globally the taxa of large size are under-represented in the extant insular record. Such a difference in size representations reflects the selective recent extinctions and extirpations, mainly anthropogenic (see section Discussion).

The taxonomic ranks of divergence (Fig. 6)

The quasi-absence of cases of differentiation at a subspecific rank in the extinct record is due to difficulties in osteological discrimination of fossils at these very low degrees of divergence (see also Brodkorb, 1959; about possible subspecific ranks for extinct *Tyto* in the Caribbean Islands).

Size classes and evolution of size (Figs. 7-8)

The slight trend noticed for extant taxa alone is per-

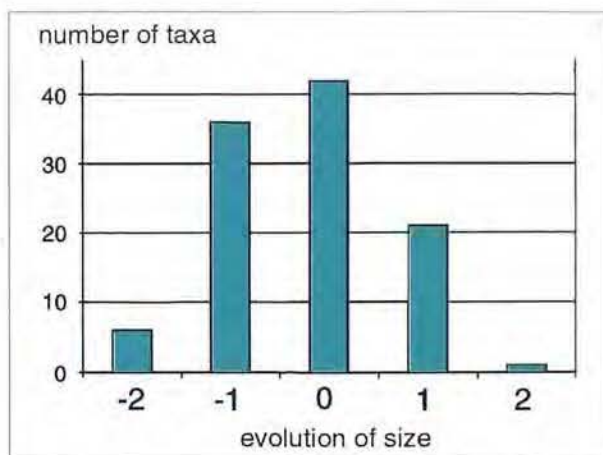


Fig. 2. Distribution of the extant endemic insular taxa of Strigiformes according to the categories of size evolution.

Fig. 2. Distribució dels taxa d'estrigiformes insulars endèmics vivents d'acord amb les categories d'evolució de talla.

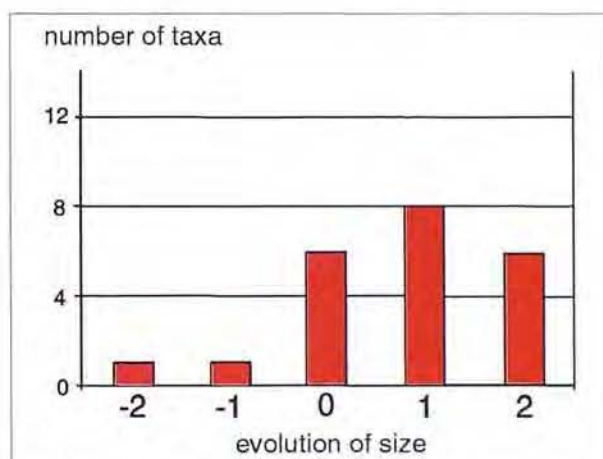


Fig. 3. Distribution of the extinct endemic insular taxa of Strigiformes according to the categories of size evolution.

Fig. 3. Distribució dels taxa d'estrigiformes insulars endèmics extingits d'acord amb les categories d'evolució de talla.

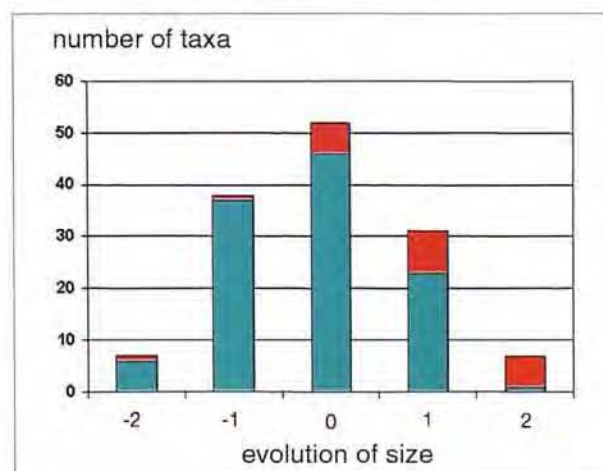


Fig. 4. Quantitative integration of the two endemic insular records: extant (in turquoise) and extinct (in red) taxa. Distribution of the taxa of Strigiformes according to the categories of size evolution.

Fig. 4. Integració quantitativa dels dos registres insulars endèmics: taxa vivents (en turquesa) i extingits (en vermell). Distribució dels taxa d'estrigiformes d'acord amb les categories d'evolució de la mida.

ceptible on the Fig. 7: smaller extant taxa show more increases in size, and larger ones show more decreases.

For extinct taxa alone, however, the pattern is different. Most of the moderate increases revealed by extinct taxa concern those which were already large before isolation (classes 4 and 5), and the gigantism essentially concerns large taxa too. The smallest taxa which evolved

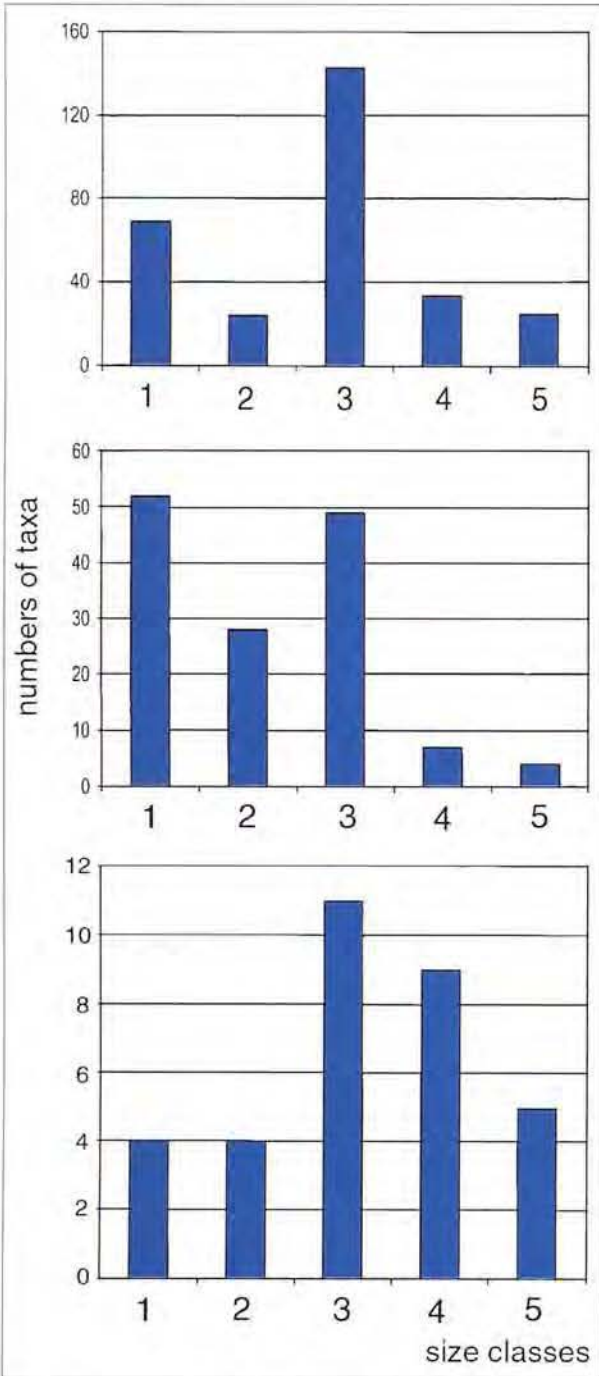


Fig. 5. Distribution of the taxa of Strigiformes according to the different size classes. Top: Extant taxa present simultaneously on islands and on the mainland. Middle: extant endemic insular taxa. Bottom: extinct endemic insular taxa.

Fig. 5. Distribució dels taxa d'estrígiformes segons les diferents classes de talla. A dalt: taxa vivents presents simultàniament a illes i continents. En mig: taxa insulars endèmics vivents. A sota: taxa insulars endèmics extingits.

toward gigantism, extinct and extant records altogether, led to *Athene angelis*, from the Pleistocene of Corsica (Louchart, 2002), and *Mimizuku (Otus) gurneyi*, living in the Philippine Islands, as well as probably the first differentiated species of *Mascarenotus*, ancestral to the others, all in the Mascarene Islands.

When the extinct and extant data are put together, there is no more correlation between the size category and the direction of size evolution (Fig. 8).

Therefore, there is no 'island rule' for owls: the smaller ones do not tend to increase in size (14 decreases and 15 increases), while the larger ones only slightly tend to decrease (31 decreases and 24 increases).

Another way to confirm the absence of 'island rule' in owls is to consider other groupings of size classes. If the size class 3 is considered the medium one, then it is useful to look at the trends in the classes of smaller size than 3 vs. the ones of larger size than 3. In addition this allows to avoid the possible bias induced by the necessary choice to assign the size class of a taxon after in situ evolution (see section Methods). This bias would affect the proportion of taxa showing an increase vs. a decrease in size only in the intermediate class (3). If a category of larger taxa is defined as separated from the category of smaller taxa by the equivalent of the class 3, then no taxon can be erroneously put in a wrong category from being classified after in situ evolution, because no case has been recorded that would cross two limits of size class in the course of its insular size modification. The best marked cases cross only one size class limit and are rare (14 cases over 84). Thus, examining the proportions of decreases and increases for taxa included in disjunct "extreme" size classes makes it possible to eliminate this possible bias (which would act against the island rule). The Table 3 confirms that the absence of island rule is not an artifact: the smaller classes (1 or 1+2) comprise similar numbers of decreases and increases, while the larger classes (4+5 or 5) comprise even slightly more increases than decreases.

		Decrease	Increase
smaller	Size class 1	11 (2)	10 (2)
	Size classes 1+2	14 (3)	16 (2)
larger	Size classes 4+5	8 (1)	11 (4)
	Size class 5	3 (0)	4 (3)

Table 3. Distribution of the cases of insular body size modification of the smallest and the largest Strigiformes (living + extinct) in the categories 'decrease' (categories -1 and -2 lumped) and 'increase' (categories 1 and 2 lumped) according to the size of the taxa. First row: size class 1 only; second row: size classes 1 and 2; third row: size classes 4 and 5; fourth row: size class 5 only. The 'medium' size class 3 is excluded. In parentheses after every total is indicated the number of best marked modifications (categories '-2' and '2').

Taula 3. Distribució dels casos de modificació de la mida corporal de les estrígiformes més petites i més grans (vivents i extingides) a les categories de "minva" (categories -1 i -2 juntes) i "increment" (categories 1 i 2 juntes) d'acord amb la mida dels taxa. Primera filera, només la classe de mida 1; segona filera, classes de mida 1 i 2; tercera filera, classes de mida 4 i 5; quarta filera, només la classe de mida 5. S'ha exclòs la classe de mida "mitjana" 3. Darrera cada total, entre parèntesi, s'indica el nombre de modificacions més marcades (categories "-2" i "2").

	Strong negative allometry (-2)	Moderate negative allometry (-1)	Moderate positive allometry (1)	Strong positive allometry (2)	Moderate shortening (-1)	Moderate lengthening (L)	Strong lengthening (LL)
Beak	1: <i>Otus pauliani</i>	3: <i>Tyto alba gracilirostris</i> ; <i>T. a. meeki</i> ; <i>Phodilus badius parvus</i>	2: <i>Tyto alba sumbaensis</i> ; <i>T. a. crassirostris</i>	1: <i>Nesasio solomonensis</i>			
Wing	1: <i>Ornimegalonyx</i> sp. †	8: <i>Tyto alba bargei</i> ; <i>Mascarenotus grucheti</i> †; <i>Bubo insularis</i> †; <i>B. osvaldoi</i> †; <i>Grallistrix</i> sp. †; <i>Athene angelis</i> †; <i>Sceloglaux albifacies</i> (†); <i>Asio otus canariensis</i>	1: <i>Tyto novaehollandiae calabyi</i>				
Tarsus			3: <i>Tyto alba gracilirostris</i> ; <i>T. a. schmitzi</i> ; <i>T. novaehollandiae calabyi</i>	1: <i>Nesasio solomonensis</i>	4: <i>Tyto pollens</i> †; <i>Athene angelis</i> †; <i>Pulsatrix arredondoii</i> †; <i>Nesasio solomonensis</i>	8: <i>Tyto alba ernesti</i> ; <i>T. a. detorta</i> ; <i>Otus insularis</i> ; <i>Pyrroglaux podarginus</i> ; <i>Ornimegalonyx</i> sp. †; <i>Athene cretensis</i> †; <i>A. trinacriae</i> †; <i>Sceloglaux albifacies</i> (†)	5: <i>Tyto robusta</i> †; <i>Otus nudipes</i> ; <i>Gymnoglaux lawrencii</i> ; <i>Mascarenotus</i> sp. †; <i>Grallistrix</i> sp. †
Foot digits and claws		3: <i>Phodilus badius parvus</i> ; <i>Otus alfredi</i> ; <i>O. collari</i>	7: <i>Tyto alba ernesti</i> ; <i>T. a. detorta</i> ; <i>T. a. gracilirostris</i> ; <i>T. a. schmitzi</i> ; <i>T. a. crassirostris</i> ; <i>T. novaehollandiae calabyi</i> ; <i>Otus alius</i>	2: <i>Athene angelis</i> †; <i>Nesasio solomonensis</i>			

Table 4. Allometrical evolution in endemic island owls, living and extinct altogether. Only the instances where a change occurred are taken in account here. The values correspond to the number of taxa falling in every category. †: extinct taxon.

Taula 4. Evolució al·lomètrica als mussols i òlibes insulars, vivents i extingits, tots junts. Només es tenen en compte els exemples en els quals s'han detectat canvis. Els valors corresponen als nombres de taxa que cauen dins cada categoria. †: taxon extingit.

Allometrical insular evolution

Allometrical trends in insular birds are well known: on the beak, wing or tarsus, in living or extinct Passeriformes (Grant, 1965a,b; 1966; Rando *et al.*, 1999; Seguí, 1998); on the wing or the tarsus in Falconiformes (e.g. Suarez & Olson, 2001), in Psittaciformes (*Necropsar rothschildi*, J.P. Hume, pers. com.), in Strigiformes (references in this study); on the wing in the numerous examples of reduction or loss of flight ability in insular (mainly extinct) taxa, known in at least 14 orders of birds (references in Louchart, 2001). The trends, when present, are in an increase of the relative size of the beak and the relative length of the tarsus, and a decrease in the relative size or length of the wing. All these are likely to be observed on fossil bones.

Allometries were recorded for extant, as well as extinct owls, when the information was available or interpretable. These data were analyzed to evaluate the place of Strigiformes in this context. The sources used to complete the database were the same as for body size.

The data for extant, and moreover for extinct taxa are not abundant. Only a qualitative comparison of the two records can be made. It reveals that the trends displayed are basically the same for both, but are more extreme in the extinct taxa.

Data and observations

Description of the variables

When a modification occurs in the length of limbs in birds, the most distal elements are affected at most and first (Rando *et al.*, 1999). It is judged pertinent to interpret osteological data of the tarsometatarsus length in terms of hindlimb length, and the recent data of length in the ornithological literature either on the « tarsus » or on the whole limb as representative of the changes in hindlimb length as well.

• Beak

Five categories are defined:

- 2: strong negative allometry
- 1: moderate negative allometry
- 0: isometry
- 1: moderate positive allometry
- 2: strong positive allometry

• Wing

Four categories are defined:

- 2: strong negative allometry
- 1: moderate negative allometry
- 0: isometry
- 1: moderate positive allometry

• Tarsometatarsus / « tarsus »

Six categories are defined:

- L: moderate shortening
- 0: isometry
- 1: moderate positive allometry (in all its dimensions)
- 2: strong positive allometry (in all its dimensions)
- L: moderate lengthening
- LL: strong lengthening

• Pedal digits and claws

Four categories are defined:

- 1: moderate negative allometry
- 0: isometry

1: moderate positive allometry

2: strong positive allometry

Univariate trends (Table 4)

Data relative to the pedal digits and claws and to the beak are available almost only in the extant record. One case is however included here (Table 4): the extinct *Athene angelis* exhibits a positive allometry on pedal digits and claws (Louchart, 2001; 2002). This information is not listed in the Table 2.

Uncertain cases are excluded in the present analysis. Isometries are widely predominant, and they are not included in the Tables 2 and 4.

Some trends appear for pedal digits and claws, the tarsus and the wing (Table 4):

- The pedal digits and claws tend to get stronger. This is a newly observed insular trend.

- The tarsus tends essentially to get longer.

- The wing tends to get reduced.

Correlations between variables

These allometrical evolutions do not tend to show clear correlations with any other variable in this study, which is probably due in part to the small size of the sample.

Between each other, the observed trends seem to

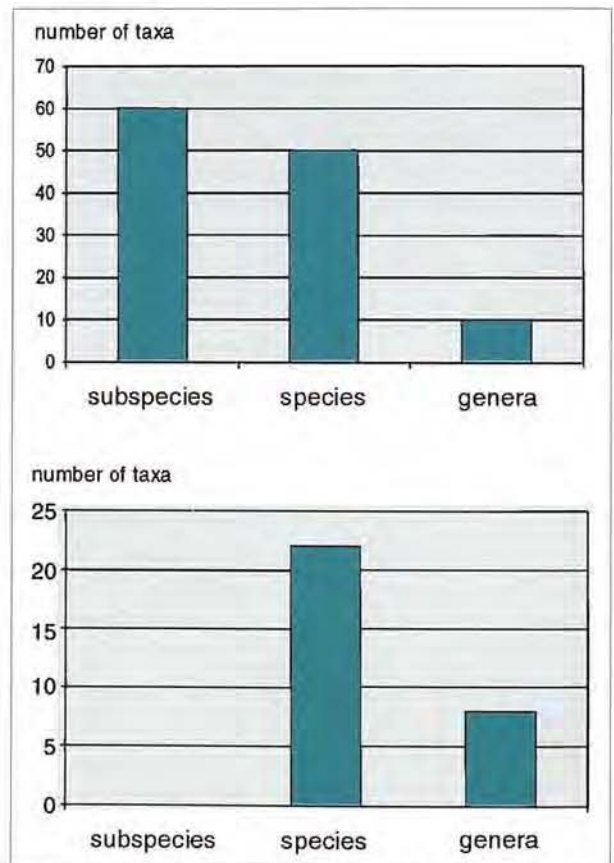


Fig. 6. Distribution of the taxa of Strigiformes according to the three categories of taxonomic rank of divergence. Top: extant insular taxa. Bottom: extinct endemic insular taxa.

Fig. 6. Distribució dels taxa d'estrigiformes d'acord amb les tres categories de rang taxonòmic de divergència. A dalt: taxa insulars endèmics vivents. A sota: taxa insulars endèmics extingits.

show some dependence, qualitatively, given the characteristics of the taxa concerned:

- the positive allometrical evolution of pedal digits and claws seems positively correlated with that of the tarsus;

- the allometrical evolution of the beak seems positively slightly correlated with the two preceding, but there is however no clear resulting univariate trend for the beak.

DISCUSSION

Grant (1965a,b) observed that in passerines, the evolutions of body size and allometries are independent. This seems to apply also to the Strigiformes, but the small sample regarding the allometries does not allow to test it statistically. Allometries and size are treated separately here.

Evolution of size

No general trend for increase or decrease in size appears for insular Strigiformes. This tends to confirm the absence of such a general trend for birds.

Secondly, no 'island rule' applies to insular Strigiformes, when extinct and extant are integrated, despite a rather important range of body sizes (spanning more than two orders of weight): there is no relation between the size of a taxon and the direction of its insular size evolution. No analogy can be drawn with the island rule known in both living (e.g. Lomolino, 1985) and extinct mammals (e.g. Mein, 1983; Guérin, 1997). This tends to support the absence of such a reliable rule observed hitherto in birds, despite the questionable statement of Clegg & Owens (2002). There is no evidence either for the 'island rule' from the Holocene native bird record of New Zealand (Cassey & Blackburn, 2004).

Considering the anthropogenic impacts that will be developed later (see below), the interpretations of the bivariate analyses on the extant database must be very cautious.

A threshold effect seems to appear between the moderate increase in size, and the giantism. The value of this threshold is difficult to precise, but the effect is clear: beyond this value, the influence of the size of preys is markedly expressed, especially for giantism, in every individual case. Giantism can generally be explained by the adaptation of the owl to indigenous and/or endemic larger mean size of preys than on mainland.

Under the threshold value, every case considered separately, no pattern related to the size of prey can be detected. Precise data on the diet of insular owls are often missing, but this observation is consistent with a lack of influence of disparate sizes of prey on the size of living *Tyto alba* (Fig. 9; Taylor, 1994).

Considering the marked decreases in size, the relatively small size of prey can be influential sometimes, but other factors certainly play a role. They are not identified yet, but sometimes a noticeably insectivore diet is reported, for example, showing the possible role of the nature of prey, not only its size.

As part of an « island syndrome », islands typically display a release of some constraints (interspecific competition, predation...), and a strengthening of some others (confinement, limitation of some resources, intraspecific competition) (e.g. Adler & Levins, 1994; Blondel, 2000). Some of these factors have been variously proposed to shape the body size trends observed in diverse Amniotes. These can be roughly summarized:

- optimal body size (Damuth, 1993; Brown, 1995) - sometimes with a reference to Cope's rule (e.g. Damuth, 1993); this concept and the value of the possible optimal body size in mammals are however disputed (e.g. Meiri *et al.*, 2004),
- release of predation by medium sized Carnivores (Thaler, 1973; van Valen, 1973; Sondaar, 1977; partly inspired by Valverde, 1964),
- change in demographic strategy (Melton, 1982),
- territoriality associated with sexual size dimorphism (Louchart, 2001),
- (near) absence of large predators (Case, 1978),
- increase in intraspecific competition, due to higher density (Robinson-Wolrath & Owens, 2003),
- increase in density of some prey; relative abundance of prey (Case, 1978),
- release in interspecific competition (Case, 1978; Lomolino, 1985; Angerbjörn, 1986, in Grant, 1998; Millien, 1999),
- increase of the ratio food resource / food requirement, associated with territoriality (Case, 1978),
- different size of prey compared with mainland (Case, 1978; Alcover *et al.*, 1992); only over a threshold value (Louchart, 2001),
- Bergmann's rule and insular climate types (Foster, 1964); incidentally this ecographic rule applies well to continental owls generally (e.g. Del Hoyo *et al.*, 1999),
- Limited surface area of islands (e.g. Grant, 1998),
- Limitation in vegetal food resources (Sondaar, 1977; Azzaroli, 1982, Lawlor, 1982; Ryan *et al.*, 1989),
- Increased sedentarity in some birds (see e.g. Louchart, 2001).

Some of these factors were proposed together in conjunction (e.g. Case, 1978). Many were dismissed recently, depending on the taxonomic group and the trend considered, but the interactions between them are so complex, and the contexts so intricate, that no synthetic satisfying explanation of the real trends emerges yet.

Considering the Strigiformes alone, there is no general insular trend to be explained, but giantism and dwarfism seem to correspond to typically insular conditions (e.g. presence of giant mammalian prey...). It seems that some explanations for size changes could be searched in the optimal size theory (especially for some decreases in size), in the prey density/availability (especially for dwarfism), in the size of prey available (over a threshold value, at least for giantism), and in the territoriality of the owl taxon (Louchart, 2001).

Allometries

The predatory nature of owls obviously has consequences on the observed allometries of the pedal digits and claws, and a priori possibly also those of the tarsus.

The trend for pedal digits and claws to get stronger in insular owls was hitherto never reported. This special adaptation is likely to be found even more regularly as more precise data become available for extant as well as extinct taxa. The Fearful Owl *Nesasio solomonensis* (Solomon Islands) feeds on unusually large prey for an owl of this size, somehow “replacing” absent *Ninox* (Burton, 1992; Doughty *et al.*, 1999; Del Hoyo *et al.*, 1999; König *et al.*, 1999). Its relatively very strong feet and claws (and strong beak and large and stout tarsus) are probably related to this habit, and in some continental owls they are associated to similarly unusually large prey (Bruce, 1999; Marks *et al.*, 1999). The case of the extinct *Athene angelis*, similarly exhibiting strong feet and claws, may be interpreted in the same manner (Louchart, 2002). It is very likely that many extant cases of strong feet and claws on insular owls (e.g. *Tyto*) can be interpreted this way as

well. For both extant and extinct taxa, the data are missing on the often overlooked phalanges, but it will be most interesting to investigate them.

A special adaptation to ornithophagy might also give rise to relatively strong feet and claws, as suggested by examples on extant Falconiformes (M. Pavia, pers. com.). This possibility deserves attention.

The other allometrical trends observed may have a large part in common with birds as a whole. Considering the reduction of the wing and the lengthening of the tarsus, the diverse explanations that have been proposed are:

- more terrestrial habits than on mainland (Arredondo, 1975; Weesie, 1982; Rando *et al.* 1999),
- ornithophagy in forested habitat (Olson & James, 1991), due to absence of mammals,
- forested habitat and specialized predation on repti-

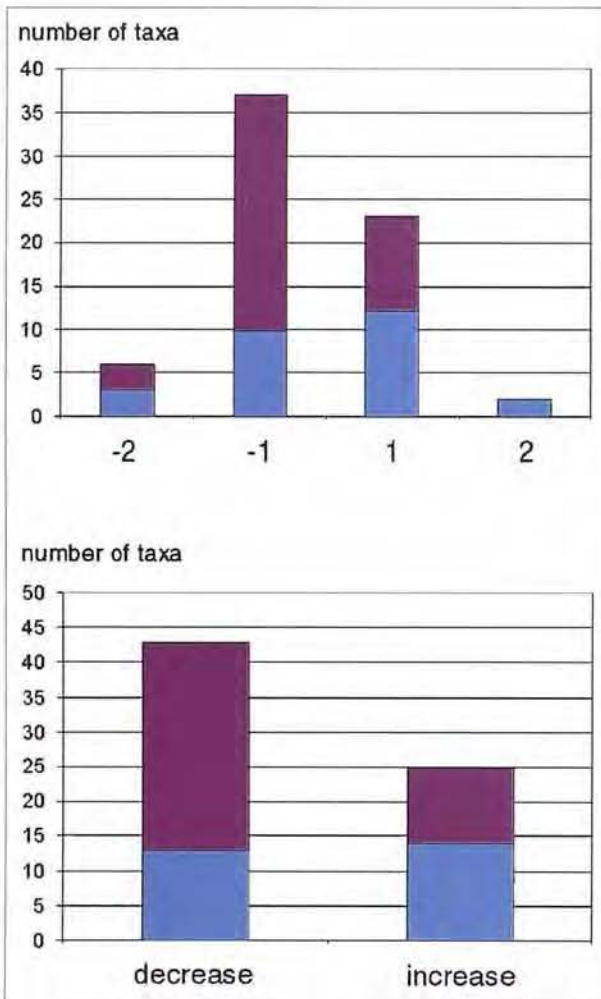


Fig. 7. Distribution of the different size classes of the extant endemic insular taxa of Strigiformes according to the categories of size evolution. In light blue: smaller taxa (size classes 1 and 2). In violet: larger taxa (size classes 3 to 5). Top: detailed categories of size evolution. Bottom: categories grouped in decreases and increases.

Fig. 7. Distribució de les diferents classes de talla als taxa d'estrígiformes endèmics insulars vivents, segons les categories d'evolució de la talla. Blau clar: taxa més petits (classes de talla 1 i 2). Violeta: taxa més grans (classes de talla 3 a 5). A dalt: categories detallades d'evolució de la talla. A sota: categories agrupades en increments i minves.

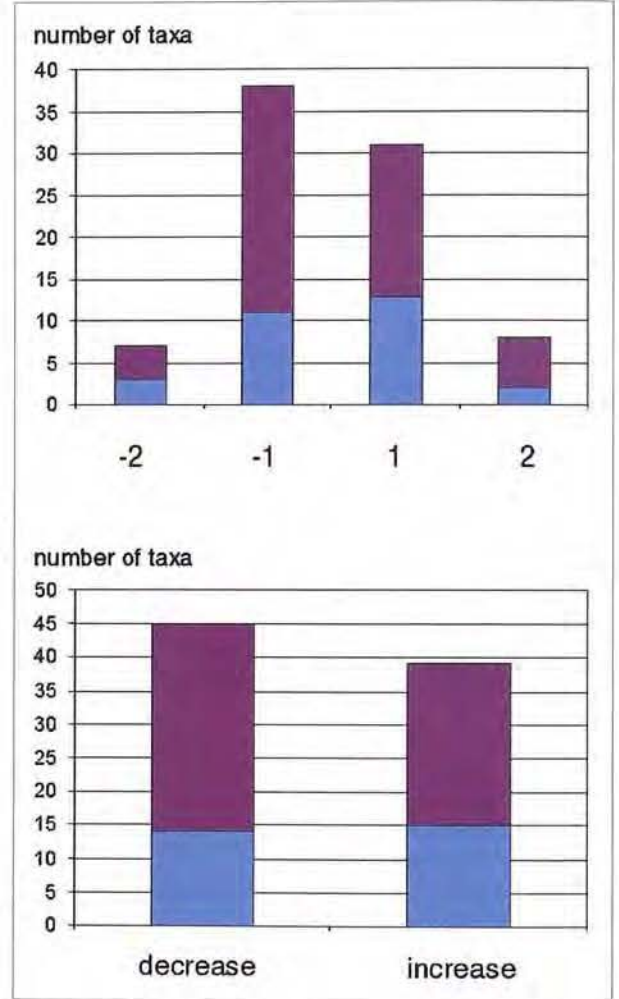


Fig. 8. Integrated distribution of the different size classes of all the endemic insular taxa of Strigiformes (living + extinct) according to the categories of size evolution. In light blue: smaller taxa (size classes 1 and 2). In violet: larger taxa (size classes 3 to 5). Top: detailed categories of size evolution. Bottom: categories grouped in decreases and increases.

Fig. 8. Distribució integrada de les diferents classes de talla de tots els taxa d'estrígiformes endèmics insulars (vivents + extingits) segons les categories d'evolució de la talla. Blau clar: taxa més petits (classes de talla 1 i 2). Violeta: taxa més grans (classes de talla 3 a 5). A dalt: categories detallades d'evolució de la talla. A sota: categories agrupades en increments i minves.

les on vertical surfaces (J.P. Hume, pers. com.; example of some historically known *Mascarenotus*),

- terrestriality and insectivory (Suarez & Olson, 2001),
- oriented extension of some dimensions of habitat niche, due to the release of interspecific competition (Blondel, 2000), like:

- for the tarsus: firmer perches on average – including the ground (Grant, 1965a,b; 1966),
- for the beak: more types of foods, including larger particles (Grant, 1965a,b; 1968; 1998),
- character displacement (Grant, 1998),
- increased sedentarity (Grant, 1998),
- Allen's rule and insular climate types (discussed e.g. in Grant, 1965b).

The factors that are likely to explain the most general insular trends observed in birds are an increased terrestriality linked with a reduced predation pressure, a special diet sometimes devoid of non-flying mammals (for predatory birds), and an increased sedentarity.

For the Strigiformes, all of these three groups of factors clearly apply, more or less independently, to account for the trends. Shorter wings are in general a consequence of sedentarity and release of predation. Longer legs can be linked with terrestriality (staying or moving on the ground, e.g. probably *Gymnoglaux lauwrencii* and *Otus nudipes* – Greater Antilles, *Otus insularis* – Seychelle Islands, or the extinct *Athene cretensis*, *Ornimegalonyx oteroi*...), or with a special diet (e.g. possibly the extinct *Grallatrix* spp., *Mascarenotus* spp...). A marked insectivore diet is shared by *G. lawrencii*, *Otus nudipes* and *Pyrroglaux podarginus* (the latter of the Palau Islands, Micronesia), all three having lengthened hindlimbs (and partly unfeathered). Thus, such a diet could also favor this allometrical change, as in the falcon *Falco kurochikini* (Suarez & Olson, 2001). All these factors are not exclusive of each other.

There is no evidence for an insular climatic influence on either body size or allometries in owls or more generally in birds. A particular climate on average on islands has not been firmly established yet, some authors having even opposite opinions on this issue (cooler, or warmer than on the mainland at the same latitudes). Actually a warmer and moister climate is likely on most

oceanic islands compared with mainland, which needs to be quantified, but the evidence is missing for continental islands.

The special diets (enhanced or exclusive ornithophagy, herpetophagy, insectivory) are consequences of the lack of indigenous non-flying mammals on oceanic islands. These terrestrial mammals are the main diet of a very large proportion of owl species on the continents.

The allometries of feet and claws seen above may sometimes « replace » the expected change in body size of the predator to follow the size of indigenous prey.

The predatory ecology of the Strigiformes appears influential in case of gigantism. The obvious examples of extinct giant owls reveal more of the pattern. Generally, the islands standing far from a continent are free of Carnivores. Alcover & McMinn (1994) indicated that the Viverridae colonized islands up to 300 km from the continent (Ethiopian and Oriental regions). In most cases, among the Carnivores, only some otters colonize farther than 30 km. The distance is therefore indirectly influential in this particular way. On these islands the Strigiformes take a predominant role of predator, as strong and complementary to that of the diurnal raptors treated by Alcover & McMinn (1994). On several islands, the largest predator before the anthropogenic impacts was an owl (Burness *et al.*, 2001).

What can be considered as parallelism was noticed by Arredondo (1976) and Olson (1978), between the evolution of the different species of *Tyto* on the palaeo-archipelago of Gargano (Mio-Pliocene), and that of the species of *Tyto* on the Greater Antillean Islands (Pleistocene): in both cases the body size of the three species are spaced out at the same values approximately. These two archipelagoes had in common the absence of Carnivores (otters excepted), and the presence, probably abundant, of often giant mammalian prey (Rodents, Insectivores, and others; Arredondo, 1976). These common traits are in part due to moderate (intermediate) distances to the respective continents. As another striking parallelism, on each one of the Galapagos and Canary Archipelagoes (the latter partly) lives a small and dark endemic species of *Tyto*: respectively *Tyto (alba) punctatissima* and *T. alba gracilirostris*. Among the other similarities between these

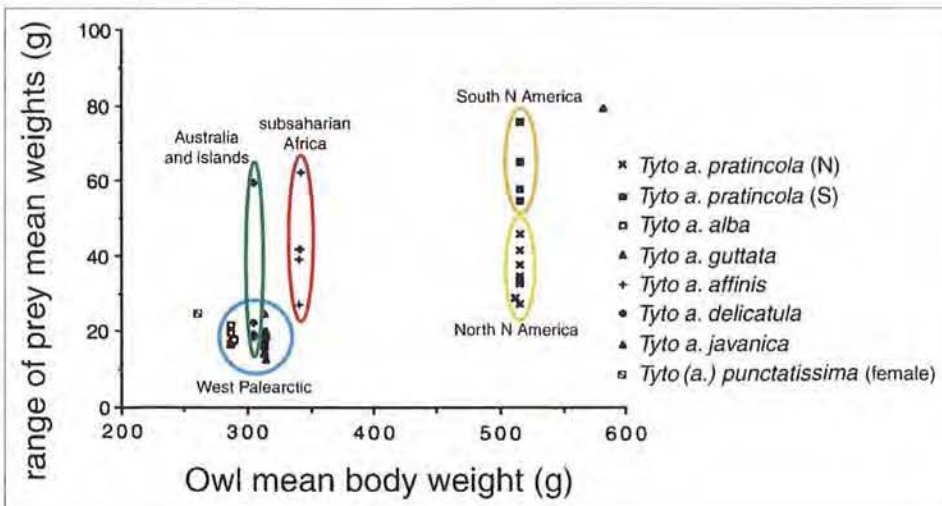


Fig. 9. Relation between the mean size of different populations of *Tyto alba* and the mean size of some samples of their preys. Modified after Taylor (1994).

Fig. 9. Relació entre la mida mitjana de diferents poblacions de *Tyto alba* i la mida mitjana de diverses mostres de les seves preses. Modificat a partir de Taylor (1994).

two archipelagoes, Rando *et al.* (1999) cited the presence of an endemic buzzard (*Buteo*), of lava mice, and of giant rats. These two archipelagoes have in common physical (volcanic origin) and geographical (east side of an ocean, intertropical) characteristics. A further common trait is the absence of indigenous Carnivores. A last remarkable example, this time of convergence, was noticed by Mourer-Chauviré *et al.* (1994). On the Hawaiian archipelago the genus *Grallistrix*, a small endemic owl of the Strigidae probably close to *Strix*, has undergone allopatric speciations (Olson & James, 1991). This genus is characterized by very lengthened hindlimbs and shortened wings. All of the four species are extinct. On the Mascarene Islands several allopatric speciations also occurred, in the extinct endemic genus *Mascarenotus*, probably close to *Otus* (Mourer-Chauviré *et al.*, 1994). *Mascarenotus* also shows very lengthened hindlimbs and shortened wings. The two archipelagoes had in common their remoteness and the absence of any non-flying mammal. These three examples show the importance – among others – of the characteristics of the mammal community in shaping the community of Strigiformes, and provide help to define the main island types biologically. The really oceanic islands are those devoid of non-flying mammals (including the Pleistocene Eivissa, Balearic archipelago, Alcover *et al.*, 1994). A further intermediate type should be defined: the islands lacking Carnivores (with the possible exception of some otters), but where some non-flying mammals (e.g. Rodents) are present. This is the case of some Caribbean Islands, including those where live *Gymnoglaux lawrencii* and *Otus nudipes*, both having lengthened hindlimbs, but not as much as *Grallistrix* and *Mascarenotus*.

Incidentally, it is remarkable that in Corsica are concentrated two rare types of evolution of size in owls: the only known extinct dwarf owl *Bubo insularis*, and the extinct giant *Athene angelis* diverging from a small owl. In addition, *B. insularis* shows the greatest known decrease in size from such a large mainland ancestor as a European *B. bubo* of today, and *A. angelis* shows one of the greatest increases from such a small owl as *A. noctua*. Many Carnivores lived on this island in the Middle Pleistocene (Pereira, 2001) and this unusual circumstance could have been influential in several ways. But insularity in other ways was marked enough to make these two evolutionary trajectories possible, in a still unclear manner (Louchart, 2001, 2002).

The selective extinctions and extirpations

The fossil record reveals the artifactual nature of the range of insular trends visible on the extant taxa alone. The selective nature of the extinctions in the Strigiformes can be summarized as follows (Figs. 2-4, 5): selective impacts have eradicated the largest species faster and more easily. Similarly the taxa resulting from extreme evolutionary pathways went extinct first. Larger species have lower population densities than the smaller ones (Peters, 1983). Therefore, insular populations of larger species, limited in surface area, are less numerous than are those of smaller species, which makes them more vulnerable to extinction risks (Soulé, 1987). The taxa with longer hindlimbs and/or shorter wings also experienced

relatively more extinctions. A major reason lies in their vulnerability to predation, being more terrestrial. Even the perception of the relation between size and size evolution is affected when extinct taxa are not considered (Figs. 7-8).

Both extinctions and extirpations occurred among island birds due to anthropogenic impacts (e.g. Steadman, 1995). For owls, extinctions seem by far the most frequent, from the fossil record available. These extinctions may have a priori two origins: natural (changes in sea level, climate; volcanic eruptions, cyclonic events, land bridge due to a tectonic or eustatic event and allowing non-indigenous animals to colonize...), or anthropogenic. The latter were by far the most common on islands, mainly in the Holocene. For the Strigiformes, even if the exact causes are often very difficult to establish, it was demonstrated in almost all the individual cases that they were anthropogenic.

CONCLUSION

There is no general trend in the insular evolution of body size for owls. Neither is there an 'island rule' for this group. This also seems to be the case for birds as a whole, but a comprehensive study including the recent fossil record remains to be done. As summarized by Case (1978), a rule is more powerful if it explains the numerous exceptions to the general trends. But such a model tends to comprise many « amendments » to the « law ». Even in mammals, the 'island rule' would better be called just an island trend. For every size, only a majority of taxa follow the rule, but still all the other ones show either no change or change in the opposite way (e.g. Lomolino, 1985; Meiri *et al.*, 2004). Then, a simple rule may hide many converging or diverging factors, acting differently on the different taxa, size categories, etc. Such a rule is likely to be an emerging property of a very complex system (*sensu* Gell Mann, 1994). Finally, many islands display marked idiosyncrasies (e.g. Quammen, 1996; Grant, 1998; Laman, 2000), which perturb the recognition of general trends. But the idiosyncrasy of many islands must be emphasized, because it is a third reason to preserve island biotas, along with their role as museums – for palaeoendemics, and laboratories – for [partly] neoendemics (Cronk, 1997, in Sadler, 1999).

Body size may not be the powerful estimator of many ecological traits, as it has been thought. It is likely to be influenced by too many factors, sometimes in opposition, related to climate, competition, predation, among others (e.g. Peters, 1983; Meiri *et al.*, 2004), and such intricate relationships make both the recognition and explanation of a clear pattern very difficult. Some allometries seem to be more informative than body size considering owls. A trend for pedal digits and claws to get stronger in island owls is reported, and seems related to unusually large prey.

Trends for longer hindlimbs and shorter wings are observed, and are the same as those known in island birds in general. The most general explanations lie in terrestriality, special diets, and sedentarity. These charac-

teristics are in turn linked with isolation and particular indigenous faunas, including prey and predators, the latter factor being partly a consequence of the previous.

The special case of Corsica is emphasized, as an original, alternative Middle Pleistocene insular context with several Carnivores, which among others revealed the extinct giant *A. angelis*, and the extinct dwarf *B. insularis*.

The probably most important intrinsic characteristics which need to be better investigated for some island owls are: their diet; other traits of their ecology like their degree of terrestriality; their territoriality (the original one of their mainland ancestor). The most important extrinsic, insular characteristics, which also need more precise quantifications, include the type and size of preys available; more generally the kinds of mammals present on the island (in part linked to, but as influential *per se* as the distance from the mainland). Here again, the palaeontological input is necessary, to reveal the original indigenous faunas, mammalian as well as reptilian for example. An intermediate type of biological islands should be defined: the islands lacking Carnivores (with the possible exception of some otters, depending on their diet), but where some non-flying mammals (e.g. Rodents) are present; as opposed to other continental islands where Carnivores are (or were recently) present.

The fossil record is indispensable to understand the insular evolutionary phenomena in owls. It is even possible to integrate quantitatively the extant and extinct records, which provides a closer approximation of the natural trends.

It is probable that the results of the bivariate analyses, carried out with extant taxa alone, are distorted too, due to the problem of selective extinctions. It is not possible to integrate the fossil data in these analyses yet. More indirectly, problems arise also from the fact that the ecology (diet for example) of living species is affected today by recent anthropogenic impacts to their habitats, available prey etc.

The fossil record is indispensable in two main ways:

- It reveals unique evolutionary pathways, the results of which are more likely to be extinct when they are extreme, for example in terms of gigantism or strong allometries. The original protective nature of islands, especially in terms of release of predation, allowed the survival of such endemics. But the same islands became a trap when man appeared. The extreme adaptations to insular contexts became a handicap. The remaining extant range of evolutionary potentials of islands is very distorted and incomplete. Incidentally, the fossil record is also necessary for purposes of insular biogeography, because in this domain it becomes evident that *in situ* evolutions have to be taken in account (e.g. Lomolino, 2000; Lomolino & Weiser, 2001).
- N.B.*: Taking in account the forms recently extinct from other causes than anthropogenic ones (rare cases, but existing), is important for taxon-scale studies of evolutionary possibilities.
- It is the only way to approximate the natural communities, contemporaneous with these evolutionary events, and which disappeared or changed drastically. The present insular communities are known to be highly residual and artificial since the

human impacts, which have already been shown to make the fossils necessary in insular biogeography (e.g. Steadman, 1995). In terms of insular evolution, the best possible knowledge of the past, natural communities, is necessary because these determine the special interactions partly responsible for many changes. Alongside the owls themselves, the whole community of birds, mammals and other groups need the same palaeontological approach.

Such an integrated approach is still unusual, and surely it will require some time before biologists and palaeontologists really share the same interests. Well beyond the domain of owls, the same issue applies to birds in general, mammals, reptiles, and many other living organisms on islands, because few have escaped the anthropogenic waves of extinctions. A striking example is that of the Mascarene Islands where, unlike on the Hawaiian Islands for example, all the extinctions are due to the European colonizers since the XVIIth Century (Blanchard, 2000).

Perspectives for the study of insular owls

The data in the extant and extinct records need to be regularly updated, because new owls are discovered quite often on islands, living as well as fossil. More precise data are needed on allometries – including toes and claws – and size for many taxa, living and fossil. The phylogenetic relationships must be ascertained between many island and mainland taxa. More ecological data are also needed. The whole record of strictly continental taxa will be integrated for the Strigidae. It will be also necessary to make analyses segregating the small and large islands (as suggested for biogeography by Lomolino & Weiser, 2001), as well as the oceanic, intermediate, and continental ones, biologically speaking.

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