

AZORES PASSERIFORMES

– A MODEL FOR EVOLUTIONARY STUDIES

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Summary: Due to the geographic location of the Azores archipelago, situated in the centre of the North Atlantic Ocean, about 1,500 km from Europe and 1,900 km from America, this group of nine islands can act as a model system for the study of evolution on remote islands. Despite the low number of native breeding Passeriformes in this archipelago (only 10 species), recent studies on its phylogeography and genetic diversity shade light on new hypothesis about the colonization of the Azores and the natural evolution of species on isolated archipelagos. The knowledge of the phylogeographic history and genetic structure of these species is fundamental to provide a basis for their conservation and protection.

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Sumário: Devido à localização geográfica do arquipélago dos Açores, situado no centro do Oceano Atlântico Norte, a cerca de 1.500 km da Europa e 1,900 km da América, este grupo de nove ilhas pode actuar como um sistema modelo para o estudo da evolução em ilhas remotas. Apesar do número reduzido de Passeriformes nativos que nidificam neste arquipélago (apenas 10 espécies), estudos recentes sobre sua filogeografia e diversidade genética revelam novas hipóteses sobre a colonização dos Açores e da evolução natural das espécies em arquipélagos isolados. O incremento do conhecimento sobre a filogeografia e a estrutura genética destas espécies é fundamental para o estabelecimento de medidas de conservação e protecção.

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BIRDS DIVERSITY AND MOLECULAR TOOLS

More than 250 years have passed since the 10th edition of Linnaeus's seminal taxonomic work *Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus differentiis, synonymis, locis* (1758). Still today however, the species concept debate remains a key issue among biologists (MALLET, 1995; SITES & MARSHALL, 2003; HEY, 2006). The most often assumed definition of a species is the biological species concept (MAYR, 1963), which defines a species as members of populations that interbreed in nature according to similarities in appearance and where phenotypic variation is grounded in their taxonomic correlations. For instance, according to this definition, the majority of bird species are distinguished solely based on their morphological traits such as anatomy, size and plumage patterns. The conventional definition of a species is, therefore, the "morphological species concept", which recognises that each species typically looks different from other species, including its closest relatives (NEWTON, 2003). The rise of genetic-based approaches capable of accurately discerning phylogenetic relationships among closely related species and/or individuals, however, has led to the common acceptance that traditional taxonomy,

based only on phenotypic variation, is not always consistent with species molecular phylogenies, i.e. incongruences between gene trees and species trees often occur (MADDISON, 1997). Avian taxonomy provides numerous examples of disagreements at the subspecies and genus levels (e.g., BALL & AVISE, 1992; PAVLOVA *et al.*, 2003; DROVETSKI *et al.*, 2004a,b, 2009; ZINK, 2004; ARBOGAST *et al.*, 2006). Taking these incongruences into account, several different species concepts have been advocated by contemporary biologists, including biological, ecological, evolutionary and phylogenetic concepts, among others (DE QUEIROZ, 2007).

After the completion of the chicken (*Gallus gallus*) mitochondrial genome (DESJARDINS & MORAIS, 1990), the first applications of polymerase chain reaction (PCR) to ornithology (KOCHER *et al.*, 1989; EDWARDS & WILSON, 1990) and, especially, commensurate upon the work of SIBLEY and AHLQUIST (1990) on DNA-DNA hybridization, molecular techniques have brought new insights into the evolutionary history, phylogeny and classification of birds. Molecular studies have a great advantage over morphological information since the determination of cryptic species resulting from convergent evolution

is more readily detected. Molecular data may also provide an estimation for the time scale over which a particular evolutionary step has taken place (the 'molecular clock') and, as a consequence, allow both the phylogenetic and geographical analyses of a group of related organisms (WINK *et al.*, 2002).

Phylogeography, a sub discipline of biogeography, allows the tracing of historical aspects of the contemporary spatial distributions of species and gene variability, especially the variation at the intraspecific level (AVISE, 1996, 1998). Phylogenetic relationships among birds are currently being clarified through analyses of DNA, providing measures of the genetic distances between species, that is, the higher genetic similarity is between two species, the more closely related they are (NEWTON, 2003; SPICER & DUNIPACE, 2004). Phylogeography, and the analyses of nuclear and mitochondrial marker genes, are currently some of the most important tools for the study of species' evolutionary history, namely birds, in the context of palaeoenvironmental changes (HEWITT, 1996, 2004; TRIBSCH & SCHONSWETTER, 2003). This information is relevant, as a detailed knowledge of the evolution and geographic variation of a given species will help to identify lineages of independent evolutionary history, and ultimately

provide the framework to infer their conservation status and future population viability. The development and integration of biogeographic and evolutionary models within programmes for the preservation of bird species, especially on islands, will help the future integrative protection of unique bird species and their habitats.

The Order Passeriformes radiated unlike any other avian group, probably due to a combination of morphological, neurological, behavioural, and ecological adaptations (FITZPATRICK, 1988). This large monophyletic group of birds, that have diversified on all continents and now occupy nearly all terrestrial ecosystems (BARKER *et al.*, 2004), has been described based on a few biometrics including the features of the palate, spermatozoa, forehand hind limb muscles, and feet (RAIKOW, 1982). Beyond these morphological characters, however, passerines also differ from other birds in terms of other biological traits. They usually have a higher metabolic rate than other birds of the same size, and they have relatively large brains and superior learning abilities, including vocalization (SHELDON & GILL, 1996). Most recent studies of passerine relationships suggest that this group began to diversify during the Cretaceous (BARKER *et al.*, 2002, 2004; ERICSON *et al.*, 2002), and it appears that they were so successful and radi-

ated so rapidly during the late Tertiary, that the lines of demarcation among-families and higher groups have now become poorly defined (FEDUCCIA, 1995; SPICER & DUNIPACE, 2004).

Currently, bird populations on islands are used to illustrate the extreme character divergence caused by geographic isolation (NEWTON, 2003). Driven by the renowned association between Darwin's theory of evolution by natural selection and the Galapagos finches (DARWIN, 1859), island bird populations have become a reference point for the study of evolution. Island systems provide critical insights to processes underlying the evolutionary diversification of species (GRANT, 1998), and contributed to the most widely accepted model of speciation. That is, the allopatric model, which considers that populations isolated geographically, differentiate due to either genetic drift

(random changes in allele frequencies over generations) or founder effects (loss of genetic variation that occurs when a new population is established by a small number of individuals from a larger population) (MAYR, 1963; NEI *et al.*, 1983). In fact, genetic drift reduces the genetic variation to a magnitude proportionally inverse to population size (CROW & KIMURA, 1970). It is, therefore, expected that drift should be pronounced in small areas, such as isolated islands, leading to divergence among populations, whereas gene flow (by migration) has a homogenizing effect (BARTON, 1998; SLATKIN, 1985). Low rates of gene flow and substantial genetic drift in small populations are, therefore, the most probable explanations for the lower genetic diversity generally observed in island populations and species when contrasted with their mainland relatives (FRANKHAM, 1997).

THE AZORES AMONG THE MACARONESIAN ARCHIPELAGOS

Archipelagos are attractive environments for the study of evolution for a number of reasons, namely: (i), they present discrete geographical entities within defined oceanic boundaries; (ii), gene flow between individual islands is reduced by oceanic barriers; (iii), their often small geographic areas allow a detailed cataloguing of

flora and fauna in contrast to continental systems; (iv), despite their small size they can contain a diversity of habitats and (v), they are often geologically dynamic, with historical and contemporaneous volcanic and erosion activities (EMERSON, 2002). In combination, the above factors typically translate into high levels of

endemism within oceanic island systems, providing us with a microcosm of evolutionary processes. However, Island populations are likely to be genetically poor, due to possible founder effects, isolation from the source population, and stochastic processes attributable to the limited size of the population (WILCOX, 1980; WILDT *et al.*, 1987; HOEZEL *et al.*, 1993). Although the premises identified herein explain the usually lower bird diversity to be found on islands, as compared with continents, 17% of all non-marine bird species occur only on these systems, giving an overall species density nearly four times greater than the average for continents (NEWTON, 2003).

BORGES & BROWN (1999) provided a comprehensive review of the four major hypotheses that typically explain the level of species richness (S) on oceanic volcanic islands according to certain geographic variables: (i), the species-area relationship introduced by PRESTON (1962) and further developed by MACARTHUR & WILSON (1967) in the *Theory of Island Biogeography* states that larger islands will provide assemblages with higher levels of S; (ii), the altitude range hypothesis (BAEZ, 1987; SJÖGREN, 1990) predicts S as a function of maximum altitude, with greater elevations promoting further habitats; (iii), in the isolation hypothesis, also

developed in the *Theory of Island Biogeography* (MACARTHUR & WILSON, 1967), S should decrease for a given taxonomic group when distance from the source of species, typically the nearest mainland, increases (i.e., remote oceanic islands will have fewer species than those located near the mainland); in addition, WILLIAMSON (1981) stated that isolation influences the number of endemic species (i.e., remote oceanic islands will have more endemic species); (iv), the time hypothesis (WILLIS, 1922) predicts that species accumulate with time and thus S matches each island's geological age. It is known that the number of bird species on islands usually respects the equilibrium theory of MACARTHUR & WILSON (1967), which correlates island area and isolation, stating that larger islands will have more species and, conversely, remote islands will have fewer species.

The archipelagos of volcanic origin are even more interesting in that they provide insights into the processes of evolutionary species' diversification, owing to them: (i), providing examples of adaptive diversification; (ii), have a well-characterized geological history and (iii), relatively simple ecologies (GRANT, 1986; BALDWIN & ROBICHAUX, 1995; JUAN *et al.*, 2000). The group of archipelagos located in the north-eastern quadrant of the

Atlantic Ocean, and comprising the Azores, Madeira (including the Salvage Islands), Canary Islands and Cape Verde, forms the biogeographic region of Macaronesia. Such islands are scattered across the North Atlantic from the Mid Atlantic Ridge to the North African coast, ranging across a

considerable latitudinal gradient from 40° to 15° N (FIGURE 1). The Azores is the most isolated Macaronesian archipelago, being separated from the nearest Continent, Europe, by almost 1,400 km. Distances between the different Macaronesian archipelagos and continents are shown in TABLE 1.

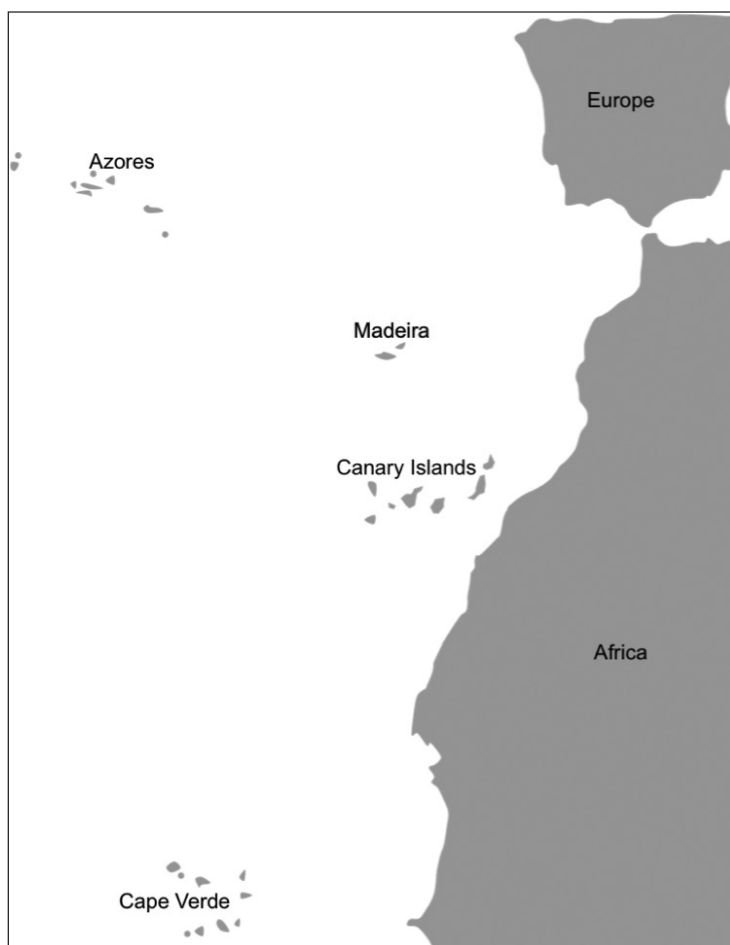


FIGURE 1: Location of the Macaronesian archipelagos.

TABLE 1. Distances (in km) of the Macaronesian archipelagos from continental Africa and Europe. Distances were obtained from Google Earth (2012)

	Azores	Madeira	Canary Islands	Cape Verde	Africa	Europe
Azores	—	842	1112	2185	1554	1370
Madeira	842	—	430	1895	635	796
Canary Islands	1112	430	—	1295	100	942
Cape Verde	2185	1895	1295	—	571	2621

With the exception of the Azores, with a volcanic activity related to the Mid-Atlantic ridge, the origins of the Macaronesian islands lie within the African plate. Their formation began around 80 million years ago (My), gradually building the submarine platforms for the East Canaries and Salvage Islands. The oldest island system to rise above sea level was the Salvage Islands, around 27 My, followed by the Canary Islands (20 My), Madeira (15 My), and finally Cape Verde and the Azores, around 10 and 8 My, respectively (FRANÇA *et al.*, 2003; WHITTAKER & FERNÁNDEZ-PALACIOS, 2007). The climatic patterns in these groups of islands range from the cool-oceanic in the Azores to the oceanic tropical monsoon-drift in Cape Verde islands, with the Mediterranean climates of Madeira and the Canary Islands between (FERNÁNDEZ-PALACIOS & DIAS, 2001).

The geographic locations of the Macaronesian islands, their volcanic formation and singular ecological conditions and isolation (they were

never part of a continent), present a distinctive biogeography with the existence of unique species and communities, and are included in the Mediterranean biodiversity hotspot (MYERS *et al.*, 2000). The numbers of unique endemic species and subspecies of terrestrial fauna and flora for these archipelagos has been estimated at >6,000: 452 for the Azores (BORGES *et al.*, 2010), 1,419 for Madeira (Borges *et al.*, 2008), 3,672 for the Canary Islands (IZQUIERDO *et al.*, 2004), and 540 for Cape Verde (ARECHAVELETA *et al.*, 2005).

In terms of bird species, there are 86 regular breeding species in the Canary Islands, 41 in Cape Verde, 38 in Madeira and 35 in the Azores (OLIVEIRA & MENEZES, 2004; LÓPEZ-JURADO *et al.*, 2005; RODRIGUES *et al.*, 2010; GARCIA-DEL-REY, 2011), but the number of regular migrants and rare vagrants in all these archipelagos is in the order of several hundred species (CLARKE *et al.*, 2006).

The Azores archipelago (FIGURE 2), due to its geographic isolation in the

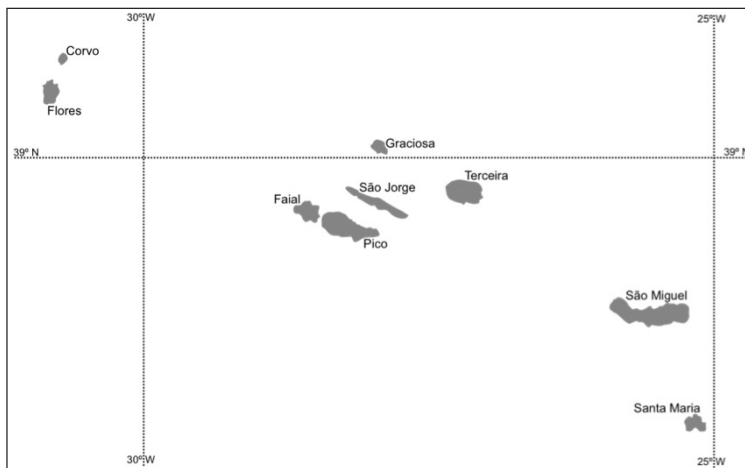


FIGURE 2: The Azores archipelago.

centre of the North Atlantic Ocean, between latitudes 36°55' and 39°43' North, and longitudes 24°46' and 31°16' West, about 1,400 km from Europe and 1,900 km from North America, could become a natural lab-

oratory with a strong potential for the study of evolution. The Azores is a volcanic oceanic archipelago consisting of nine islands and several islets of recent volcanic origin (TABLE 2), which are spread over >600 km along

TABLE 2: **Physical and geological features of the Azores islands; geological data adapted from FRANÇA (2003) and HILDENBRAND *et al.* (2008); 2001 physical features adapted from Instituto Hidrográfico (2010)**

Island	Area (km ²)	Inhabitants	Density (Inhab./km ²)	Maximum altitude (m)	Maximum isotopic age (My)
Santa Maria	97	5500	58	587	8,12
São Miguel	757	132000	176	1103	4,01
Terceira	402	56000	141	1023	3,52
Graciosa	62	4800	78	402	2,5
São Jorge	246	11000	41	1053	1,3
Pico	433	15000	33	2351	0,25
Faial	172	15000	87	1043	0,73
Flores	142	4000	28	915	2,16
Corvo	17	400	25	718	0,71
Total	2344	241763	103		

a northwest-southeast line (FRANÇA *et al.*, 2003). The oceanic distribution of these islands and, as a consequence, their relative positions, has led to the formation of the following groups: (i), a western group, comprising the islands of Flores and Corvo;

(ii), a central group, with the islands of Faial, Pico, São Jorge, Terceira and Graciosa and (iii), an eastern group, made up of the islands of São Miguel and Santa Maria. Distances between the various Azorean islands are shown in TABLE 3.

TABLE 3: Distances (in km) among the Azores islands.
Distances obtained from Google Earth (2012)

Island	Corvo	Flores	Faial	Pico	S. Jorge	Graciosa	Terceira	S. Miguel	S. Maria
Corvo	—	18	230	256	261	269	336	497	596
Flores		—	220	247	265	267	332	491	585
Faial			—	6	31	68	108	253	345
Pico				—	18	60	66	200	295
S. Jorge					—	37	38	183	285
Graciosa						—	57	223	330
Terceira							—	137	245
S. Miguel								—	80
Santa Maria									—

The geological and geographic characteristics of the Azores plus its ecological heterogeneity have led to the inclusion of the archipelago, along with the rest of the Macaronesian biogeographic archipelagos, in an Endemic Bird Area (STATTERSFIELD *et al.*, 1998).

The Azores have a temperate, maritime climate and the weather is influenced by the anticyclonic conditions present on the eastern side of the North Atlantic (the Azorean anticyclone), and the islands are situated in the junction

of the temperate and subtropical zones. When the Azorean anticyclone extends to the south of the islands, the weather conditions are typical of a temperate zone, with depressions, coming from the west (the prevailing winds). When the Azorean anticyclone is centred south of the islands, subtropical weather conditions prevail, with winds from the east (AZEVEDO, 2006). The annual median air temperature is $\sim 17^{\circ}\text{C}$, varying between 13°C and 14°C during the winter and 22 to 23°C in the summer. Precipitation rises with latitude and

altitude, with Santa Maria being the driest island. Rainfall also varies greatly from place to place on each island and from year to year. Over the archipelago, the annual average precipitation is 1,930 mm (DROTRH/INAG, 2001; CLIMAAT, 2011).

At the time of the discovery of the Azores archipelago by the Portuguese in 1427, a dense Laurel forest

covered the islands. However, since then, production forests and pasture have replaced the natural habitat, and even the surviving remnants of natural habitats are almost all invaded by an invasive flora. Nevertheless, it is still possible to find small areas of pristine natural forest in Flores, Pico and Terceira (BANNERMAN & BANNERMAN, 1966; SJÖGREN, 1984).

AN OVERVIEW OF THE BREEDING AVIFAUNA OF THE AZORES

In spite of the isolated geographical location of the Azores in the middle of the Atlantic Ocean, and the prevailing westerly winds, all regularly breeding species have a Palearctic origin (TABLE 4).

Among the breeding species, there is the Azores bullfinch (*Pyrrhula murina*), the only Azorean endemic passerine and one of the most threatened European species, which nests exclusively in the Laurel forest of Pico da Vara, on the eastern part of São Miguel (RAMOS, 1994), and Monteiro's storm-petrel (*Oceanodroma monteiroi*), the only Azorean endemic seabird, which nests on only two small islets off Graciosa (BOLTON *et al.*, 2008).

The remaining populations of marine birds are among the most important in Europe (MONTEIRO *et al.*, 1996a). The Azores archipelago harbours the larg-

est population of Cory's shearwater (*Calonectris diomedea borealis*) in the world. Although this species is not considered globally threatened (BirdLife International, 2009), its distribution is restricted to the subtropical north-eastern Atlantic and the Mediterranean and their breeding population has declined abruptly in the recent years (RODRIGUES *et al.*, 2012). The concentrations of the band-rumped storm-petrel (*Oceanodroma castro*) and little (or Macaronesian) shearwater (*Puffinus baroli*) in the Azores are also significant. Further, the archipelago has a small population of Manx shearwater (*Puffinus puffinus*) on the islands of the western Group, and a residual population of Bulwer's petrel (*Bulweria bulwerii*) on Santa Maria. Individuals of one of the most threatened European species, Fea's petrel (*Pterodroma*

feae), have also been captured in the Azores (MONTEIRO and FURNESS, 1995a,b; MONTEIRO *et al.*, 1996b; MONTEIRO *et al.*, 1999). According to the chronicles of Frutuoso (1561), this species very likely bred in the Azores in the past.

The Azores populations of two other seabird species, namely the roseate tern (*Sterna dougallii*) and the common tern (*Sterna hirundo*), represent a large element of the European and Portuguese populations, respectively, even though both species are relatively common on the global scale (GOCHFELD, 1983; DEL NEVO *et al.*, 1993, BirdLife International, 2004). Among the passerines, besides the Azores bullfinch, the Azores has populations of the canary (*Serinus canaria*), endemic to Macaronesia, and several endemic subspecies, similar to the situations in the majority of insular systems. Current taxonomy indicates that the endemic passerines include three subspecies of the goldcrest (*Regulus regulus* [*R. r. azoricus*, *R. r. inermis* and *R. r. sanctaemariae*]), and one subspecies of the grey wagtail (*Motacilla cinerea patriciae*), the blackbird (*Turdus merula azorensis*), the starling (*Sturnus vulgaris granti*) and the chaffinch (*Fringilla coelebs moreletti*). There is also an endemic subspecies of Falconiformes, the Azorean buzzard (*Buteo buteo rothschildi*), and one Columbiformes,

the Azorean wood pigeon (*Columba palumbus azorica*).

Among the species that sporadically nest in the Azores (TABLE 4), there are the American black duck (*Anas rubripes*) and the killdeer (*Charadrius vociferous*), both from the Nearctic origin, and the sooty tern (*Onychoprion fuscatus*), that reaches the northern limit of its distribution in the Azores, where its presence has been known since 1902 (HARTERT & OLGIVIE-GRANT, 1905). The Eurasian collared dove (*Streptopelia decaocto*) has greatly expanded its local distribution in the last few decades, having already arrived in the Azores, and breeding was confirmed in 2009 in Terceira (Birding Azores team, 2011). The rose-ringed parakeet (*Psittacula krameri*) and the common waxbill (*Estrilda astrild*) were recently (and accidentally) introduced (Birding Azores Team, 2011).

The importance of the Azorean avifauna extends beyond breeding species, given that every year several migratory species originating from the Occidental Palearctic and the Nearctic arrive on the archipelago. The archipelago also provides a refuge to rest and regain strength before continuing their journeys (RODRIGUES *et al.*, 2010).

The breeding birds of the Azores and the recognized importance of the archipelago for migratory seabirds are

are a natural heritage not just locally but also within the global context (RODRIGUES & CUNHA, 2011). Because of their uniqueness, there is a great need to protect and conserve

the Azorean birds and their habitats, especially several endemic terrestrial species, namely passerines, and highly important colonies of seabirds (RODRIGUES & CUNHA, 2012).

AZOREAN PASSERINES AS EVOLUTIONARY MODEL SPECIES

A good evolutionary model should provide evidence of ancient colonisation events, non-mediated by humans; evidence of phenotypic and/or genetic differentiation, either by classic taxonomic studies or by genetic sampling; abundant breeding populations on several islands; and isolation of insular populations from migratory continental populations, which would confuse genetic signatures. According to these features, not all the species meet the necessary requirements to be a good evolutionary model. For example, species that recently colonised an isolated region are not suitable, such as the common sparrow (*Passer domesticus*) that colonized the Azores in 1960 (LE GRAND, 1977). Some examples of good Azorean passerine models for evolutionary studies are shown on FIGURE 3.

There are also orders that act as a better evolutionary model than others; Passeriformes show more evolutionary plasticity in relation to environmental conditions (e.g. diet, habitats) than other kinds of animals (e.g. reptiles)

and other types of birds (e.g. marine birds). The same or related species of Passeriformes have also been able to colonise different island systems, allowing for the comparison of different island radiations within the same taxa (NEWTON, 2003).

Azorean native Passeriformes can act as a model species for evolutionary studies because, from the majority of the birds that are known to have colonised islands, they show smaller dispersal rates and reduced gene flow between islands and continents due to a great geographical isolation, hence increasing the probability of population differentiation.

Recent decades have seen several studies focusing the phylogeography and the genetic diversity of the Azores passerines, raising new theories about the colonization of the Azores and the natural evolution of species on isolated archipelagos.

Based on the genetic study of the genus *Pyrrhula* from Eurasia (TÖPFER *et al.*, 2010), that revealed the genetic distance of the Azores bullfinch to



FIGURE 3: Photographic documentation of good evolutionary model species.

1 – Robin (*Erithacus rubecula*); 2 – Blackbird (*Turdus merula*); 3 – Blackcap (*Sylvia atricapilla*);
4 – Goldcrest (*Regulus regulus*); 5 – Chaffinch (*Fringilla coelebs*).

other bullfinches' populations, it was possible to assign a species status to *Pyrrhula murina* from São Miguel Island.

Based on the studies of MARSHALL & BAKER (1999), and more recently on RODRIGUES *et al.* (2013a), it was possible to determine that chaffinches have colonized the Azores archipelago around 1.5 million years ago; and unveil the genetic distance of the chaffinches from the Azores to the other populations from Macaronesia and from the Continental Western Palearctic, raising the hypothesis of a new endemic species to the Azores. PÄCKERT & MARTENS (2004), revealed two metapopulations of goldcrests inhabiting the Azores, which are recent descendants of continental European populations. RODRIGUES (2012), based on genetic and morphometric issues raises the hypothesis of a new evolutionary unit present solely on Flores Island.

NEVES *et al.* (2010) investigated the

genetic divergence between the European starling in the Azores and other European populations, and their results showed a significant genetic differentiation between the Azores and the other European populations. On the other hand, other studies revealed that some Azorean native passerines have a small or no genetic differentiation to other populations from Macaronesia and from Europe, namely the canary (DIETZEN *et al.*, 2006), blackcap (DIETZEN *et al.*, 2008), and robin (RODRIGUES *et al.*, 2013b), meaning that the colonization of the Azores by these species occurred very recently.

It is therefore important to provide a comprehensive and accurate description of the phylogeographic history of the Azorean passerines. This would provide a framework to understand the role of evolutionary processes in shaping the past ecology of these species, so that we can assist with their conservation in a near future.

REFERENCES

- ARBOGAST, B. S., S. V. DROVETSKI, R. L. CURRY, P. BOAG, P. GRANT, R. GRANT, G. SEUTIN & D. J. ANDERSON, 2006. Origin and diversification of Galápagos mockingbirds. *Evolution*, 60: 370-382.
- ARECHAVELETA, M., N. ZURITA, M. C. MARRERO & J. L. MARTÍN, 2005. *Lista preliminar de especies silvestres de Cabo Verde (hongos, planta y animals terrestres)*, 155 pp. Consejería de Medio Ambiente y Ordenación Territorial, Gobierno de Canarias.
- AVISE, J. C., 1996. Space and time as axes in intraspecific phylogeography. In: B. HUNTER, W. CRAMER, A. V. MORGAN, H. C. PRENTICE & J. R. M. ALLEN (eds.), *Past*

- and Future Rapid Environmental Changes: The Spatial and Evolutionary Responses of Terrestrial Biota*, pp. 381-388. Springer-Verlag, New York.
- AVISE, J. C., 1998. The history and purview of phylogeography: a personal reflection. *Molecular Ecology*, 7: 371-379.
- AZEVEDO, A., 2006. *Património natural açoriano. O anticiclone dos Açores*, 73 pp. João Azevedo editor. Portugal.
- BAEZ, M., 1987. Caractères liés à l'insularité de la faune de l'archipel des Canaries. *Bulletin de la Société Zoologique de France*, 112: 143-152.
- BALDWIN, B. G. & R. H. ROBICHAUX, 1995. Historical biogeography and ecology of the Hawaiian silversword alliance. In: W. W. WAGNER & V. A. FUNK (eds.), *Hawaiian Biogeography*, pp. 259-287. Smithsonian Institution Press, Washington, DC.
- BALL, JR R. M., & J. C. AVISE, 1992. Mitochondrial DNA phylogeographic differentiation among avian populations and the evolutionary significance of subspecies. *Auk*, 109: 626-636.
- BANNERMAN, D. A. & W. N. BANNERMAN, 1966. *Birds of the Atlantic Islands*. Vol. 3: *A History of the Birds of the Azores*, 262 pp. Oliver & Boyd. Edinburgh and London.
- BARKER, F. K., G. F. BARROWCLOUGH & J. G. GROTH, 2002. A phylogenetic hypothesis for passerine birds: taxonomic and biogeographic implications of an analysis of nuclear DNA sequence data. *Proceedings of the Royal Society of London B*, 269: 295-308.
- BARKER, F. K., A. CIBOIS, J. SCHIKLER & J. CRACRAFT, 2004. Phylogeny and diversification of the largest avian radiation. *Proceedings of the National Academy of Sciences of the United States of America*, 101: 11040-11045.
- BARTON, N. H., 1998. Natural selection and random genetic drift as causes of evolution on islands. In: P. R. GRANT (ed.), *Evolution on islands*, pp. 102-123. Oxford University Press, New York.
- Birding Azores Team, 2011. <http://www.birdingazores.com/>. Accessed in 2011-12-08.
- BirdLife International, 2004. *Birds in Europe: population estimates, trends and conservation status*, 374 pp. BirdLife International, Cambridge.
- BirdLife International, 2009. Species fact-sheet: *Calonectris diomedea*. <http://www.birdlife.org>. Accessed in 2011-12-08.
- BOLTON, M., A. L. SMITH, E. GÓMEZ-DÍAZ, V. L. FRIESEN, R. MEDEIROS, J. BRIED, J. L. ROSCALES & R. W. FURNES, 2008. Monteiro's Storm-petrel *Oceanodroma monteiroi*: a new species from the Azores. *Ibis*, 150: 717-727.
- BORGES, P. A. V. & V. K. BROWN, 1999. Effect of island geological age on the arthropod species richness of Azorean pastures. *Biological Journal of the Linnean Society*, 66: 373-410.
- BORGES, P. A. V., C. ABREU, A. F. AGUIAR, P. CARVALHO, S. FONTINHA, R. JARDIM, I. MELO, P. OLIVEIRA, M. M. SEQUEIRA, C. SÉRGIO, A. R. M. SERRANO, M. SIM-SIM & P. VIEIRA, 2008. Terrestrial and freshwater biodiversity of the Madeira and Selvagens archipelagos. In: P. A. V. BORGES, C. ABREU & A. M. F. AGUIAR (eds.), *A list of the terrestrial fungi, flora and fauna of Madeira and Selvagens archipelagos*, pp. 13-26. Direcção Regional do Ambiente da Madeira and Universidade dos Açores, Funchal and Angra do Heroísmo.

- BORGES, P. A. V., A. COSTA, R. CUNHA, R. GABRIEL, V. GONÇALVES, A. F. MARTINS, I. MELO, M. PARENTE, P. RAPOSEIRO, P. RODRIGUES, R. S. SANTOS, L. SILVA, P. VIEIRA & V. VIEIRA (eds.), 2010. *A list of the terrestrial and marine biota from the Azores*, 429 pp. Príncipe, Cascais.
- CLARKE, T., C. ORGILL & T. DISLEY, 2006. *Field guide to the birds of the Atlantic islands: Canary Islands, Madeira, Azores, Cape Verde*, 368 pp. Helm Field Guides, London.
- CLIMAAT, 2011. Anuários climatológicos. <http://www.clima.angra.uac.pt/>. Accessed in 2011-10-04.
- CROW, J. & M. KIMURA, 1970. *An Introduction to Population Genetics Theory*, 591 pp. Harper & Row, New York.
- DARWIN, C., 1859. *On the Origin of Species by Means of Natural Selection*, 434 pp. (Reprint of first edition, 1950). Watts, London.
- DE QUEIROZ, K., 2007. Species concepts and species delimitation. *Systematic Biology*, 56: 879-886.
- DEL NEVO, A. J., E. K. DUNN, F. M. MEDEIROS, G. LE GRAND, P. AKERS, M. I. AVERY, L. R. MONTEIRO, 1993. The status of Roseate Terns *Sterna dougallii* and Common Terns *Sterna hirundo* in the Azores. *Seabird*, 15: 30-37.
- DESJARDINS, P. & R. MORAIS, 1990. Sequence and gene organization of the chicken mitochondrial genome. *Journal of Molecular Biology*, 212: 599-634.
- DIETZEN, C., C. VOIGT, M. WINK, M. GAHR & S. LEITNER, 2006. Phylogeography of Island Canary (*Serinus canaria*) populations. *Journal of Ornithology*, 147: 485-494.
- DIETZEN, C., E. GARCIA-DEL-REY, G. CASTRO & M. WINK, 2008. Phylogenetic differentiation of *Sylvia* species (Aves: Passeriformes) of the Atlantic islands (Macaronesia) based on mitochondrial DNA sequence data and morphometrics. *Biological Journal of the Linnean Society*, 95: 157-174.
- DROTRH/INAG, 2001. *Plano Regional da Água. Relatório técnico. Versão para consulta pública*, 414 pp. DROTRH-INAG, Ponta Delgada.
- DROVETSKI, S. V., R. M. ZINK, I. V. FADEEV, E. V. NESTEROV, E. A. KOBLIK, Y. A. RED'KIN & S. ROHWER, 2004a. Mitochondrial phylogeny of *Locustella* and related genera. *Journal of Avian Biology*, 35: 105-110.
- DROVETSKI, S. V., R. M. ZINK, S. ROHWER, I. V. FADEEV, E. V. NESTEROV, I. KARAGODIN, E. A. KOBLIK & Y. A. RED'KIN, 2004b. Complex biogeographic history of a Holarctic passerine. *Proceedings of the Royal Society of London B*, 21: 545-551.
- DROVETSKI, S. V., R. M. ZINK & N. A. MODE, 2009. Patchy distributions belie morphological and genetic homogeneity in rosifinches. *Molecular Phylogenetics and Evolution*, 50: 437-445.
- EDWARDS, S. V. & A. C. WILSON, 1990. Phylogenetically informative length polymorphism and sequence variability in mitochondrial DNA of Australian songbirds (*Pomatostomus*). *Genetics*, 126: 695-711.
- EMERSON, B. C., 2002. Evolution on oceanic islands: molecular phylogenetic approaches to understanding pattern and process. *Molecular Ecology*, 11: 951-966.
- ERICSON, P. G. P., L. CHRISTIDIS, A. COOPER, M. IRESTEDT, J. JACKSON, U. S. JOHANSSON & J. A. NORMAN, 2002. A Gondwanan ori-

- gin of passerine birds supported by DNA sequences of the endemic New Zealand wrens. *Proceedings of the Royal Society of London B*, 269: 235-241.
- FEDUCCIA, A., 1995. Explosive evolution in Tertiary birds and mammals. *Science*, 267: 637-638.
- FERNÁNDEZ-PALACIOS, J. M. & E. DIAS, 2001. El marco biogeográfico Macaronésico. In: J. M. FERNÁNDEZ-PALACIOS & E. J. L. MARTÍN (eds.), *Naturaleza de las Islas Canarias: Ecología y conservación*, pp. 45-52. Turquesa Ediciones, Santa Cruz de Tenerife.
- FITZPATRICK, J. W., 1988. Why so many passerine birds? A response to Raikow. *Systematic Zoology*, 37: 71-76.
- FRANKHAM, R., 1997. Do island populations have less genetic variation than mainland populations? *Heredity*, 78: 311-327.
- FRANÇA, Z., J. V. CRUZ, J. C. NUNES & V. H. FORJAZ, 2003. Geologia dos Açores: uma perspectiva actual. *Açoreana*, 10: 11-140.
- FRUTUOSO, G., 1561. *Saudades da terra*. 2nd edition published in 6 volumes from 1978 to 1983. J. B. O. RODRIGUES (ed.). Instituto Cultural de Ponta Delgada, Ponta Delgada.
- GARCIA-DEL-REY, E., 2011. *Field Guide to the Birds of Macaronesia. Azores, Madeira, Canary Islands, Cape Verde*, 342 pp. Lynx Edicions, Bellaterra, Barcelona.
- GOCHFELD, M., 1983. The Roseate Tern: World distribution and status of a threatened species. *Biological Conservation*, 25: 103-125.
- Google Earth, 2012. Accessed in 2012-04-08.
- GRANT, P. R., 1986. *Ecology and Evolution of Darwin's Finches*, 492 pp. Princeton University Press, Princeton, NJ.
- GRANT, P. R., 1998. *Evolution on islands*, 334 pp. Oxford University Press, Oxford.
- HARTERT, E. & W. R. OGILVIE-GRANT, 1905. On the Birds of the Azores. *Novitates Zoologicae*, 12: 80-128.
- HEY, J., 2006. On the failure of modern species concepts. *Trends in Ecology and Evolution* 21: 447-450.
- HEWITT, G. M., 1996. Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society*, 58: 247-276.
- HEWITT, G. M., 2004. Genetic consequences of climatic oscillations in the Quaternary. *Philosophical Transactions of the Royal Society of London B*, 359: 183-195.
- HILDEBRAND, A., P. MADUREIRA, F. O. MARQUES, I. CRUZ, B. HENRY & P. SILVA, 2008. Multi-stage evolution of a sub-aerial volcanic ridge over the last 1.3 Myr: S. Jorge Island, Azores triple junction. *Earth and Planetary Science Letters*, 233: 289-298.
- HOEZEL, A. R., J. HALLEY, S. J. O'BRIEN, C. CAMPAGNA, T. ARNBOM, B. LE BOEUF, K. RALLS & G. A. DOVER, 1993. Elephant seal genetic variation and the use of simulation models to investigate historical population bottlenecks. *Journal of Heredity*, 84: 443-449.
- Instituto Hidrográfico, 2010. *Roteiro da costa de Portugal – Arquipélago dos Açores*. 3rd edition published in 2 volumes. Instituto Hidrográfico, Lisboa.
- IZQUIERDO, I., J. L. MARTÍN, N. ZURITA & M. ARECHAVELETA (eds.), 2004. *Lista de especies silvestres de Canarias (hongos, plantas y animales terrestres)*, 579 pp. Consejería de Política Territorial y Medio Ambiente del Gobierno de Canarias, Spain.

- JUAN, C., B. C. EMERSON, P. OROMÍ & G. M. HEWITT, 2000. Colonization and diversification: towards a phylogeographic synthesis for the Canary Islands. *Trends in Ecology & Evolution*, 15: 104-109.
- KOCHER, T. D., W. K. THOMAS, A. MEYER, S. V. EDWARDS, S. PAABO, F. X. VILLABLANCA & A. C. WILSON, 1989. Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. *Proceedings of the National Academy of Science of the USA*, 86: 6196-6200.
- LE GRAND, G., 1977. Apparition du moineau domestique à São Miguel (Açores). *Alauda*, 45: 339-340.
- LINNAEUS, C., 1758. *Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus differentiis, synonymis, locis*. Tomus I. Editio Decima, Reformata. Holmiae, Impensis Direct, Laurentii Salvii.
- LÓPEZ-JURADO, L. F., J. A. MATEO & A. I. FAZERES, 2005. Chordata. In: M. ARECHA-VALETA, N. ZURITA, M. C. MARRERO & J. L. MARTÍN (eds.). *Lista preliminar de especies silvestres de Cabo Verde (hongos, planta y animals terrestres)*, pp. 101-104. Consejería de Medio Ambiente y Ordenación Territorial, Gobierno de Canarias.
- MACARTHUR, R. H. & E. O. WILSON, 1967. *The theory of island biogeography*, 215 pp. University Press, Princeton, NJ.
- MADDISON, W. P., 1997. Gene trees in species trees. *Systematic Biology* 46: 523-536.
- MALLET, J., 1995. A species definition for the modern synthesis. *Trends in Ecology and Evolution* 10: 294-299.
- MARSHALL, H. D. & A. J. BAKER, 1999. Colonization History of Atlantic Island Common Chaffinches (*Fringilla coelebs*) Revealed by Mitochondrial DNA. *Molecular Phylogenetics and Evolution*, 11: 201-212.
- MAYR, E., 1963. *Animal species and speciation*, 797 pp. Harvard University Press, Cambridge, MA.
- MONTEIRO, L. R. & R. W. FURNESS, 1995a. Fea's Petrel *Pterodroma feae* in the Azores. *Bulletin of the British Ornithologists' Club*, 115: 9-14.
- MONTEIRO, L. R. & R. W. FURNESS, 1995b. Seabirds as monitors of mercury in the marine environment. *Water, Air & Soil Pollution*, 80: 851-870.
- MONTEIRO, L. R., J. A. RAMOS & R. W. FURNESS, 1996a. Past and present status and conservation of the seabirds breeding in the Azores archipelago. *Biological Conservation*, 78: 319-328.
- MONTEIRO, L. R., J. A. RAMOS, R. W. FURNESS & A. J. DEL NEVO, 1996b. Movements, morphology, breeding, molt, diet and feeding of seabirds in the Azores. *Waterbirds*, 19: 82-97.
- MONTEIRO, L. R., J. A. RAMOS, J. C. PEREIRA, P. R. MONTEIRO, R. S. FEIO, D. R. THOMPSON, S. BEARSHOP, R. W. FURNESS, M. LARANJO, G. HILTON, V. C. NEVES, M. P. GROZ & K. R. THOMPSON, 1999. Status and distribution of Fea's Petrel, Bulwer's Petrel, Manx Shearwater, Little Shearwater and Band-rumped Storm-Petrel in the Azores Archipelago. *Waterbirds*, 22: 358-366.
- MYERS, N., R. A. MITTERMEIER, C. G. MITTERMEIER, G. A. B. da FONSECA & J. KENT, 2000. Biodiversity hotspots for conservation priorities. *Nature*, 403: 853-858.
- NEI, M., T. MARUYAMA & C. I. WU, 1983. Models of evolution of reproductive isolation. *Genetics*, 103: 557-579.

- NEVES, V. C., K. GRIFFITHS, F. R. SAVORY, R. W. FURNESS & B. K. MABLE, 2010. Are European starlings breeding in the Azores archipelago genetically distinct from birds breeding in mainland Europe? *European Journal of Wildlife Research*, 59: 95-100.
- NEWTON, I., 2003. *The Speciation & Biogeography of Birds*, 668 pp. Academic Press, London, UK.
- OLIVEIRA, P. & D. MENEZES, 2004. *Aves do Arquipélago da Madeira*, 111 pp. Serviço do Parque da Madeira Arquipélago Verde produtos promocionais, Ida. Funchal.
- PÄCKERT, M. & J. MARTENS, 2004. Song dialects on the Atlantic islands: Goldcrests of the Azores (*Regulus regulus azoricus*, *R. r. sanctae-mariae*, *R. r. inermis*). *Journal of Ornithology*, 145: 23-30.
- PAVLOVA, A., R. M. ZINK, S. V. DROVETSKI, Y. A. RED'KIN & S. ROHWER, 2003. Phylogeographic patterns in *Motacilla flava* and *M. citreola*: species limits and population history. *Auk*, 120: 747-758.
- PRESTON, F. W., 1962. The canonical distribution of commonness and rarity: Part I. *Ecology* 43: 185-215 and 431-432.
- RAIKOW, R. J., 1982. Monophyly of the Passeriformes: test of a phylogenetic hypothesis. *Auk*, 99: 431-445.
- RAMOS, J. A., 1994. Fern frond feeding by the Azores Bullfinch. *Journal of Avian Biology*, 25: 344-346.
- RODRIGUES, P., J. BRIED, S. RODEBRAND & R. CUNHA, 2010. Aves. In: P. A. V. BORGES, A. COSTA, R. CUNHA, R. GABRIEL, V. GONÇALVES, A. F. MARTINS, I. MELO, M. PARENTE, P. RAPOSEIRO, P. RODRIGUES, R. S. SANTOS, L. SILVA, P. VIEIRA & V. VIEIRA (eds.), *A list of the terrestrial and marine biota from the Azores*, pp. 255-271. Principia, Lisboa.
- RODRIGUES, P. & R. T. CUNHA, 2011. Azorean birds – a natural heritage. *Açoreana*, 7: 319-330.
- RODRIGUES, P., 2012. *Phylogeography and genetic diversity of the Azores passerines. Thesis for the Doctoral degree in Biology*, 185 pp. University of the Azores, Ponta Delgada.
- RODRIGUES, P. & R. T. CUNHA, 2012. Birds as a tool for island habitat conservation and management. *American Journal of Environmental Sciences*, 8: 5-10.
- RODRIGUES, P., C. AUBRECHT, A. GIL, T. LONGCORE & C. ELVIDGE, 2012. Remote sensing to map light pollution stress on Cory's Shearwater, *Calonectris diomedea borealis*, on São Miguel Island, Azores Archipelago. *European Journal of Wildlife Research*, 58: 147-155.
- RODRIGUES, P., R. J. LOPES, S. REIS, R. RESENDES, J. A. RAMOS & R. T. CUNHA, 2013a. Genetic diversity and morphological variation of the common chaffinch (*Fringilla coelebs*) in the Azores. *Journal of Avian Biology*. DOI: 10.1111/j.1600-048X.2013.00229.x.
- RODRIGUES, P., R. J. LOPES, S. V. DROVETSKI, S. REIS, J. A. RAMOS & R. T. CUNHA, 2013b. Phylogeography and genetic diversity of the Robin (*Erithacus rubecula*) in the Azores islands: evidence of a recent colonisation. *Journal of Ornithology*, 154: 889-900.
- SHELDON, F. H. & F. B. GILL, 1996. A reconsideration of songbird phylogeny with emphasis on the evolution of titmice and their Sylvioidean relative. *Systematic Biology*, 45: 473-495.

- SIBLEY, C. G. & J. E. AHLQUIST, 1990. *Phylogeny and Classification of Birds: a study in molecular evolution*, 976 pp. Yale University Press, New Haven, CT.
- SITES, Jr J. W., & J. C. MARSHALL, 2003. Delimiting species: A Renaissance issue in systematic biology. *Trends in Ecology and Evolution*, 18: 462-470.
- SJÖGREN, E., 1984. *Azores Flowers*, 176 pp. Direcção Regional de Turismo, Horta.
- SJÖGREN, E., 1990. Bryophyte flora and vegetation on the island of Graciosa (Azores), with remarks on floristic diversity of the Azorean islands. *Arquipélago*, 8: 63-96.
- SLATKIN, M., 1985. Gene flow in natural populations. *Annual Review of Ecology and Systematics*, 16: 393-430.
- SPICER, G. S. & L. DUNIPACE, 2004. Molecular phylogeny of songbirds (Passeriformes) inferred from mitochondrial 16S ribosomal RNA gene sequences. *Molecular Phylogenetics and Evolution*, 30: 325-335.
- STATTERSFIELD, A., M. CROSBY, A. LONG & D. WEGE, 1998. *Endemic Bird Areas of the World. Priorities for Biodiversity Conservation*, 846 pp. Birdlife Conservation, Series N° 7. Cambridge.
- TÖPFER, T., E. HARING, T. R. BIRKHEAD, R. J. LOPES, L. L. SEVERINGHAUS, J. MARTENS & M. PACKERT, 2010. A molecular phylogeny of bullfinches *Pyrrhula* Brisson, 1760 (Aves: Fringillidae). *Molecular Phylogenetics and Evolution*, 58: 271-282.
- TRIBSCH, A. & P. SCHONSWETTER, 2003. Patterns of endemism and comparative phylogeography confirm palaeo-environmental evidence for Pleistocene refugia in the Eastern Alps. *Taxon*, 52: 477-497.
- WILCOX, B., 1980. Insular ecology and conservation. In: M. SOULÉ & B. WILCOX (eds.), *Conservation biology: an evolutionary ecological perspective*, pp. 95-117. Sinauer, Sunderland, MA.
- WILDT, D. E., M. BUSH, K. L. GOODROWE, C. PACKER, A. E. PUSEY, J. L. BROWN, P. JOSLIN & S. J. O'BRIEN, 1987. Reproductive and genetic consequences of founding isolated lion populations. *Nature* 329: 328-331.
- WILLIAMSON, M., 1981. *Island Populations*, 286 pp. Oxford University Press, Oxford.
- WILLIS, J. C., 1922. *Age and area, A Study in Geographical Distribution and Origin of Species*. Cambridge University Press, Cambridge.
- WINK, M., H. SAUER-GÜRTH & E. GWINNER, 2002. Evolutionary relationships of stonechats and related species inferred from mitochondrial-DNA sequences and genomic fingerprinting. *British Birds*, 95: 349-355.
- WHITTAKER, R. J. & J. M. FERNÁNDEZ-PALACIOS, 2007. *Island Biogeography. Ecology, evolution and conservation*, 412 pp. Second Edition. Oxford University Press. New York.
- ZINK, R. M., 2004. The role of subspecies in obscuring biological diversity and misleading conservation policy. *Proceedings of the Royal Society of London B*, 271: 561-564.