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An Overview of the Genus *Athene* in the Pleistocene of the Mediterranean Islands, with the Description of *Athene trinacriae* n. sp. (Aves: Strigidae)

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Abstract

The Little Owls of the genus *Athene* are small strigiform birds commonly present in Mediterranean islands during the Pleistocene and Holocene with four species: *Athene angelis* from the Middle and Late Pleistocene of Corsica, *Athene cretensis* from the Late Pleistocene of Crete and Armathia, *Athene trinacriae* n. sp. from the Middle Pleistocene of Sicily, and *Athene noctua* from the Pleistocene of the Balearic Islands, Sardinia, Cyprus, Karpathos, and from the Late Pleistocene of Sicily. This work takes into account the distribution of the genus *Athene* in the Mediterranean islands and tries to explain the relationships between the endemic mammal faunas of the islands and the presence of endemic *Athene* species. In addition, the present distribution of *Athene noctua* on Mediterranean islands, probably due to recent colonization, is discussed. An extinct species, *Athene trinacriae* n. sp., is described within the fossil assemblage of some Middle Pleistocene locali-

ties of Sicily. The species is similar in size to the extant *A. noctua*, but differs from it by its longer legs and some morphological characteristics, probably as a result of a mainly terrestrial life style. *Athene trinacriae* n. sp. is smaller than *A. angelis*, from the Pleistocene of Corsica, and has longer and thinner tibiotarsus and tarsometatarsus; it also differs by its smaller size and by its relatively longer legs from the endemic form of the Pleistocene of Crete and Armathia, *Athene cretensis*.

Introduction

The fossil avifauna of Sicily is little known, except for a few studies of bird remains from some archaeological sites in which only extant species and continental-like bird associations are listed (Tyrberg, 1998), and a preliminary analysis of the late Middle Pleistocene birds from Contrada Fusco (Siracusa, South-Eastern Sicily) (Cassoli and Tagliacozzo, 1996).

In the revision of the avifaunas of isolated Mediterranean islands during the Middle and Late Pleistocene (Alcover *et al.*, 1992), the avifaunas of Sicily were excluded because it was supposed that a connection had existed between the island and the mainland. During the last two centuries, many Sicilian localities with fossil vertebrate assemblages have been found and excavated (Bonfiglio and Burgio, 1992). Palaeontological analysis made it possible for the authors to arrange the Pleistocene vertebrates into five faunal complexes. Four of them include mainly endemic fossil mammals, reptiles, and amphibians, while the fifth, dating from the latest Pleistocene, contains extant continental species, which accompany Palaeolithic artefacts (Bonfiglio *et al.*, 1997, 2001; Di Maggio *et al.*, 1999). Fossil bird remains were found in each faunal complex (Bonfiglio and Insacco, 1992; Bonfiglio *et al.*, 1997), except in the oldest one “Monte

Pellegrino Faunal Complex” which contains only small mammals and reptiles (Burgio and Fiore, 1988).

In 1959 and 1960 fossil bones were collected in Spinagallo Cave, near Siracusa (South-Eastern Sicily), by a team from the University “La Sapienza” of Rome (Accordi *et al.*, 1959). The fossil assemblage contains the dwarf elephant *Elephas falconeri*, endemic Gliridae, the endemic shrew *Crocidura esuae*, bats, reptiles, amphibians, and birds (Kotsakis, 1984). This assemblage is typical of the “*Elephas falconeri* Faunal Complex” which is referred to the early Middle Pleistocene (Bonfiglio *et al.*, 1997). In a preliminary report on the fossil avifauna of Spinagallo Cave, Pavia (1999) recognized 61 taxa, some of them with characteristics of endemism.

This paper describes the fossil remains from Spinagallo Cave and other Sicilian localities of same age (Luparello Cave, Marasà Cave and Poggio

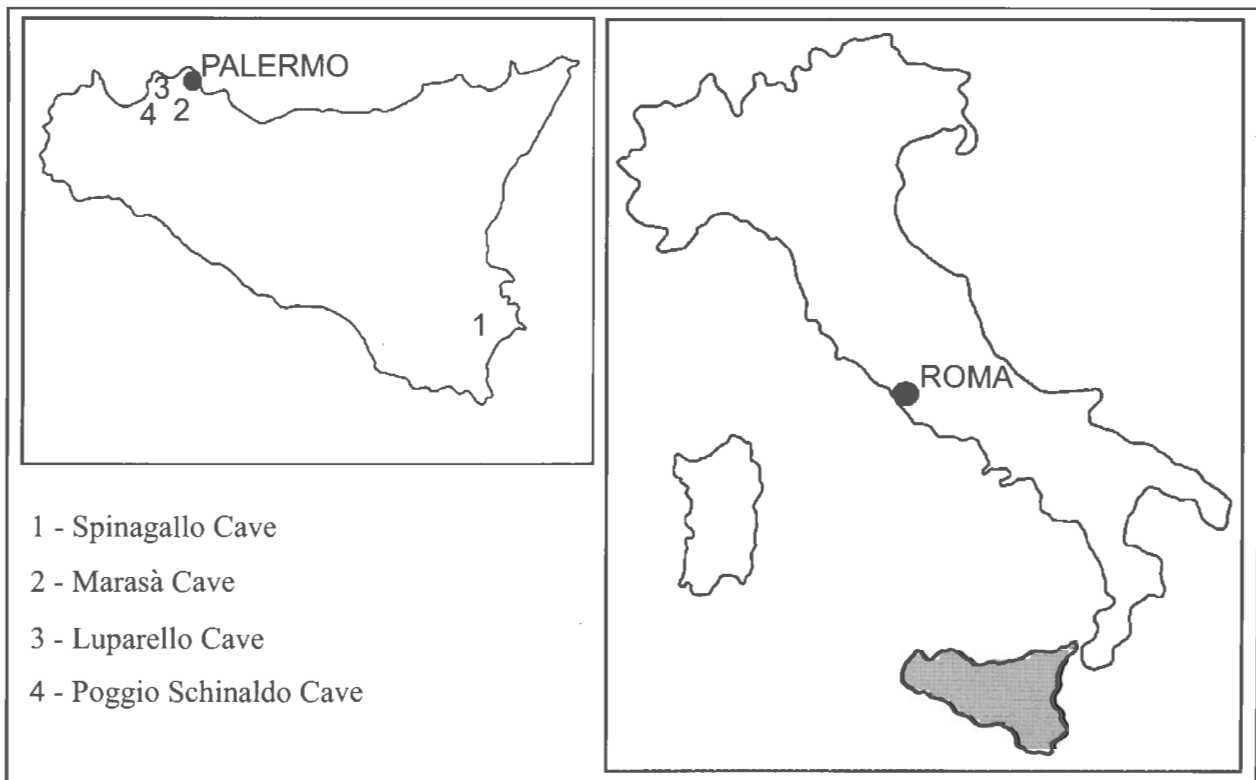


FIGURE 1. Map of Sicily (shaded). The inset shows the position of the localities with *Athene trinacriae* remains cited in the text.

Schinaldo Cave) (Fig. 1) that belong to the genus *Athene* and have been attributed to a new species, *Athene trinacriae*. It also analyses the distribution of the genus *Athene* in the Mediterranean islands during the Pleistocene and Holocene.

The fossil specimens are deposited in the Museo di Paleontologia dell' Università "La Sapienza", Roma (MPUR), in the Museo Geologico "G. G. Gemmelaro", Palermo (MGUP), in the Museo di Geologia e Paleontologia dell' Università, Torino (PU) and in the Insacco Collection in the Museo Civico di Storia Naturale, Comiso (CI). The osteological terminology follows Baumel and Witmer (1993).

Systematic Paleontology
Class Aves Linnaeus, 1758
Order Strigiformes (Wagler, 1830)
Family Strigidae Vigors, 1925
Genus *Athene* Boie, 1822
Athene trinacriae n. sp.

Athene n. sp. Tyrberg, 1998

Athene species undescribed Pavia, 1999

Holotype MPUR 5537 complete right tarsometatarsus.

Paratypes MPUR 5127 right coracoid, MPUR 5234 left tarsometatarsus, MPUR 5259 left coracoid, MPUR 5285 right femur, MPUR 5510 right tarsometatarsus, MPUR 5572 distal left humerus, MPUR 5713 proximal left ulna, PU 100023 left humerus, PU 100024 distal right ulna, PU 100026 left carpometacarpus, PU 100029 distal right tibiotarsus, CI 1150-1 right tibiotarsus.

Hypodigm Material from Spinagallo Cave: MPUR 5003 distal right coracoid, MPUR 5004 left coracoid, MPUR 5006 left humerus, MPUR 5009 right coracoid, MPUR 5014 right carpometacarpus, MPUR 5094 right coracoid, MPUR 5096 left coracoid, MPUR 5098 distal right coracoid, MPUR 5128 right coracoid, MPUR 5214 left humerus, MPUR 5231 right tarsometatarsus, MPUR 5239 left tarsometatarsus, MPUR 5249 right coracoid, MPUR 5255 left coracoid, MPUR 5256 proximal left coracoid, MPUR 5257 left coracoid, MPUR 5258 left coracoid, MPUR 5260 left coracoid, MPUR 5261 left coracoid, MPUR 5273 left femur, MPUR 5288 proximal left femur, MPUR 5424 proximal right carpometacarpus, MPUR 5507

proximal left humerus, MPUR 5512 proximal right tarsometatarsus, MPUR 5513 distal right tarsometatarsus, MPUR 5528 distal right tarsometatarsus, MPUR 5532 distal right tarsometatarsus, MPUR 5535 distal left tarsometatarsus, MPUR 5718 proximal left tibiotarsus, MPUR 5719 right tibiotarsus, MPUR 5721 distal left ulna, MPUR 5723 right tibiotarsus, MPUR 5725 distal right humerus, MPUR 5730 proximal right tibiotarsus, PU 100025 left coracoid, PU 100028 right coracoid, PU 100027 left mandible, PU 100030 proximal left tarsometatarsus, CI 1150-2 right ulna, CI 1150-3 distal left ulna, CI 1150-5 distal left tibiotarsus, CI 1150-6 proximal left humerus, CI 1150-7 proximal left humerus, CI 1150-8 left humerus, CI 1150-9 distal left ulna. Material from Marasà Cave: MGUP MA 227-012 proximal right humerus, MGUP MA 227-042 proximal left humerus, MGUP MA 227-044 distal right humerus, MGUP MA 229-013 left coracoid, MGUP MA 229-014 left carpometacarpus, MGUP MA 229-017 left coracoid, MGUP MA 229-019 left carpometacarpus, MGUP MA 229-027 left tarsometatarsus, MGUP MA 229-035 proximal left ulna, MGUP MA 229-134 proximal right ulna, MGUP MA 230-015 right tarsometatarsus, MGUP MA 230-077 proximal left carpometacarpus, MGUP MA 230-079 distal right tarsometatarsus, MGUP MA 230-084 proximal right coracoid, MGUP MA 230-099 proximal right coracoid, MGUP MA 231-015 right humerus, MGUP MA 231-024 distal right humerus, MGUP MA 231-033 proximal right humerus, MGUP MA 234-005 distal left carpometacarpus, MGUP MA 235-003 right carpometacarpus, MGUP MA 237-051 distal right tarsometatarsus, MGUP MA 237-066 proximal right coracoid, MGUP MA 237-090 proximal right humerus. Material from Poggio Schinaldo Cave: MGUP PS 77/1 cranium, MGUP PS 78/1 right tarsometatarsus, MGUP PS 78/2 left tarsometatarsus, MGUP PS 79 sternum. Material from Luparello Cave: MGUP GL 405 distal right tibiotarsus, MGUP GL 432-4 proximal right tarsometatarsus (Table 1).

Etymology From Trinacria, the ancient name of Sicily.

Type locality Spinagallo Cave, near Siracusa, South-Eastern Sicily, Italy.

Additional localities Luparello Cave, Marasà Cave and Poggio Schinaldo Cave, near Palermo, North-Western Sicily.

TABLE 1. Measurements (in mm) of the complete limb bones of *Athene trinacriae* n. sp. The measurements are taken following Mourer-Chauviré (1975). (TL, Total length; PW, Proximal width; PD, Proximal depth; DW, Distal width; DD, Distal depth; WM, Width in the middle. Other acronym abbreviation, see text.)

| | TL | PW | PD | DW | DD | WM |
|------------------------|------|-----|-----|-----|-----|-----|
| Coracoid | | | | | | |
| MGUP MA 229-013 | 25.0 | | 3.5 | | | 2.3 |
| MGUP MA 229-017 | 25.1 | 5.4 | 2.9 | 7.3 | 2.0 | 2.4 |
| MGUP MA 230-084 | 22.9 | 4.6 | 2.8 | | 1.8 | 2.4 |
| PU 100025 | 26.3 | 5.0 | 3.2 | 8.0 | 2.3 | 2.2 |
| PU 100026 | 24.7 | 4.7 | 3.0 | 7.8 | 2.1 | 2.1 |
| MPUR 5004 | 27.8 | 5.3 | 3.3 | | | 2.5 |
| MPUR 5009 | 26.3 | 5.4 | 3.0 | 7.5 | 2.3 | 2.2 |
| MPUR 5096 | 26.1 | 4.8 | 2.9 | 7.6 | 2.5 | 2.1 |
| MPUR 5127 | 26.9 | 5.0 | 3.1 | 7.6 | 2.1 | 2.3 |
| MPUR 5128 | 25.6 | 4.5 | 3.5 | 6.9 | 2.3 | 2.2 |
| MPUR 5249 | 25.1 | 4.6 | 3.2 | | | 2.2 |
| MPUR 5255 | 26.0 | 4.5 | 3.2 | 7.3 | 2.1 | 2.4 |
| MPUR 5257 | 26.4 | 4.2 | 2.9 | 8.1 | 2.4 | 2.5 |
| MPUR 5258 | 26.3 | 5.1 | 3.5 | 7.7 | 2.1 | 2.2 |
| MPUR 5259 | 26.6 | 4.8 | 2.9 | 7.8 | 2.3 | 2.3 |
| MPUR 5260 | 25.3 | 5.0 | 2.9 | 8.1 | 2.0 | 2.2 |
| MPUR 5261 | 26.6 | 5.2 | 2.8 | 7.5 | 2.3 | 2.2 |
| Humerus | | | | | | |
| CI 1150-8 | 50.1 | 9.5 | 5.9 | | | 3.4 |
| MGUP MA 231-015 | 47.6 | 9.2 | 5.7 | 8.4 | 4 | 3.5 |
| PU 100023 | 49.2 | 9.3 | 5.8 | 8.9 | 4.4 | 3.4 |
| MPUR 5006 | 52.7 | | | 9.4 | 4.7 | 3.5 |
| MPUR 5725 | 50.4 | 9.2 | 6.3 | 9.1 | 4.3 | 3.5 |
| Ulna | | | | | | |
| CI 1150-2 | 59.6 | | | | | 2.6 |
| Carpometacarpus | | | | | | |
| MGUP MA 229-014 | 26.7 | 3.1 | 6.4 | 4.8 | 2.5 | 1.8 |
| MGUP MA 229-019 | 28.7 | 6.5 | 3.5 | 4.4 | 2.6 | 1.7 |
| PU 100028 | 28.2 | 3.2 | 6.3 | 4.1 | 2.5 | 1.8 |
| MPUR 5014 | 28.1 | 3.2 | 6.3 | 4.5 | 2.3 | 2.1 |
| Femur | | | | | | |
| MPUR 5273 | 40.5 | 7.1 | 4.5 | 7.7 | 6.4 | 3.2 |
| MPUR 5285 | 40.9 | 7.2 | 4.8 | 7.6 | 5.9 | 3.5 |
| Tibiotarsus | | | | | | |
| CI 1150-1 | 66.1 | | | | | 3.4 |
| Tarsometatarsus | | | | | | |
| MGUP MA 230-015 | 40.1 | 6.8 | 6.9 | 7.2 | 6.0 | 3.2 |
| MPUR 5231 | 40.8 | | | 7.5 | 5.4 | 3.2 |
| MPUR 5233 | 39.6 | 6.7 | 6.1 | | | 2.6 |
| MPUR 5234 | 40.7 | 6.9 | 6.6 | 7.5 | 5.4 | 2.9 |
| MPUR 5239 | 40.8 | | | | | 3.7 |
| MPUR 5510 | 41.6 | | | 7.4 | 5.6 | 3.1 |
| MPUR 5537 | 42.7 | 7.1 | 6.7 | 8 | 5.7 | 3.4 |

Age Early Middle Pleistocene, “*Elephas falconeri* Faunal Complex” according to Bonfiglio *et al.* (1997, 2001).

Diagnosis Body size similar to that of *Athene noctua* but with very long legs. Coracoid with the distal outline of the facies articularis clavicularis forming an acute angle with the major axis of the bone. Tibiotarsus elongated, with muscular impression in the medial side of the diaphysis, close to the condylus medialis. Tarsometatarsus thin and elongated; the crista medialis hypotarsi is well developed and its proximal outline slopes toward the distal end.

Description and Comparison with Extant Forms of the Genus *Athene*

The coracoid presents the typical features of the genus (Fig. 2A). The facies articularis scapularis is not as wide as in *A. noctua*, and in addition the angle between the processus procoracoideus and the diaphysis is more open. The distal outline of the facies articularis clavicularis forms an acute angle with the major axis of the bone (Fig. 2F) while in *A. noctua* the angle is obviously more open (Fig. 2G).

In the humerus of *Athene noctua*, the condylus ventralis is more elongated and pointed in cranial view; the fossa musculi brachialis has a more pronounced lateral border in *A. trinacriae* than in *A. noctua*.

In the proximal part of the ulna the impressio brachialis is well marked in *Athene trinacriae*, and the tuberculum ligamenti collateralis ventralis is more protruding too. In *A. trinacriae* the olecranon is clearly projecting proximally, while in *A. noctua* it is less projecting and it is in the prolongation of the caudal outline of the cotyla dorsalis. In the new species a clearly marked tuberculum is visible on the dorsal part of the bone, close to the crista intercotylaris, that is also more evident than in *A. noctua* (Fig. 2H). On the distal part of the bone, the incisura tuberculi carpalis of *A. trinacriae* is deep and wide, and forms a sort of right angle between the tuberculum carpalis and the condylus ventralis ulnae.

The tibiotarsus of *A. trinacriae* is thinner and more elongated than in *A. noctua*, with a muscular impression on the medial side of the distal part of the diaphysis, close to the condylus medialis (Fig. 2C, D).

The tarsometatarsus of *A. trinacriae* is very slender

and elongated (Fig. 2K). In *A. trinacriae* the crista medialis hypotarsi is more developed than in *A. noctua* and its proximal outline slopes towards the distal end (Fig. 2I). In *A. noctua* the lateral side of the trochlea metatarsi III, forms a small backward point in caudal view (Weesie, 1982), whereas in *A. trinacriae*, as shown also in *A. angelis* (Mourer-Chauviré *et al.*, 1997), there is not a point but a kind of blade that is more developed in a proximo-distal direction.

According to Del Hoyo *et al.* (1999), the other extant species of the genus *Athene* are *A. brama* from Southeast Asia, *A. blewitti* from the Indian subcontinent, and *A. cunicularia* from America.

Athene brama is smaller than *A. noctua* and thus smaller than *A. trinacriae*; it also shows different proportions of limb elements, with relatively longer wings and shorter legs. *Athene blewitti* is a very rare bird; nevertheless, it was possible to obtain significant measurements from an incomplete specimen preserved at the Natural History Museum at Tring (Louchart, pers. comm.). These measurements, together with others reported by Mourer-Chauviré *et al.* (1997) taken from bones preserved in study skins, fall within the variation range of *A. noctua*, except for the tarsometatarsus, which is shorter. *Athene trinacriae* differs from both *A. brama* and *A. blewitti* by its relatively longer legs, as a result of adaptation to a partially terrestrial life in open dry country, whereas the other two species are adapted to arboreal life in dense tropical forests. *Athene cunicularia* lives in the open semi-desertic countries of North and South America; its very elongated hindlimbs, especially the tarsometatarsus, reflect an adaptation to a terrestrial life-style. We were not able to study any skeleton of *A. cunicularia*, but according to the measurements taken from two specimens at the Natural History Museum at Tring (Louchart, pers. comm.), it is larger than *A. noctua*, with larger wings and obviously longer legs. *Athene trinacriae*, even with a similar adaptation to a terrestrial life-style, differs from *A. cunicularia* in having shorter legs, especially the tarsometatarsus.

Description and Comparison with Extinct Forms of the Genus *Athene*

Some fossil species and subspecies belonging to



the genus *Athene* have been described from the Pliocene and the Pleistocene of Europe. *Athene noctua lunellensis*, from the Middle Pleistocene of France (Mourer-Chauviré, 1975) is slightly larger than *A. noctua*, with a similar ratio between wings and legs, while *A. trinacriae* has elongated legs. *Athene angelis* from the Middle and Late Pleistocene of Corsica (Mourer-Chauviré *et al.*, 1997) is a large endemic form, with strong leg bones, from which *A. trinacriae* differs by its smaller size and more slender legs. *Athene cretensis*, from the Late Pleistocene of Crete and Armathia (Weesie, 1982; Pieper, 1984), has longer legs than *A. trinacriae*. *Athene cretensis* also has a diagnostic feature in the proximal humerus: the crista bicipitalis extends distally in a kind of an arch in *A. noctua*, and this arch is absent in *A. cretensis* (Weesie, 1982), but clearly developed in *A. angelis* (Mourer-Chauviré *et al.*, 1997) and *A. trinacriae*. The taxon *Athene (noctua) veta* described by Jánossy (1974) from the Late Pliocene-Early Pleistocene of Rebielice Królewskie in Poland, on the basis of an incomplete left coracoid, was synonymized with *Aegolius funereus* by Mlíkovský (1992).

The scatter diagrams of the total length and width in the middle of carpometacarpus and humerus (Figs. 3-4) show similarities between *Athene trinacriae* and *A. noctua*, while the scatter diagrams of tibiotarsus and tarsometatarsus (Figs. 5-6) show similarities with *A. cretensis*. The osteology of *Athene trinacriae* suggests its adaptation to a terrestrial life-style, similar to that indicated for *A.*

cretensis by Weesie (1982).

The island of Sicily during the Early and Middle Pleistocene was inhabited by an impoverished, highly endemized vertebrate fauna. The absence of terrestrial predators, the presence of endemic rodents of the genera *Leithia* and *Malthamys*, together with the long period of isolation from the mainland, favoured the structural modifications as far as the formation of the endemic species *Athene trinacriae* is concerned. The presence of a large quantity of rodent remains together with bones of *Athene trinacriae* suggests that these animals represented the main food source for this species. Simpson's ratio-diagram (Fig. 7) shows that the leg bones of *A. trinacriae* are proportionally longer than in *A. cretensis*, especially the tarsometatarsus, while the wings are shorter. This fact suggests a greater adaptation of *A. trinacriae* to a terrestrial life-style compared with *A. cretensis*.

The elongation of the hindlimb elements, especially tarsometatarsi, has also been reported in a large number of insular Strigiformes (Ballmann, 1973; Mourer-Chauviré *et al.*, 1994) and has been interpreted as an adaptation to a terrestrial life-style.

Distribution of the Genus *Athene* in Mediterranean Islands

The genus *Athene* has been known in the western Palaearctic since the Late Miocene of Rudabanya, Hungary (Mlíkovský, 1996), while the extant species *Athene noctua* has been known since the Early Pleistocene of the continental Europe (Tyrberg, 1998).

At the present time, *Athene noctua* is widespread on all major Mediterranean islands, even if it is absent in the Maltese Archipelago and very rare in Corsica and the Balearics. This species in Corsica was considered to be an occasional breeder by Thibault and Bonaccorsi (1999). In recent years the records for the Balearic Islands have been increasing in number, and now the species probably breeds locally in Mallorca and Menorca (Snow and Perrins, 1997). *A. noctua* has also been reported from some Pleistocene deposits of the Mediterranean islands, such as Menorca (Seguí, 1999), Mallorca and Tylos (Alcover *et al.*, 1992), Karpathos (Weesie, 1984), Sardinia (Alcover *et al.*, 1992; Weesie, 1999), and Sicily.

FIGURE 2. *Athene trinacriae* n. sp.: paratype left coracoid MPUR 5259, dorsal view (A), enlargement of the proximal end, medial view (F); paratype right tibiotarsus, distal end, PU100029, cranial view (C); paratype right tibiotarsus CI 1150-1, cranial view (E); holotype right tarsometatarsus MPUR 5537, dorsal view (J), enlargement of the medial side of the proximal end (H); paratype left ulna, proximal end, MPUR 5713, cranial view (L); *Athene noctua* recent, Marco Pavia Osteological Collection 38, for comparison (B, E, G, I and K). The scale bar represents 0.5 cm. The specimens are coated with ammonium chloride to enhance contrasts.

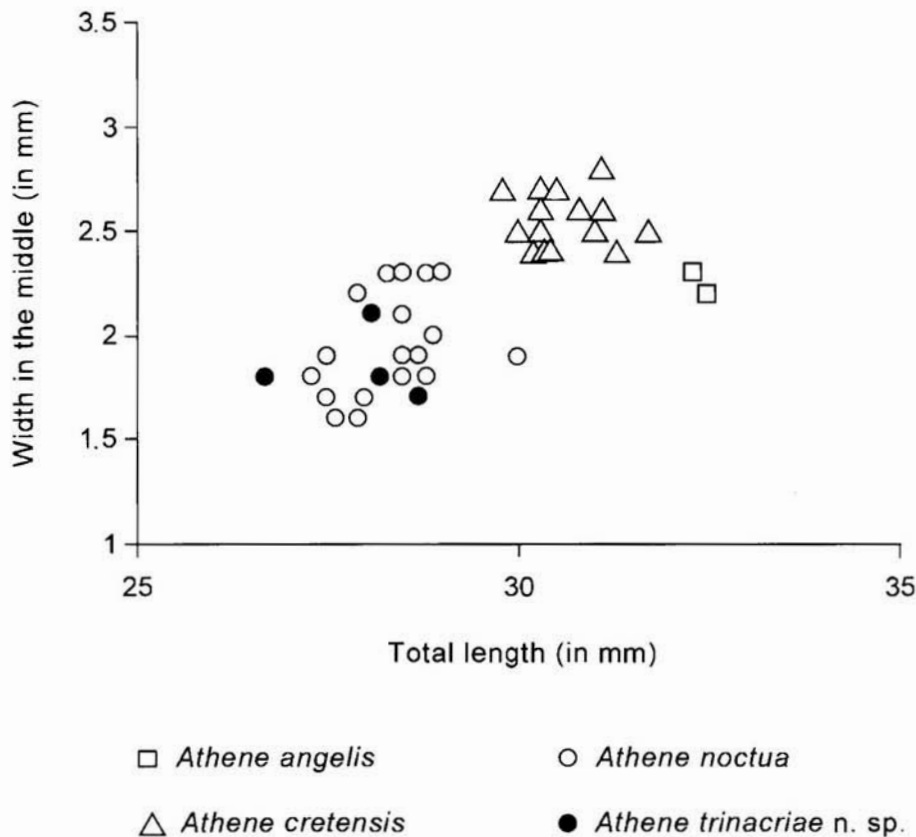


FIGURE 3. Scatter diagram with the measurements of the carpometacarpus of *Athene angelis*, *A. noctua*, *A. cretensis* and *A. trinacriae* n. sp.

On the island of Karpathos, Weesie (1984) determined some bones, which are morphologically identical to the recent *Athene noctua* from a Pleistocene cave deposit. The bones of an endemic murid were collected together with bird remains. The island of Karpathos is close to the Turkish mainland, thus it was probably not so isolated during the Pleistocene as to allow the formation of an endemic form of *Athene*, although the isolation of the island from the mainland has been sufficient to generate endemic mammals. Pieper (1984) reported the discovery of a humerus of *A. cretensis* in a Pleistocene deposit of unknown age on the island of Armathia, close to Kasos and Karpathos. A single bone does not provide very much information, but Weesie (1984) indicated that the islands of Kasos and Karpathos had the same mammalian fauna, different from that of Crete.

Therefore, we think that the fossil from Armathia needs to be re-examined. Besides, the morphological characteristic indicated by Weesie (1982) that separates the humerus of *Athene cretensis* from that of *A. noctua* might have not been well expressed if the bone was not well preserved. In a recent paper, Mourer-Chauviré (1999) reported the presence of *Athene noctua* in an archaeological deposit, dating from the latest Pleistocene, on Cyprus. The geographical position of the island and the absence of other endemic fossil birds suggest a lesser degree of isolation of Cyprus during the Late Pleistocene.

In a paper on fossil birds from the Late Pleistocene of Corbeddu Cave, in Sardinia, Weesie (1999) indicated a complete left tarsometatarsus of small size as *Athene* sp. The author puts forward the hypothesis that it could represent a new insular form. The

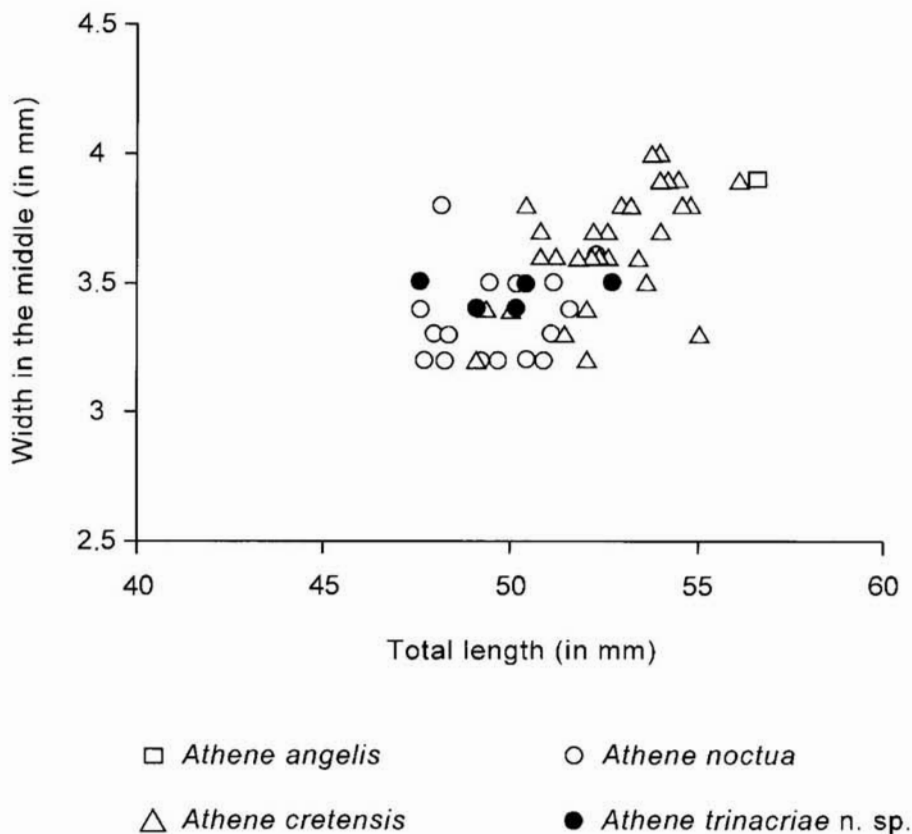


FIGURE 4. Scatter diagram with the measurements of the humerus of *Athene angelis*, *A. noctua*, *A. cretensis* and *A. trinacriae* n. sp.

measurements of the bone fall within the size range of *Athene noctua* and this bone could actually belong to a small individual of this species. We found an indication of aff. *Athene noctua* from Sardinia (Alcover *et al.*, 1992), but according to Comaschi Caria (1969) all the bird material from Sardinia, as well as the bones studied by Malatesta and Suriano (1970), needs to be restudied. Therefore we do not take into account the indication given by Alcover *et al.* (1992).

In Sicily, *Athene noctua* has been present since the late Middle Pleistocene and bones of this species were found in some localities associated with the vertebrates of the “*Elephas mnaidriensis* Faunal Complex”, such as Contrada Fusco (Cassoli and Tagliacozzo, 1996; Pavia, 2001), Baida, Cannita Cave, and Favignana (Pavia, 2000, and unpublished data). All these localities are late Middle Pleistocene in age (Bonfiglio *et al.*, 1997).

During the Middle Pleistocene, Sicily was often connected with the mainland; and some continental species, such as deer and terrestrial carnivores, entered the island. During the same period, *Athene trinacriae* and some other elements of the early Middle Pleistocene “*Elephas falconeri* Faunal Complex” disappeared. The causes of the extinction of these animals are still unknown, but are probably related to palaeoenvironmental changes and to competition with continental animals. *Athene noctua* replaced *A. trinacriae*; in fact, the former taxon was a fairly common bird in the late Middle Pleistocene and Late Pleistocene deposits of Sicily.

Thus, the Mediterranean islands were inhabited by different endemic species of *Athene* during the Pleistocene. The extant species of this genus are generally sedentary and inclined to a terrestrial way of life, as illustrated by the American *A. cunicularia*.

This sedentary habitus contributes to genetic isolation, which favours the formation of endemic forms. Such an endemization is also related to the presence of endemic micromammals, one of the main food sources. In the Mediterranean islands at least three extinct species of *Athene* are known: *Athene trinacriae* n. sp. from Sicily, *A. cretensis* from Crete (Weesie, 1982), and *A. angelis* from Corsica (Mourer-Chauviré *et al.*, 1997).

Athene trinacriae n.sp. is known in some localities of Sicily associated with fossils of the “*Elephas falconeri* Faunal Complex” of the early Middle Pleistocene (Bonfiglio *et al.*, 1997). The presence of highly modified mammals and other endemic species of birds (Pavia, 1999) suggests a great degree of isolation of Sicily during the Early Pleistocene and part of the Middle Pleistocene. This isolation from the mainland, the great abundance of prey, and the absence of terrestrial predators may have determined the

formation of this endemic form, which is highly modified for a terrestrial life-style.

Weesie (1982) suggested the same habitus for the endemic *Athene cretensis*, known from some Pleistocene cave deposits of Crete. This form has very long legs, which suggest an adaptation to a terrestrial way of life. Its occurrence is probably also related to the presence of the endemic murid *Mus minotaurus*, which in all likelihood represented its most common prey, as shown by the analysis of fossil owl pellets found in Liko Cave (Crete). The age of the Cretan fossil bird assemblage is probably Late Pleistocene (Weesie, 1988). The considerable modification that *A. cretensis* underwent took place over a short period of time, as shown by the material from Liko Cave in which the mean lengths of femora and tarsometatarsi are significantly longer in the upper levels of the cave than in the lower levels, while this is not the case for humeri,

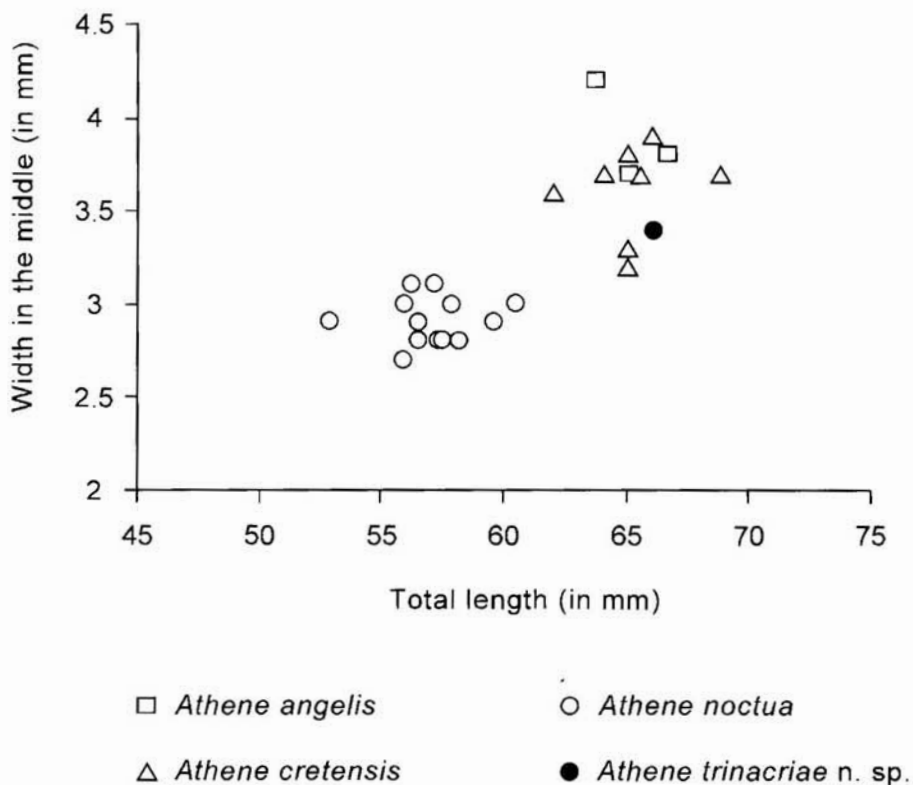


FIGURE 5. Scatter diagram with the measurements of the tibiotarsus of *Athene angelis*, *A. noctua*, *A. cretensis* and *A. trinacriae* n. sp.

ulnae, carpometacarpi and tibiotarsi. The extinction of the species is possibly related to the arrival of terrestrial carnivores on the island, arrival that may have been connected to the colonization by man. This fact led to the extinction of *Mus minotaurus* and to high predation and niche competition between the terrestrial *A. cretensis* and the new terrestrial predators (Weesie, 1982). In the same way, the extinction of *A. trinacriae* n. sp. is probably due to competition with terrestrial predators, which arrived in Sicily together with some large mammals in the late Middle Pleistocene (Bonfiglio *et al.*, 1997).

In the Middle and Late Pleistocene fissure deposits of Castiglione (Northern Corsica), Mourer-Chauviré *et al.* (1997) described the endemic taxon *Athene angelis*. The other fauna of Castiglione includes, amongst others, two extinct strigiforms, *Tyto balearica* and *Bubo insularis*, and some endemic mammals, both

macro- and micromammals. Unlike the other two species of *Athene* from Sicily and Crete, *A. angelis* shows a general increase in the body size with an elongate femur and a robust tarsometatarsus. This massive structure with normal proportions between wings and legs, suggests a different life-style, much less terrestrial than in *A. cretensis* and *A. trinacriae* n. sp., and more similar to that of the extant *A. noctua*. The causes of extinction and the relationships between this species and the other vertebrates of Corsica are under study by A. Louchart.

From the Late Pliocene-Early Pleistocene of Cova de Ca Na Reia on Eivissa, Alcover (1989) reported the presence of *Athene* cf. *veta*. This species was described by Janossy (1974) from the Late Pliocene of Poland, and was recently synonymized with *Aegolius funereus* by Mlikovský (1992). Nevertheless,

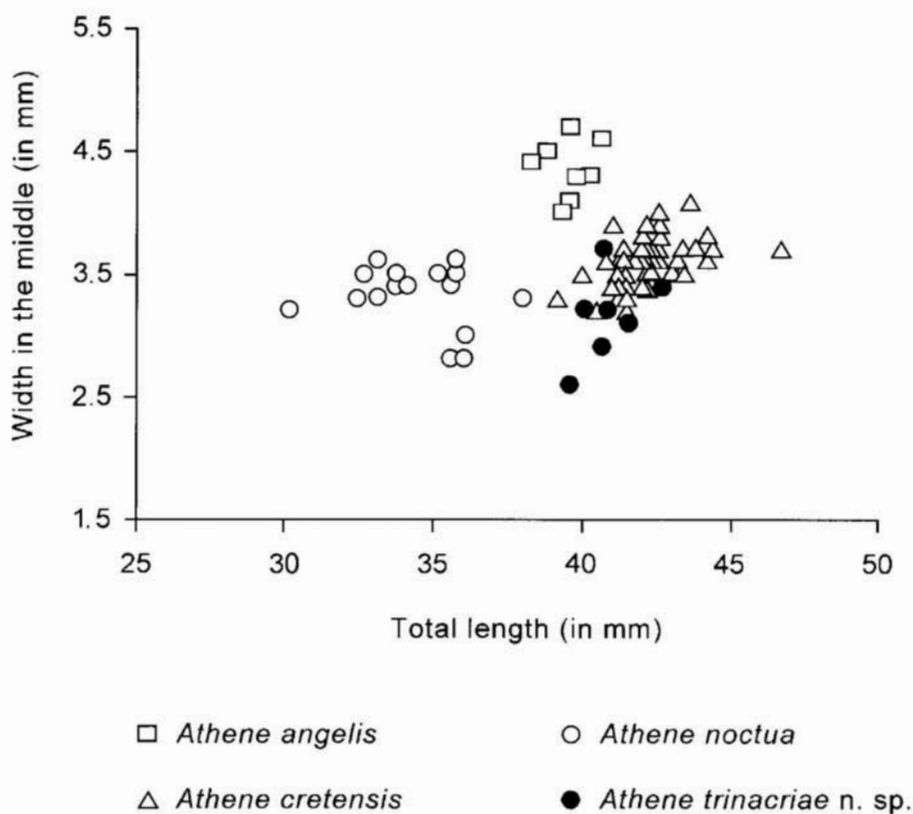


FIGURE 6. Scatter diagram with the measurements of the tarsometatarsus of *Athene angelis*, *A. noctua*, *A. cretensis* and *A. trinacriae* n. sp.

since the tarsometatarsus from the Cova de Ca Na Reia shows typical features of *Athene*, it may represent a new, undescribed form of this genus. Recently, Sondaar *et al.* (1995) reviewed the current knowledge on the vertebrate fauna from the Pliocene and Pleistocene of the Gymnesic and Pityusic Islands; the specimen of *Athene cf. veta* from the Cova de Ca Na Reia were listed as *Athene sp.*

Another still undescribed extinct form is also present on the Aegean island of Évvoia, and is larger than *Athene noctua* but smaller than *A. cretensis* (S. L. Olson, pers. comm.).

The absence of fossil species of *Athene* on Malta is probably due to the incompleteness of the fossil record. Alcover *et al.* (1992) reported some references for Pleistocene Maltese avifaunas, but most of these papers concern species of larger size. Moreover, the Maltese fossil vertebrate fauna has some elements in common with that of Sicily, for example in the micromammals, therefore the presence of *Athene* remains in the Pleistocene of Malta should not be unexpected.

Conclusions

During the Pleistocene and Holocene, various

species of *Athene* inhabited different Mediterranean islands (Fig. 8): *A. angelis* lived in Corsica during the Middle and Late Pleistocene; *A. cretensis* in the Late Pleistocene of Crete; *A. trinacriae* n. sp. in the early Middle Pleistocene of Sicily; and *A. noctua* in various places after the late Middle Pleistocene. The presence of endemic species of *Athene* on Mediterranean islands during the Pleistocene is related to particular environmental and ecological conditions. The long geographical isolation of the islands from the mainland, the presence of abundant terrestrial prey, and the absence of terrestrial carnivores, together with the sedentary habitus of the genus, favoured genetic isolation and the formation of endemic forms, as was also suggested by Weesie (1982). The extinction of the endemic forms is probably related to other ecological factors, such as palaeoenvironmental changes or competition with terrestrial predators, e.g. foxes and hedgehogs, which arrived from the mainland. Their arrival is due either to natural colonization after the new connection of the mainland with the island, as in the case of Sicily, or to human introduction, as in the case of Crete (Weesie, 1982), or both. Such colonization would be the cause concerning the extinction of *Athene*

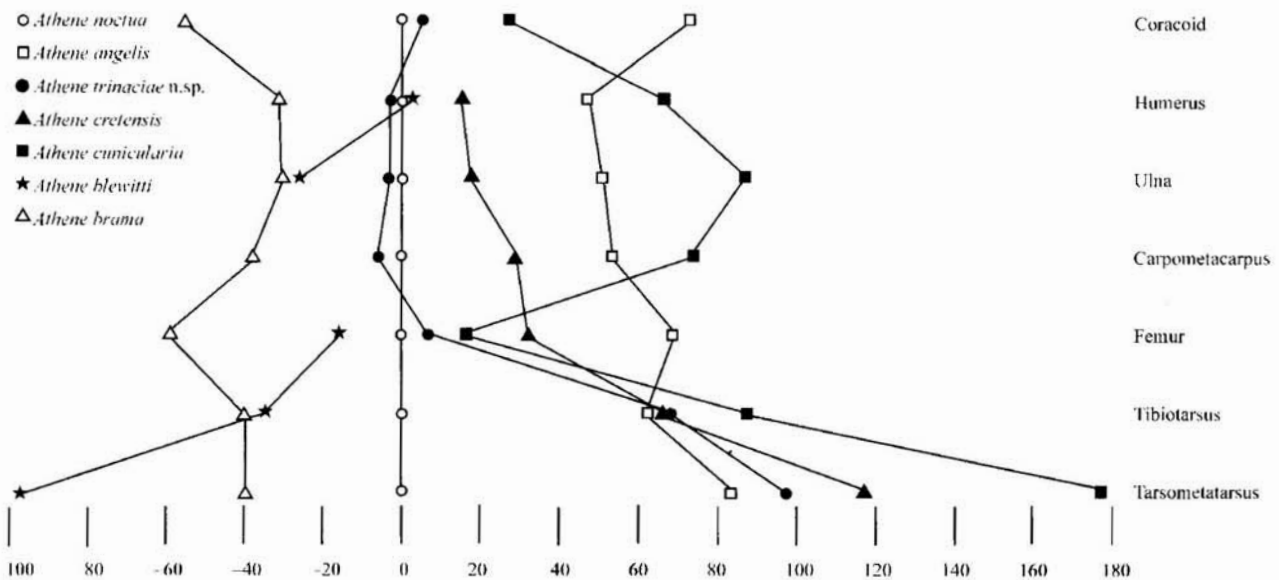


FIGURE 7. Ratio-diagram of the log differences of the mean dimensions of the long bones of *Athene trinacriae* n. sp. compared with those of *A. noctua*, *A. angelis*, *A. cretensis*, *A. cunicularia*, *A. blewitti*, and *A. brama*.

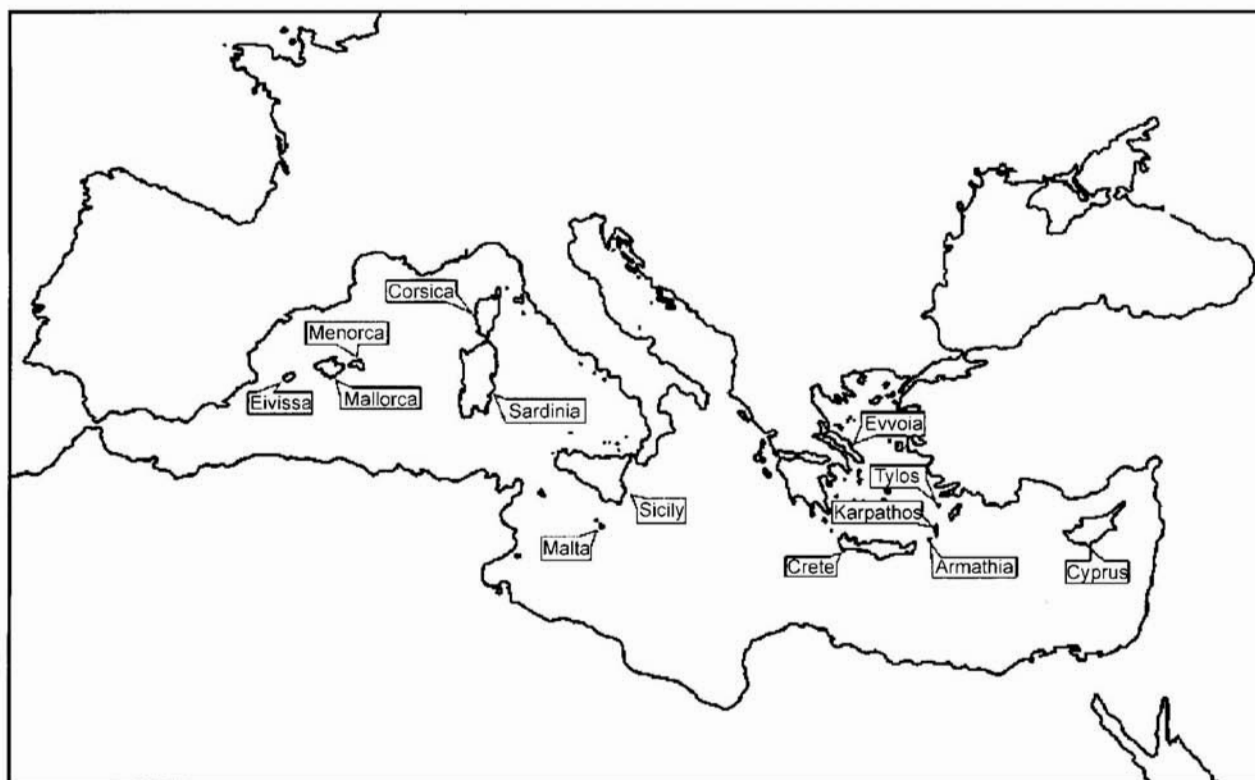


FIGURE 8. Map of the Mediterranean islands with *Athene* remains considered in this paper.

trinacriae n. sp.; this species in fact probably mainly fed on small endemic rodents and its extinction is related to the arrival of the new faunistic elements of the “*Elephas mnaidriensis* Faunal Complex”.

The present distribution of *Athene noctua* on the major Mediterranean islands is probably due to recent colonization during the Late Pleistocene. During the Early and Middle Pleistocene, in fact, most of the Mediterranean islands were much more isolated because of the higher sea level.

During the Late Pleistocene the lower sea level, as a result of eustatic changes and tectonic activity, made it possible for some terrestrial animals, or sedentary birds like *Athene noctua*, to spread on many Mediterranean islands.

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