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SHORT COMMUNICATIONS

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CONVERGENT EVOLUTION OF *ELANUS* KITES AND THE OWLS

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Within the diurnal raptors (hawks and allies, Order Falconiformes), familial relationships are among the most problematic of all avian orders (Feduccia 1999) and there are no less than six recent conflicting classifications based on morphology, molecular evidence, or both (Sibley and Ahlquist 1990, Griffiths 1994, Holdaway 1994, Mindell et al. 1997, Wink et al. 1998, Mayr et al. 2003). The owls (Order Strigiformes), on the other hand, are currently classified separately (e.g., del Hoyo et al. 1999) from the diurnal raptors, but their possible relationships have been debated since the 19th century (Garrod 1874, Cracraft 1981, Mayr et al. 2003). Here we will show that the *Elanus* kites present unique ecological and phenotypic traits, most overlooked so far, suggesting evolutionary convergence with the owls. Recent phylogenetic studies have determined, nonetheless, that the *Elanus* kites belong with the Accipitridae as an ancestral and basal group which may be recognized as a subfamily.

Elanus is composed of four species having comparable plumage patterns and sizes (about 300 g adult weight). Three of the species, the Black-shouldered Kite *E. caeruleus* from southern Asia and Africa, White-tailed Kite *E. leucurus* from the Americas and Australian Black-shouldered Kite *E. axillaris* from Australasia, are so similar in plumage characteristics and behavior that, until recently, they have been considered a cosmopolitan super-species with geographically-replacing forms (Parkes 1958, Husain 1959, Mendelsohn and Jaksic 1989). Slight differences in size, proportions, plumage and behavior led Clark and Banks (1992) to propose separate species recognition for the White-tailed Kite. The fourth species, the Letter-winged Kite *E. scriptus*, is endemic to Australia, breeds colonially, and hunts mainly at night (Ferguson-Lees and Christie 2001).

The *Elanus* kites inhabit savannah-like habitats in temperate and arid zones (Brown and Amadon 1968) and often prey on small rodents out-breaking at annual (Dunk 1995) or irregular intervals (Mendelsohn 1982, Mendelsohn and Jaksic 1989, Ferguson-Lees and Christie 2001, Jaksic and Lima 2003). They are able to disperse over long distances (up to many hundreds of kilometers) between their birth sites and first breeding sites, and even between successive breeding sites (Mendelsohn 1983, Scott 1994, Ferguson-Lees and Christie 2001). A few studies have indicated the osteological (Holdaway 1994), genetic (Wink et al. 1998), and karyotypic (Bed'Hom et al. 2003) distinctiveness of *Elanus*, but without challenging their inclusion within the Accipitridae.

In the southern hemisphere, *Elanus* appears to fill the niche of the nomadic owls of northern latitudes, which prey on multi-annually cyclic populations of small mammals (Korpimäki 1992) and are able to disperse over long distances to find local density peaks of small rodents (Korpimäki et al. 1987, Korpimäki 1993). As with some owls (e.g., Barn Owls *Tyto alba*; Taylor 1994), it is one of the few diurnal raptors able to raise more than one brood in a year, and can reproduce practically at any time (Mendelsohn 1984). In temperate regions, such as California or the Argentine Pampas, the White-tailed Kite has a long breeding season (mid-winter to late summer, see Dunk 1995). In Spain, the Black-shouldered Kite has the longest breeding period for any raptor; even though there is a peak of clutches in early spring, breeding attempts have been recorded at all seasons (authors unpubl. data).

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Figure 1. Primary feathers of *Elanus caeruleus* showing owl-like velvety barbules in the inner vane.

Recent studies based on Cytochrome-b sequences (Roulin and Wink 2004) and Cyt-b plus RAG nuclear genes (Lerner and Mindell 2005) have provided genetic evidence that *Elanus* evolved from a group of raptors basal to the largest falconiform family (i.e., Accipitridae) and only distantly related to the Falconidae. The lack of a fossil record clearly attributable to *Elanus* may explain why the importance of this ancient group for inferring evolutionary relationships in raptors has been overlooked.

Phenotypical Affinities between Elanus and the Owls. *Elanus* may resemble true kites (i.e., Milvinae) in general appearance and behavior, showing for instance, and unlike any owl, carotenoid-pigmented tarsi and ceres, and nest-building abilities (Brown and Amadon 1968). However, while handling wild kites (>50 adult and 200 nestling *E. caeruleus*), examining museum specimens ($N = 20$ *E. caeruleus* and *E. leucurus*), and consulting the literature, we noticed that *Elanus* have species-specific traits, the majority unreported, that are absent in other members of the order Falconiformes but present in owls. First, the upper surface of the primary and secondary feathers has a velvety comb structure (Fig. 1), an adaptation for silent flight also exhibited by nightjars (Caprimulgiforms). Second, unlike all other Falconiformes except the fish-eating Osprey *Pandion haliaetus*, the *Elanus* kites are zygodactilous, with a reversible outer toe. Third, they have long vibrissae around the beak and disproportionately large, frontally-placed eyes (Ferguson-Lees and Christie 2001). Fourth, the pellets regurgitated by *Elanus* are owl-like in shape and compactness (Brown and Amadon 1968), and contain some undigested bones indicating low stomach acidity (Duncan 2003). Owls' stomach pH ranges from 2–4, whereas hawks' pH ranges from 1–2. The acidity of one *E. caeruleus* stomach that we measured was pH 3.4. Fifth, *Elanus* often ingest their small-mammal prey whole, a task facilitated by a large gape (larger prey are, however, pulled apart; J. Dunk pers. comm.). Sixth, *E. scriptus*, the most nocturnal species in the genus, has asymmetrical placement of the ear openings (Burton 1989), like owls of the genera *Aegolius* and *Tyto* (Norberg 1978, Taylor 1994), that may help them to locate prey by sound. In this respect, it is worth mentioning that other Accipitridae, the harriers of the genus *Circus*, which also tend to prey on rodents and are often crepuscular, seem to have converged with the owls in having facial disks and a very slight asymmetry in the ears (J. Lazell pers. comm.).

Phylogenetic analyses (Roulin and Wink 2004, Lerner and Mindell 2005) suggest that *Elanus* and the other diurnal raptors share a common ancestor, and that the ecological and morpho-physiological similarities to the owls likely resulted from evolutionary convergence. Although most *Elanus* kites are diurnal and crepuscular hunters (Mendelsohn and Jaksic 1989), at least Letter-winged Kites are nocturnal hunters (Brown and Amadon 1968, Burton 1989, Pettigrew 1991). Nonetheless, the evolution of nocturnal activity may not face significant physiological barriers (Mrosovsky 2003), and it has recently been suggested that the dark-activity phenotype characteristic of the strigiform and caprimulgiform orders is also an example of convergent evolution (Fidler 2004). All *Elanus* kites are specialized to feed on small rodents, the populations of which, particularly in arid zones, may show irregular den-

sity outbreaks, which differ from the multi-annually cyclic small mammals of the northern hemisphere (Lima et al. 2002, Korpimäki et al. 2004). The ability to disperse over long distances and to produce many broods annually likely helps *Elanus* kites to take full benefit from local rodent outbreaks. These traits, unusual for the diurnal raptors in the family Accipitridae, may have driven the independent evolution of the characteristics that give *Elanus* the appearance of a hybrid between a hawk and an owl.

CONVERGENCIA EVOLUTIVA DE LOS ELANIOS (*ELANUS*) Y LOS BÚHOS

RESUMEN.—Hay cuatro especies de elanios (género *Elanus*) en el mundo. La mayor parte de las poblaciones se encuentran en el hemisferio sur, o en latitudes bajas del hemisferio norte. Las poblaciones que se encuentran en zonas intertropicales se comportan ecológicamente como los búhos nómadas de zonas boreales: pueden desplazarse a grandes distancias y se reproducen cuando hay explosiones demográficas de las presas que les sirven de alimento. Además, son crepusculares o nocturnos. Morfológicamente, los elanios también presentan similitudes con los búhos: plumas de vuelo con bárbulas aterciopeladas, zigodactilia, ojos grandes y frontales, largas cerdas peribucales y tarsos gruesos y cortos. Estas y otras características descritas en el texto pueden ser el resultado de convergencia evolutiva o de ascendencia común. Estudios recientes basados en distintos marcadores moleculares indican que los elanios son un grupo basal de la familia Accipitridae, que hasta ahora ha estado mal clasificados entre los milanos, y que sus similitudes ecomorfológicas con los búhos serían, por tanto, el resultado de convergencia evolutiva por ocupar nichos ecológicos similares.

[Traducción de los autores editada]

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