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New Idea

Stick supply to nests by cliff-nesting raptors as an evolutionary load of past tree-nesting

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Abstract

The supply of sticks to cliff nests by many European raptors has been explained only as a functional means of decreasing ectoparasite loads in nests and for signalling nest occupancy. We provide here a historical explanation of this behaviour as we consider it represents an evolutionary load of formerly tree-nesting species. Basically, from this perspective, facultative tree/cliff-nesting species reproduce the nests they used to build originally on top of trees, but on cliffs. Facultative species (likely evolved in forested areas) that supply their cliff nests with sticks include *Pandion haliaetus*, *Haliaetus albicilla*, *Milvus migrans*, *Circaetus gallicus*, *Buteo buteo*, *Aquila fasciata*, *A. pennata*, *A. chrysaetos*, *A. heliaca*, *Gypaetus barbatus Gyps fulvus and Neophron percnopterus.* On the contrary, the only *Falco* species that solely nests in cliffs (*F. eleonorae*)) and does not supply its nests with sticks and should be considered a true cliff-nester, likely evolved in non-forested areas. All other *Falco* species that do not supply their cliff nests with sticks but can make use of tree nests made by other non-raptorial species, should also be considered as true cliff-nesters, likely evolved in more forested areas or times. *Milvus milvus*, *Elanus caeruleus*, *Accipiter nisus*, *A. gentilis*, *Pernis apivorus*, *Aquila adalberti*, *A. clanga*, *A. pomarina* and *Aegypius monachus* are true tree nesters, likely evolved in forested areas, which did not evolve the plasticity to nest directly on cliffs.

Key Words: cliff nesting; tree nesting; birds of prey; evolutionary load; stick supply.

Introduction

The supply of greenery by some large eagles to cliff nests (e.g. golden eagle, Bonelli's eagle, booted eagle, osprey) has been explained so far only by means of functional causes, notably the role of pine aromatic compounds used as ectoparasite repellents (Wimberger, 1984, but see also Ontiveros and Pleguezuelos 2007) and for signalling nest occupancy. However, a historical explanation has never been suggested. Here we propose the idea that the supply of sticks to cliff nests identifies those raptor species whose original nesting substrate was trees or large shrubs rather than cliffs. On the contrary we suggest that cliff-nesting species that do not supply sticks to nests should be considered the only true cliff-nester species.

Methods

We compiled data from 32 Eurasian raptor species, recording whether they were known to breed on trees, on cliffs, or both, and whether they have been reported to supply sticks to their nests (see Appendix I). Tree or cliff nesting was recorded as 1 (i.e. present) even if it was rare or extremely rare because we assumed that a tree-nesting event for a typical current cliff nester could be providing hidden information about past and almost lost habits. Cases of raptor species nesting only on the ground or in tree hollows were not considered. Information was extracted mainly from general ornithological handbooks (Cramp and Simmons 1980, del Hoyo et al. 1994) except for a few cases found in other general literature sources

(e.g. Fergusson-Lees and Christie 2001) and in old literature.

Results

The set of species that nested facultatively on trees or cliffs and supplied cliff nests with sticks were *Pandion haliaetus, Haliaetus albicilla, Milvus migrans, Circaetus gallicus, Buteo buteo, Aquila fasciata, A. pennata, A. chrysaetos, A. heliaca, Gypaetus barbatus, Gyps fulvus* and *Neophron percnopterus*. On the contrary, *Falco eleonorae* was the only species found to nest only on cliffs, and did not supply sticks to their nests. All other *Falco* species nested facultatively on trees or cliffs. When breeding on trees, they reused the nests of other bird species, and when nesting on cliffs, they did not supply their nests with sticks. The set of species building their own nests only on trees were *Milvus milvus, Elanus caeruleus, Accipiter nisus, A. gentilis, Pernis apivorus, Aquila adalberti, A. clanga*, and *A. pomarina*.

Discussion

Pandion haliaetus, Haliaetus albicilla, Milvus migrans, Circaetus gallicus, Buteo buteo, Aquila fasciata, A. pennata, A. chrysaetos, A. heliaca, Gypaetus barbatus, Aegypius monachus, Gyps fulvus and *Neophron percnopterus* would be—from the perspective we defend in this paper—species evolved in forests, that originally used to build their nests on trees, but that secondarily acquired the plasticity to reproduce their tree nests on cliffs.

The case of the Egyptian vulture is a particular one seen from our Iberian perspective. An uncommon case of Egyptian vultures nesting on trees in Iberia was first recorded by Irby (1879) near Gibraltar, and it involved a pair nesting on a tree nest built by a short-toed eagle on a cork oak. However, this species commonly breeds on tall trees in India (Irby 1879, Verner 1909, Mishra et al. 2018), among other nesting substrates, including cliffs or old historical monuments and temples; they supply their own nests with sticks (Mishra et al. 2017).

The only *Falco* species nesting solely in cliffs was *F. eleonorae,* which most likely reflects the fact that this species evolved in semi-desert landscapes where trees are either rare or absent (Walter 1979). All other *Falco* species nest facultatively on trees or cliffs but utilize other species' nests when nesting on trees (notably corvid nests), and do not supply their cliff nests with sticks. This may imply that these *Falco* species are true cliff nesters too, although more plastic ones, perhaps having evolved in more forested areas or times.

Some large *Aquila* species such as Adalbert's eagle (*A. adalberti*), Greater spotted eagle (*A. clanga*) or Lesser spotted eagle (*A.pomarina*) (together with *Milvus milvus, Elanus caeruleus, Accipiter nisus, A. gentilis, Pernis apivorus and Aegypius monachus)* have never been recorded nesting on cliffs. This would mean from our perspective that they evolved in forests and are true tree nesters, never evolving secondarily the ability to reproduce tree nests on cliffs. It is interesting that, although *A. heliaca* has been reported to breed facultatively on cliffs, its sister species from Iberia, *A. adalberti*, is less plastic and has never been recorded breeding on cliffs.

The case of *A. monachus* (the Cinereous vulture) is a bit different compared with the other true tree-nesting species because although they always nest on trees, they can breed on trees growing directly in abrupt cliffs, as it happens in some isolated populations such as that on Majorca Island. Despite this being so, this vulture species would also have evolved in forested areas and should be considered an obligate tree nester too.

This new idea should be tested in the future by making use of phylogenetically informed data, linking each group identified by us (true cliff nesters, true tree nesters and facultative tree/cliff nesters) with particular environmental conditions and evolutionary pressures present during the time and region of evolution of each group.

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Referees

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Response to referee

Ferrer (2019) raised in his review an interesting derivative of our idea that the supply of raptor cliff nests with sticks may actually represent an evolutionary load of past tree-nesting. He addresses the case of raptors breeding directly on the ground and explains that even in that situation one can tell what species come from a tree-nesting past or not, based only on the fact of building nests with sticks or not. We absolutely agree with this interesting corollary of our hypothesis.

In fact a typical forest bird species, such as the wood pigeon (*Columba palumbus*) keeps building stick nests when breeding on top of human constructions that are functionally equivalent to cliffs (Xavier Ferrer, *personal communication*; see Figure 1). Nesting on human buildings is actually characteristic of rock pigeons (*C. livia*) that originally bred on cliffs and do not provide sticks to their nests. This behaviour is in favour of our hypothesis developed with raptors.

Ferrer finally suggests that having the plasticity to be a tree or cliff facultative nester must have been a critical conservation factor to respond to human disturbance during the 20th century, as obligate tree-nesters must have been more vulnerable to human persecution than facultative tree/cliff nesters. Again, we not only agree with that applied derivative of our hypothesis but we already have a whole manuscript under review analysing what caused the shift of original tree nesting raptors to cliffs and the applied consequences of having or not that plasticity.

Ferrer, M. 2019. Cliffs, trees, and ground-nesting raptors. Ideas in Ecology and Evolution 12: 26–27. CrossRef

Figure 1. A wood pigeon (*Columba palumbus*) pair nesting on a human construction built its nest with sticks as an evolutionary load of what they do when nesting on trees, their original nesting habitat. Nests on human constructions are typical of rock pigeons (*C. livia*) that are cliff-nesting species and do not supply nests with sticks. Human constructions are functionally equivalent to cliffs and are typically used by cliff-nesting bird species (Photo credit: Andreu Ubach).

Appendix I. Supply of sticks as nest material in European raptors and type of nesting substrate (tree or cliff) in which nesting has been recorded in the literature (Cramp and Simmons 1980; del Hoyo et al. 1994).

Species	Tree	Cliff	Sticks
Pandion haliaetus	1	1	1
Haliaetus albicilla	1	1	1
Milvus milvus	1	0	1
Milvus migrans	1	1	1
Elanus caeruleus	1	0	1
Circaetus gallicus	1	1	1
Accipiter nisus	1	0	1
Accipiter gentilis	1	0	1
Buteo buteo	1	1	1
Buteo lagopus	1	1	1
Pernis apivorus	1	0	1
Aquila fasciata	1	1	1
Aquila pennata	1	1	1
Aquila chrysaetos	1	1	1
Aquila adalberti	1	0	1
Aquila heliaca	1	1	1
Aquila clanga	1	0	1
Aquila pomarina	1	0	1
Neophron percnopterus	1	1	1
Gypaetus barbatus	1	1	1
Aegypius monachus	1	1	1
Gyps fulvus	1	1	1
Falco rusticolus	1	1	0
Falco cherrug	1	1	0
Falco biarmicus	1	1	0
Falco peregrinus	1	1	0
Falco eleonorae	0	1	0
Falco subbuteo	1	1	0
Falco columbarius	1	1	0
Falco vespertinus	1	1	0
Falco naumanni	1	1	0
Falco tinnunculus	1	1	0