On the Origin of Raptor-Pattern and Hawk-Mimicry of Cuckoos

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I have elsewhere described ('Jap. J. Zool.' March 1966) the hawk-mimicry pattern of cuckoos, based on the behaviour of a captive Himalayan Cuckoo *Cuculus saturatus*, which suddenly spread its wings and tail in a threatening attitude to my finger, thus displaying the hawk-like pattern of underwing and tail. This was very similar in appearance to a photograph of *Accipiter nisus* in a threatening posture. In that note I mention that the hawk-pattern of birds of prey may have an intimidatory effect against the prey (even to human eyes), and here I want to extend this idea a little more.

The hawk-pattern, the bold black barring on white, is more distinct on the under-than upper-surface of the wings and tail of the birds of prey, and this pattern is most strikingly exhibited at the moment when they swoop down upon the prey with fully spread wings and tail (as is often shown by excellent photographs). After they have caught the prey, their wings and tail are kept spread to help maintain balance over the struggling victim, and their underwing hawk-pattern should further intimidate the prey, and thus facilitate the kill. If this is so, the hawk-pattern should be found better developed, as the result of natural selection, in the species which pursue prey of their own size and are therefore more difficult to kill. We can say that this is generally the case in *Falco*, *Accipiter*, *Spizaetus*, and notably in the mighty Crowned Eagle *Stephanoaetus coronatus* or the Harpy Eagle *Harpia harpyja*; while the pattern is not so marked in many *Buteo* species or kites, etc. which chiefly prey on rodents or reptiles, nor in fish-eating sea-eagles (though the Osprey *Pandion haliaetus* is hawk-patterned) and carcass-eating vultures and condors, although there are exceptions to this rule (e.g. the Golden Eagle *Aquila chrysaetos* which is however considered to have evolved from smaller species (*A. pomarina*, etc.) that only prey on weakened animals). The above suggestion could be demonstrated if birds reacted to hawk-patterned models more than to non- or less markedly patterned ones. This I tried only tentatively with a tame jay and a few other cage birds, but with inconclusive results. However, such experiments pursued more systematically would be worthwhile.

One of the exceptions to the above supposed rule is the Honey Buzzard *Pernis apivorus*, which has a bold hawk-pattern on wings and tail. The explanation may be as follows: *P. apivorus* is a weak hawk, in reality, with bill and claws princi-
pally adapted for digging and eating wasps and its development of a hawk-pattern is a safeguarding device (adaptation) against potential enemies and stronger birds of prey. In flight, with its bold pattern, it certainly looks like some strong raptor, and I actually saw chickens in a mountain farm terrified by its over-head flight. Thus, its bold pattern may have been selected for by escape from the attack of stronger birds of prey, particularly the hawk-eagles Spizaetus. That raptors prey upon weaker raptors, as well as on other birds, has been proved by Warncke (1961, ‘Vogelwelt’ 82: 6–12) and März (1954, ‘Vogelwelt’ 75: 181–188) who report several species of owls and hawks in the diet of the Eagle-Owl Bubo bubo and Goshawk Accipiter gentilis. The Honey Buzzard and Hawk–Eagle are both of tropical origin, possibly living in the same forests (as in Japan), and it can be supposed that on islands or in restricted habitats the survival of the Honey Buzzard would have been much favoured by mimicking the Hawk–Eagle pattern. The striking resemblance of the plumage of Pernis celebensis to Spizaetus lanceolatus in Celebes (Meyer & Wiglesworth 1898, ‘The Birds of Celebes and the Neighbouring Islands’), adult with adult and very different young with young, may have thus also evolved as a Batesian mimicry under strict predatory pressure by Spizaetus and through natural selection.

In cuckoos, as discussed in my another paper, the hawk-pattern is found almost only in parasitic species, most markedly in Cuculus, which has the most developed parasitic habit, and non-parasitic species are non-hawk-patterned. Cuckoos’ hawk-patterns are most marked on the under-surface of wings and tail as in true hawks and should therefore have an intimidatory effect in threat flight against their host species, the ‘Scheuch-Flug’ (Makatsch 1955, ‘Der Brutparasitismus in der Vogelwelt’) or ‘Raptor-flight’ (Pounds 1965, ‘Brit. Bds.’ 58 (4): 154) by which ground-nesting host species are flushed, thus facilitating the cuckoo in locating the nest to parasitise. It is also known that a female Cuculus canorus will defend herself with this effect against the attack of the host species while sitting on its nest to deposit her egg.

Thus considered, the hawk-pattern developed on the under-surface of the wings and tail both of birds of prey and of parasitic cuckoos should have a similar origin in that one is used to intimidate the oponents, which are prey, and the other to intimidate the host species. Genetically, this kind of pattern should be nothing more than one of the ordinary plumage patterns among birds (a similar pattern can be found in pheasants for example, where its use is as a disruptive pattern), but one which has been selected for because of efficacy in catching prey or parasitising a host-nest. In the case of Clamator spp. however, this pattern is not effective because they parasitise stronger hosts (crows, etc.) and hence need no hawk-pattern. Thus, cuckoos’ mimetic resemblances to hawks should have arrived
by convergence, being Müllerian in nature.

However, the phenomenon is not a simple one and may include true predator-mimesis, as suggested by the Drongo Cuckoo’s *Sericulus lugubris* mimicry to a pugnacious drongo which is predatory to small birds’ nests which this cuckoo parasitises. This is a Batesian mimicry of the particular species, but the Drongo Cuckoo sometimes parasitises the drongo’s nest itself. Thus in this case, it is a host-mimesis. This host-mimesis is most marked as in well-known case of *Eudynamis scolopaces*; the male as black as the crow whose nest it parasitises, while the chick is black-headed, mimicking the host’s chicks.

In both these predator-mimetic and host-mimetic cuckoos, the male may attract the attention of host species and lead them away from the nest by provoking their mobbing or their territorial attacks and thus help the female cuckoo to deposit her egg secretly (cf. Kuroda l. c.).

It would seem therefore that the hawk-pattern in the cuckoo along with the egg-mimicry and other mimetic adaptations, has played an important role in the evolution of the cuckoos' breeding parasitism.

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猛禽斑とカッコウ類のタカ斑の起原について

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筆者は 1965 年度生態学会総会でカッコウ類のタカ斑擬態の意義について考察を述べた（動物学集報 3 巻 1966) その後、タカ斑自体を害鳥の攻撃に態であることが知られた。この短報では、それをさらに詳しくいきたい。白石・黒の太い帯をなす猛禽斑は、猛禽類の翼や尾の下で著しい。猛禽斑は獲物を捕える瞬間その翼尾の下面の斑を最大限に展開するので獲物をすくませ、捕えてからから翼を揚げるので（体のバランスをとるため）、ますます相手を深くして捕食を容易にするだろう。タカ斑は困難な獲物を捕える種類でより著しく発達していることは、この種を支配する。例えば、*Falco, Accipiter, Spizaetus,* とくに最強の *Stephanoetus* やヘビイーグル *Harpyia* に至る種は著しく、オーストラリアの鳥類のタカ斑は例外だが、このグループは比較的弱いものを捕えるアンサガワなどの小型種から進化したものと考えられる。

この仮説は、タカ斑とそうでない模様で鳥類の反応を試み実験的に証明ができるよう、筆者が簡単な実験を行ようになったところでは、明らかではなかったが、組織的な実験を試みる必要がある。

ハチヌマはハチを食べる弱い種でありながら、タカ斑を示す（とくに尾）例外といえるが、これは他の猛禽と同様なタカ斑の効果に対する予防的態であると考える。この両種は共に熱帯系の森林の鳥で、セレベスのクマクマ *Spizaetus lanceolatus* とハチヌマ *Pernis celebensis* は、幼鳥は幼鳥、成鳥は成鳥に極めて類似している。この両種は、前者はその態によって種を維持できたとさえ考えられる（幼

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鳥と幼鳥、成鳥と成鳥の類似は、タカ類に多い幼鳥の羽の多い型が両者にあり、擬態淘汰を経たのであろう。猛禽がより弱い猛禽を他の鳥と同様に獲物として扱うことは、ワシミミズクやオオタカの食の物に多くのクサやフクロウの類が含まれている例で明らかである。

また、カッコウ類でもタカ類はすばやく尾の下面にのみみられ、地上の伏しの穂を発見するのに威嚇飛行を行なって観察を追い出す習性や産卵中伏しの攻撃を受けた時など尾を閉じ、その裏のタカ麻を展開する習性があり、獲鳥が人に対してこの動作をしたことは昨年報じた。

かようにみると、猛禽やカッコウ類のタカ類は、共に捕食を威圧する効果があり、それにより、前者では獲物の捕獲を容易にし、カッコウ類では伏しの巣に寄生産卵の成功率を高め、共に生存に有利なため淘汰進化したものと考えられる。そこで、機能的には捕食と寄生産卵の違いがあるが、その起源は鳥類の羽斑の一つの遺伝子（タカ斑因子）が選択強化されたものに過ぎない。そして、それに似た斑は、例えば、キジ類の親にもみられるが、この場合は保護色効果として発達した（山階鳥類研究所）。