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TIZIANO LONDEI(*)

RELATIONSHIPS OF THE CAPE VERDEAN KESTRELS *FALCO (TINNUNCULUS) ALEXANDRI* AND *FALCO (TINNUNCULUS) NEGLECTUS* AS SUGGESTED BY FIELD OBSERVATIONS

Riassunto – *Parentele dei gheppi capoverdiani* Falco (tinnunculus) alexandri *e* Falco (tinnunculus) neglectus *quali indicate da osservazioni sul campo*

Queste due forme di gheppio, che vivono in parti diverse dell'arcipelago di Capo Verde, vengono paragonate tra loro e con altre forme del Gheppio, *Falco tinnunculus*, o affini. Nonostante qualche differenza tra loro, le forme capoverdiane hanno in comune modelli morfologici e comportamentali che fanno pensare a una separazione da un antenato comune già presente a Capo Verde, piuttosto che a colonizzazioni distinte. Questi uccelli, al largo della costa atlantica dell'Africa, hanno un aspetto intermedio tra alcune sottospecie del Gheppio presenti nell'Africa continentale e specie insulari sparse nell'Oceano Indiano. Lo scenario è a favore dell'origine africana dei gheppi tipo *tinnunculus*, essendo probabile che i caratteri ancestrali siano rimasti più evidenti nelle forme insulari, meno soggette a cambiamento.

Parole chiave – *Falco tinnunculus*, morfologia, comportamento, parentele, Capo Verde.

Abstract – *Falco (tinnunculus) alexandri* and *Falco (tinnunculus) neglectus*, which inhabit different areas of the Cape Verde Islands, are compared to each other and to other forms of, or close to, the Common Kestrel *Falco tinnunculus*. Notwithstanding some differences between the Cape Verdean forms, common patterns in their morphology and behaviour suggest local divergence from a common ancestor, rather than separate colonizations of the Cape Verdes. These birds, off the Atlantic coast of Africa, look as intermediates between Common Kestrel subspecies in mainland Africa and insular species scattered in the Indian Ocean. The scenario supports the African origin of the *tinnunculus*-like kestrels, with ancestral traits persisting more obviously in more conservative, insular forms.

Key words – *Falco tinnunculus*, morphology, behaviour, relationships, Cape Verde.

(*) Collaboratore del Museo Civico di Storia Naturale - Corso Venezia, 55 - 20121 Milano. E-mail: londeit@tin.it

Introduction

Originally described as a distinct species (SCHLEGEL, 1873), the kestrels from the northwestern components of the Cape Verde Islands have traditionally been treated as a subspecies of the Common Kestrel, with the name *Falco tinnunculus neglectus*. BOURNE (1955a) was in the latter perspective when he described a new "race" for the southeastern islands, *Falco tinnunculus alexandri*. By separating them as phylogenetic species, *Falco alexandri* and *Falco neglectus*, HAZEVOET (1995) simply acknowledged diagnosable characteristics in the two forms without any implication in the relationships with each other or with the Common Kestrel. However, he questioned BOURNE's (1955b) explanation for more *tinnunculus*-like traits in *alexandri* - more likely interbreeding with migrants on the inner islands, closer to mainland Africa - and suggested, instead, that differences between *alexandri* and *neglectus* might be due to either local divergence or separate colonizations. Assuming that genetic drift, gene flow from continental populations, and phylogenetic inertia were negligible for the Cape Verdean kestrels, HILLE & WINKLER (2000) searched for adaptive divergence among birds in different islands. They found significant differences in body proportions between the kestrels on Santo Antão (*neglectus*) and those on Boavista (*alexandri*), but did not report either on behavioural observations in support of their ecological explanation - adaptations to different prey type and availability - or on any comparison with continental kestrels.

It would therefore be interesting to compare the two Cape Verdean forms both with each other and with continental forms of (or close to) the Common Kestrel. Morphological data seem to have been at least equal to molecular data for phylogenetic inference in the Falconidae (GRIFFITHS, 1999). Considering that molecular analysis (OLSEN *et alii*, 1989) failed to separate even accepted species among the typical (rufous-backed) kestrels, relationships between presumed subspecies might be better assessed through a combination of morphological and behavioural observations in the search for common traits, provided that convergent evolution could reasonably be excluded.

Study area and methods

I observed kestrels in Cape Verde from 8 to 22 August 2003, in fine weather, taking photographs and videotaping movements and vocalizations. Birds seen on Sal and Boavista (*alexandri*) totalled nine, those on São Vicente and Santo Antão (*neglectus*) 14. As it is common opinion that Cape Verdean kestrels show weak sexual dimorphism (if any) for

colours, though sexual differences in size and shape emerged in HILLE & WINKLER's (2000) study, two breeding pairs, one for each form, were repeatedly observed at their nest sites and served to identify male and female traits through direct comparison.

Morphology: results and discussion

No matter they were perched or flying, both *alexandri* and *neglectus* looked like compact kestrels. Short wings and tails can be inferred from the measurements in BOURNE (1955a), if these are considered with respect to the measurements of tarsus, or culmen. The shorter and more rounded wings of *neglectus* compared to *alexandri* (HILLE & WINKLER, 2000) were not apparent in the field. In flight, both *alexandri* and *neglectus* showed short outerwings relative to innerwings, the ratio being decidedly lower than 2 (vs. higher than 2 in nominate *tinnunculus*) in images of birds with outstretched wings. Unfortunately, as other insular raptors may have tended to such wing and tail proportions during their evolution from continental forms (LONDEI, 2003), these traits may be of little value to lean to the idea of common insular ancestry rather than separate adaptations to insular life.

Colours conformed to a common pattern in *alexandri* and *neglectus*, and differences in tone and tinge - paler and more rufous for *alexandri*, darker and greyer for *neglectus* - seemed superimposed. The more heavily barred appearance of *neglectus* (Fig. 1A, see also HAZEVOET, 1995) may result from the fusion of larger spots. The markings on the lower underparts, especially the flanks, of both *alexandri* and *neglectus* were spots tending to bars rather than to streaks, a clear difference from the usual Common Kestrel. This trait, which may be characteristic of adults, as young birds were found more streaked below (SALVADORI, 1899), was rather reminiscent of the Madagascar Kestrel *Falco newtoni*, or the Mauritius Kestrel *Falco punctatus*, though the Cape Verdean kestrels looked more *tinnunculus*-like in body size and proportions. Two males and two females for each form, whose colours were examined in close-range photographs and video tape frames, showed constant differences in the males having more grey on the plumage and brighter, orange-yellow bare parts. A common trait of *alexandri* and *neglectus* might be sufficient to tell the sex, should direct comparison be impossible: while the females featured entirely whitish cheeks, neatly bordered not only by the usual, dark moustachial stripes but also by rather dark eye stripes and nape sides, the males had a grey wash on the cheeks which reduced the contrast with the dark borders. Some males - at least one of them breeding (Fig. 1B) - featured cheeks only partially grey, the lower part being conspicuously lighter. Although first-winter male

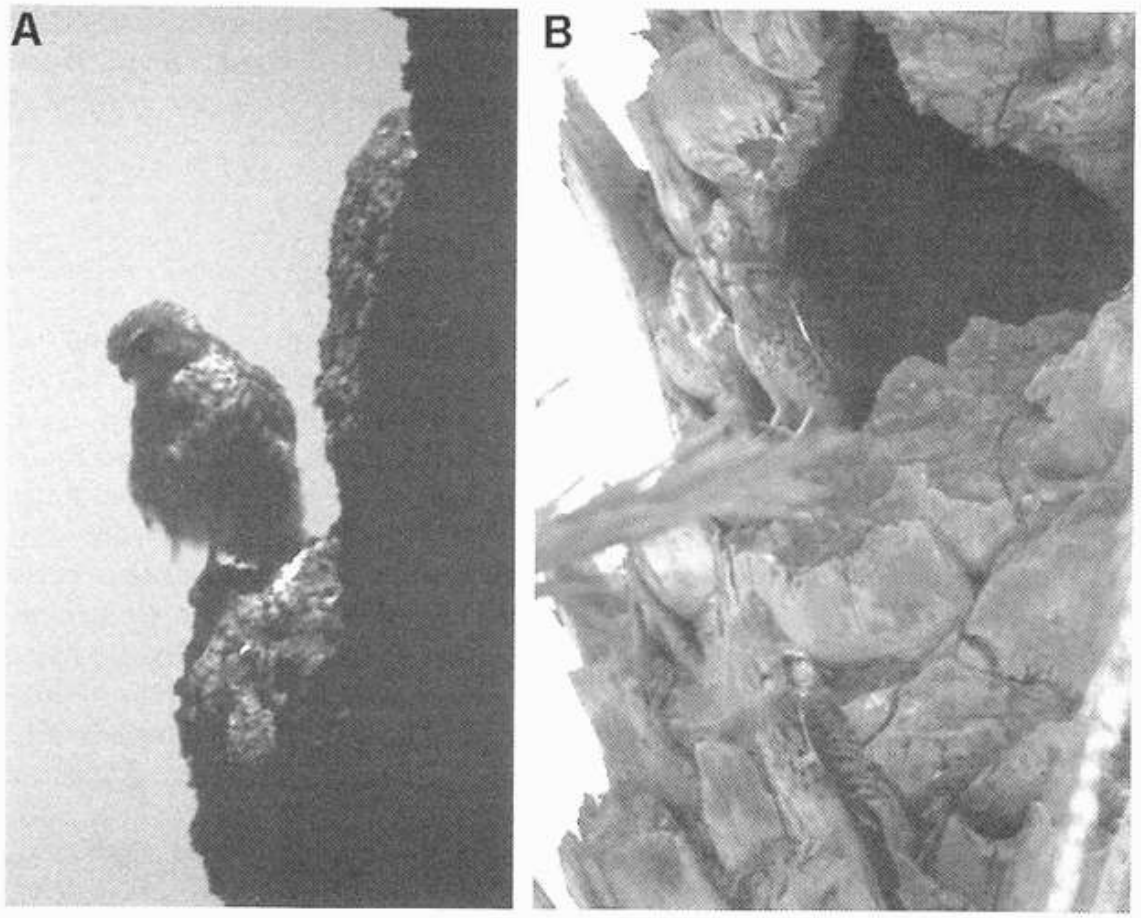

Fig. 1 - Cape Verdean kestrels at nesting sites. A) Male *Falco (tinnunculus) neglectus* erecting feathers in response to his mate's "*vriii*" calls (Santo Antão, 14 August 2003). B) Pair of *Falco (tinnunculus) alexandri* just after nest inspection by the male (Boavista, 22 August 2003).

Common Kestrels, moulting from juvenile to adult plumage, show such two-tone cheeks, the adult male cheeks are usually uniformly grey in this species.

It is worth considering that the superficially more *tinnunculus*-like coloration of *alexandri* may be an adaptation to more arid habitat on the eastern Cape Verdes. This difference is paralleled in the Canarian kestrels, with the eastern subspecies, *Falco tinnunculus dacotiae*, much paler and more rufous than *Falco tinnunculus canariensis*. However, as *dacotiae* averages smaller than *canariensis* (BANNERMAN 1963), the difference in size is reverted with respect to the Cape Verdean kestrels. This suggests that chance (genetic drift) rather than adaptation, is the cause of some trait variation among insular kestrels.

Birds appeared more often perched than flying. Their frequent staying near goat herds probably served to have small prey animals started up by grazing animals, and thus made more detectable. More active kestrels appeared in a bushy area of Boavista infested by large locusts. Twice I saw a locust caught in flight, dismembered on a branch, and remnants taken to a date palm, where they were cached among the scales of the trunk. There was a nest in the hollow trunk of another palm nearby (Fig. 1B) and the male of the nesting pair performed these actions.

I agree with BOURNE (1995b) that Cape Verdean kestrels hover infrequently, as I saw this behaviour on two occasions only (both with *alexandri*) and for a short time. As hovering is perhaps the most *tinnunculus*-typical behaviour, its rarity in *alexandri* and *neglectus* adds to the similarity between the two. Although BOURNE pointed to this behavioural feature of the Cape Verdean kestrels as an example of insular adaptation, which might suggest convergent evolution, I would not understand the adaptive value. From a description of kestrel habits on Madeira (BANNERMAN & BANNERMAN, 1965) it seems that birds were frequently seen hovering, even in places "constantly bathed in cloud". When in the Azores, I saw the local buzzards much more inclined to hovering than their continental counterparts (LONDEI, 1995), in spite of the Azores Buzzard *Buteo buteo rothschildi* having somewhat paralleled the Cape Verdean kestrels in the evolution of wing shape. Thus it seems more likely that a common ancestor of *alexandri* and *neglectus* was, for unknown reasons, already less inclined to hovering than a typical Common Kestrel.

Although rather reluctant to take flight, Cape Verdean kestrels were swift fliers, less buoyant than the usual Common Kestrel. Three videotaped sequences of powered flight for each form, obtained on different occasions and matched for different conditions, showed similar wing beat frequencies for both *alexandri* and *neglectus* (6-9/sec), whereas lower frequencies appeared for nominate *tinnunculus* (4-6/sec). Although wing beat frequency in closely related birds likely depends on the size of the bird in inverse proportion, which would explain lower values for nominate *tinnunculus*, it should be considered that the smaller *neglectus* produced the lowest, and the larger *alexandri* the highest, of all the values I obtained from Cape Verdean kestrels.

I agree with BOURNE (1955b) that the voice of the Cape Verdean kestrels differs (a little) in pitch from that of the typical Common Kestrel. The higher pitch might be due to the smaller size. My only two recorded sequences of "*kik-kik-kik*" (alarm) calls do not suggest any difference between *alexandri* and *neglectus*, and recorded "*vriii*" (greeting

or food begging) calls of the identified males and females near the nest suggest that differences between the two forms, if any, are fewer than the differences between the sexes (the smaller-sized male producing higher-pitched notes).

The described *alexandri* nesting site was 3 km south-east of Sal Rei, Boavista, in a sand-covered plain near sea level. The *neglectus* nesting site was a rocky ledge on a precipice near Pico da Cruz, Santo Antão, at about 1300 m above sea level. Both pairs appeared to be at the same stage of the breeding cycle. They showed a lot of interest in the nesting site - for example, they flew to it when the observer approached it - but their behaviour was focused on male-female interactions rather than nest content (which I could not inspect). The situation seemed comparable to that observed by BOURNE (1955b) in August-September - "The birds were displaying freely, but had not begun to lay" - which would confirm an overlooked, early onset of sexual activity, as the known breeding season for the Cape Verdean kestrels is October to April (NAUROIS, 1987; HAZEVOET, 1995).

General discussion

Whenever a difference was found in this study, *alexandri* and *neglectus* differed more from nominate *tinnunculus* than from each other, and some of the common traits (colour markings and infrequent hovering) of the Cape Verdean forms might hardly have resulted from convergent evolution. Thus the idea of separate kestrel colonizations of the Cape Verde archipelago should be discarded and that of local divergence accepted. Too few observations exist, however, to suggest a cause for this local divergence.

While for both morphology (general colour pattern and degree of sexual dimorphism) and behaviour (tendency to hovering), the Canarian kestrels are more similar to European Common Kestrels, the Cape Verdean kestrels are reminiscent of a range of Afrotropical continental subspecies of the Common Kestrel (*rufescens* to *rupicolus*), for morphology. Unfortunately the behaviour of these subspecies is still poorly known. It seems that pairs continue to frequent their nesting sites even when not breeding, and some display occurs throughout the year (BROWN *et alii*, 1982). This trait would match the early onset of sexual activity of the Cape Verdean kestrels.

The even more striking similarity, in colour markings, of the Cape Verdean kestrels to the Madagascar and the Mauritius Kestrels points to common traits of tropical insular kestrels - low degree of sexual dimorphism and conspicuously marked plumage, with spotted to barred, rather than streaked, underparts in adulthood - which suit a

widespread (ancestral?) pattern of falcons though not the *tinnunculus* model. This pattern also emerges from the rather plain, *tinnunculus*-like appearance of the Seychelles Kestrel *Falco araea*, and more eastwards, it is fully evident in the Spotted Kestrel *Falco moluccensis*. Unfortunately, hovering behaviour among these species may depend on open vs. forested habitats, hence subtler comparisons would be needed to infer phylogeny from behaviour. With their intermediate shape, size, and coloration, the Cape Verdean kestrels suggest a link between these insular species and the abovesaid subspecies of the Common Kestrel in mainland Africa. This would support BOYCE & WHITE's (1987) idea of an African origin of the typical kestrels, though not from the Fox Kestrel *Falco alopex*, an overall streaked form (see LONDEI, 2002 for further reasons).

Ancestral traits would have disappeared from most of the continental forms of typical kestrels (the Fox Kestrel, most populations of the Common Kestrel, the Australian Kestrel *Falco cenchroides*, and the Lesser Kestrel *Falco naumanni*), though traces would remain in the African continent with the Greater Kestrel *Falco rupicoloides* and some Common Kestrel populations. The ancestral traits would be more visible in more conservative, insular forms.

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