

Ecomorphology of island populations of the Kestrel *Falco tinnunculus* on Cape Verde

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ABSTRACT

Data comprising 23 morphological characters from 55 Kestrels *Falco tinnunculus* from three island populations of the Cape Verde archipelago show significant variation in shape of bill, tarsus, and talon. Since the variation refers to trophic structures, we suggest that ecological factors are largely responsible for the morphological differences in these island populations. Kestrels of the population on Brava (*Falco tinnunculus alexandri*) are intermediate between those of Boavista (*Falco tinnunculus alexandri*) and Santo Antao (*Falco tinnunculus neglectus*).

The data also revealed a distinct sexual dimorphism in morphological shape. The differences pertain mainly to trophic structures. This suggests that the dimorphism, previously only discussed with respect to body size, is due, at least in part, to ecological factors relating to prey type and availability. This assumption is strengthened by the fact that the degree of sexual dimorphism varies among these ecologically very different islands.

INTRODUCTION

Islands offer divergent environments with geographically separated animal populations that are subject to several evolutionary forces like genetic bottle-necks, drift, gene flow and selection driven by local conditions. Therefore, islands are an ideal field laboratory to study differentiation within a species and the corresponding covariation among behavioural and morphological characteristics and ecological conditions. Studies of the morphological variation of island vertebrate populations range from comparisons between continental and island forms to meticulous analyses of micro evolutionary change (Gorman 1979, Losos *et al.* 1997). Ecomorphological arguments were also used to describe and explain extant biogeographic patterns (Wunderle 1983).

Populations of the same species often differ among islands of an archipelago. These differences may be caused by genetic drift or selection for individuals best equipped for the prevailing local conditions. Drift is strongly dependent on population size and constitutes the major force counteracting selection in isolated populations. Gene flow from other islands or from continental populations can effectively swamp local adaptations. Population bottle-necks have ambiguous effects. On the one hand they exacerbate drift, but they may also increase additive genetic variance and hence allow for

bursts of effective selection (Carson & Templeton 1984). Selection of individuals well adapted to local ecology can be strong and island populations may differentiate within astonishingly few generations (Losos *et al.* 1997).

One precondition for answering functional questions using comparative studies of island populations is that these populations are sufficiently different in the characters of interest. These differences should mainly be due to adaptations to local conditions rather than drift. Gene flow from large continental populations and phylogenetic inertia leading to adaptive differences should be low or absent.

In many bird species sexual dimorphism contributes greatly to within population differentiation. The so-called reversed sexual dimorphism, with females being larger than males, occurs in most birds of prey (hawks, owls, skuas) and in some charadriiform waders. It is greatest in species that feed on large prey (Amadon 1975). Explanations for sexual dimorphism abound (Mueller 1986, Owens & Hartley 1998). They can be grouped as those that invoke sexual selection, reproductive biology, or competition.

Small-sized males may be favoured if small and agile prey is abundant and important for small nestlings (Storer 1966). Small males also spend less energy while hunting (Reynolds 1972, Balgooven 1976). Big females are best suited to contribute to offspring care when food demand of the young is high. The female's size will offer her a variety of advantages concerning reproduction, including better nest defence (Storer 1966, Selander 1972). Selection for female dominance seems to be a major reason for the reversed sexual dimorphism, too (Amadon 1975, Mueller 1986).

Morphological differences between the sexes may also be due to niche differentiation to avoid competition for food (Storer 1954, van Valen 1965, Selander 1966, Wilson 1969, Snyder & Wiley 1976, Newton 1979). They should be more common if fewer competing species are present (Willson 1969, Ebenmann 1986) as is generally the case on islands. However, it has also been argued that a large number of competitors would select for greater efficiency and hence higher dimorphism (van Valen 1965, Willson 1969). In woodpeckers, at least, sexual dimorphism is more pronounced on islands (Wallace 1974).

The Kestrel *Falco tinnunculus* is an ideal study object for this kind of question because it is widespread on the mainland and occurs with two allopatric taxa *Falco tinnunculus neglectus* (Schlegel, 1873) and *Falco tinnunculus alexandri* (Bourne, 1955) on the entire Cape Verde archipelago (for distribution see Figure 1). They are ubiquitous and generalists in hunting modes and prey choice.

We have chosen the Cape Verde archipelago as a study area because it exhibits a variety of different environments. It consists of nine inhabited islands and some remote islets, and is situated 460 km off the West African coast. The islands in the east differ greatly from those in the west. The former are flat and sandy and aeolian activity including wandering dunes determine geomorphological traits. The western islands are less eroded and exhibit a mountainous relief with peaks up to 3000 m and little flat land. The monsoon rains are unpredictable and not annual. The islands belong to the hyper-arid areas (Barrow 1991) and there is continuing desertification of the land. Humidity and precipitation outside the monsoon are only possible at higher elevations (over 600 m).

Because of the differences in the environments on the islands adaptation may lead to divergence in morphological structures in the Kestrel among island populations. Many ecomorphological studies have shown the close relationship between habitat, behaviour and morphology (Leisler *et al.* 1989, Stiles 1995, Gamauf *et al.* 1998). The larger islands may have greater environmental heterogeneity, and so a greater width of environmental selective pressures (Williamson 1981). Further, morphological features correlate with hunting behaviour (Leisler *et al.* 1989, Carrascal *et al.* 1994).

Gene flow that potentially retards differentiation among island populations may occur between the island populations and between the archipelago and resident or migratory mainland populations (*Falco t. tinnunculus* (Linnaeus, 1758) and *Falco tinnunculus rufescens* (Swainson, 1837)).

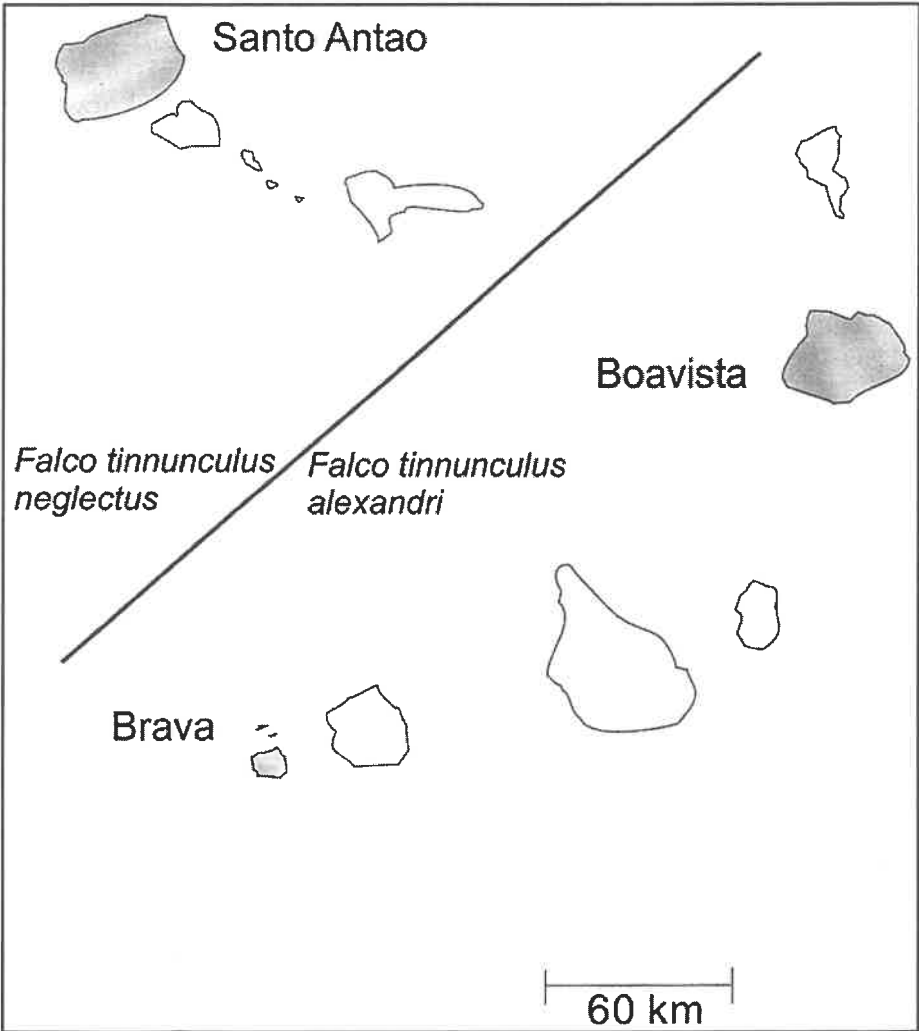
Data sets for the analysis of morphological parameters in bird populations are mostly restricted to a basic set of a few parameters. But larger sets of morphological characters are crucial for detecting variation within one species. Leisler *et al.* (1997) stress that the number of relevant characters is still low in most studies. By taking 23 characters into account, including some which play a crucial role

in subduing (tarsus, toe, talon) and manipulating prey (bill), we made sure that we could detect even low levels of morphological variation.

The study focuses on three islands which represent main Cape Verdian landscape units: Santo Antao, Brava and Boavista (see Fig. 1). Santo Antao and Brava offer a mountainous relief, the latter showing most intensive agriculture and land degradation due to drought and human impact. Boavista is one of the eastern flat and sandy islands, where agriculture is only possible in oasis-like riverbeds.

In this paper we will assess variation of external morphological characters among island populations and between sexes of the Kestrel on the archipelago to test the basic assumption that divergence among islands does occur and that it is driven by ecological factors rather than random processes.

Figure 1: Map of the Cape Verde Islands. The line separates the island populations of *F. t. neglectus* and *F. t. alexandri*.



MATERIAL AND METHODS.

To examine morphometric variation in three populations of both subspecies, we measured 55 living birds from 3 islands (Boavista 21, Santo Antao: 17, Brava: 17). On the head, feet, wing and tail we measured 23 variables. These comprised bill width (gape), maxilla height from nostril until lower edge, nostril distance, cere length, cranium maximum length, tarsometatarsus length, diameter of intertarsal joint, length of toes (middle, hind, inner), length of claws (outer, middle, hind), height of claws (outer, middle, hind, inner), wing-length, Kipp's distance (wing tip to secondary 1), wing tip to primary 6, wing tip to primary 7, wing tip to primary 8 and ulna length. For details see Leisler & Winkler (1985,1991).

Data were adjusted by dividing all characters by the cube root of the weight and transformed to natural logarithms. We analyzed data with canonical variate analysis (CVA, ter Braak 1995).

RESULTS

First we grouped the individuals according to their geographical origin (island). With CVA we obtained one highly significant factor (Chi-Square= 95.925, F.G.= 24., $p < .0001$). It correlates mainly with seven variables: height of hind claw, gape, maxilla height, height of inner claw, distance between wing tip and 6p, height of outer claw and nostril distance (Table 1).

Table 1. Univariate F-tests and correlations of the first factor with the original characters in a CVA of 23 external characters with the birds grouped according to their origin (three islands).

<i>Character</i>	<i>univariate F</i>	<i>p</i>	<i>factor</i>
Gape	17.7827	.00000	-0.661
Maxilla height	11.6228	.00007	-0.584
Nostril distance	9.3425	.00034	-0.542
Cere			
Cranium			
Tarsometatarsus			
Knuckle			
L. toe middle			
L. toe hind			
L. toe inner			
L. claw outer			
L. claw middle	8.9692	.00045	-0.533
L. claw hind			
H. claw outer	9.5791	.00029	0.543
H. claw middle			
H. claw hind	20.7185	.00000	0.702
H. claw inner	10.8255	.00012	0.571
Wing length			
kipp			
Ulna			
Tip to p6	9.4112	.00032	-0.544
Tip to p7			
Tip to p8			
Percentage of total variance			91.7

Then the individuals were grouped according to sex. The highly significant factor (Chi-Square=77.721; F.G= 23; $p < .0001$) (Table 2). relates mainly to maximum cranium length, tarsometatarsus, nostril distance, cere length, and length of the hind claw.

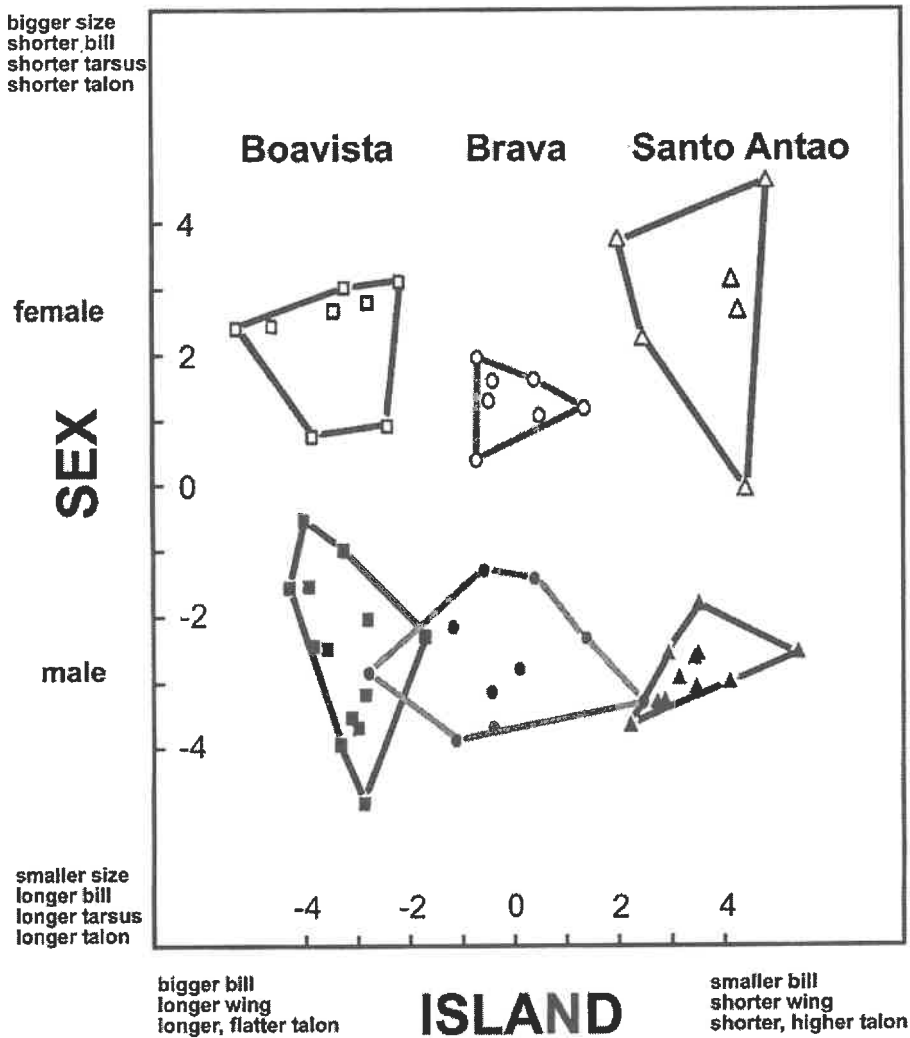
Table 2: Univariate F-tests and correlations of the factor with the original characters in a CVA of 23 external characters, with the birds grouped according to sex.

<i>Character</i>	<i>univariate F</i>	<i>p</i>	<i>factor</i>
Gape			
Maxilla height			
Nostril distance	20.0439	.00004	-0.572
Cere	16.7181	.00015	-0.534
Cranium	55.1159	.00000	-0.779
Tarsometatarsus	23.3671	.00001	-0.604
Knuckle			
L. toe middle			
L. toe hind			
L. toe inner			
L. claw outer			
L. claw middle			
L. claw hind	15.6326	.00023	-0.521
H. claw outer			
H. claw middle			
H. claw hind			
H. claw inner			
Wing length			
kipp			
Ulna			
Tip to p6			
Tip to p7			
tip to p8			
Percentage of total variance			100.03

A plot of the scores on one plane obtained from these analyses (Figure 2) shows how the six groups separate according to sex and island. On the first, the "island" axis, *Falco tinnunculus neglectus* of Santo Antao is found at the far positive end, the Brava Kestrels hold an intermediate position, and the Kestrels of Boavista are on the far left (negative) end of the axis. This corresponds to the high and short claws of the Santo Antao Kestrels, their small bill (gape, maxilla height, nostril distance), and their short and somewhat rounded wings. Towards the left (negative) of the axis, bills get bigger, claws longer and flatter, and the wings are more elongated, as is typical for the Kestrels on Boavista (Figure 2). The second axis separates the sexes with the females being found on the upper (positive) end. Since the data were corrected for size, this analysis reveals that females are not only the bigger sex, but also different in shape with respect to trophic structures. They differ from the males by their shorter cranium, shorter tarsometatarsus, smaller cere, shorter distance between nostrils, and shorter claws.

The females do not overlap morphologically between islands, but the males do as differences between the males are less strong. Sexual dimorphism according to those variables appears to be larger on Santo Antao than on Brava and Boavista. Also the females on Santo Antao vary more in these variables than do the males.

Figure 2: Plot of the results (first axes) of CVAS with respect to island and sex. Unit of scale is the standard deviation of the scores relative to the mean. For details of the analyses see Tables 1 and 2, and text.



DISCUSSION

There is variation in morphological structures between the island populations of the Kestrel. This variation occurs not just in size, but also in shape, related to traits of the prey-catching apparatus, namely the bill, talons, as well as tarsus and wing. These differences in trophic structures lead us to the assumption that adaptation to local environments with their respective habitat characteristics and prey abundance played a crucial role in forming morphologically distinct island populations (Figure 2). We suggest that small bill, short distal wing, and shorter and higher talons are well adapted to capture small, terrestrial prey. The longer wing, bigger bill, and longer and flatter talons of Boavista Kestrels may indicate frequent aerial hunting of bigger prey types.

The data also open new aspects for the discussion of the sexual dimorphism in birds of prey. Sexual dimorphism in birds of prey has been exclusively discussed in terms of differences in size. Our study shows that sexual dimorphism does not only refer to the difference in size but also to shape. The heavier females possess relatively short tarsi and a short bill (Figure 2). As far as we know, variation in shape has not been described and analyzed in previous studies on sexual dimorphism in raptors. As the data reveal sexual dimorphism in trophic structures, it indicates that ecological factors like availability of different prey types are important for the evolution of sexual dimorphism in raptors. Since environments differ among islands it is not surprising in this context that the extent of sexual dimorphism in the Kestrels varies among islands.

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