

Dispersion in the Seychelles Kestrel

Falco araea

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ABSTRACT

A study of Seychelles Kestrel dispersion behaviour was carried out in a 1270 ha area on Mahé in 1975/76, with a re-survey of part of the area in 1998. Nest sites were over-dispersed with nearest-neighbour-distances typically around 450m. Some 34 pairs nested within the study area which was mainly dense secondary forest. The kestrels occupied year-round territories that were actively defended along boundaries between pairs, and territorial defence was most frequent in March-June, immediately after the breeding season. Disputes typically involved prolonged bouts of vocalisation with birds perched in trees or on small rock faces. Territory size varied from 33.5-46.5 ha (mean 40.3 ha) and smaller territories contained proportionately more 'structured' forest and less 'open' habitat. Occupancy of the territory was advertised by characteristic display flights that occurred most frequently in May-July, prior to the breeding season. The same study area was re-surveyed in February 1998 and occupancy was checked in 22 of the original territories. Mated pairs or adult birds with recently fledged young were detected in 20 of these territories confirming the expected long-term stability in the pattern of dispersion in this tropical island raptor living in a forest environment.

INTRODUCTION

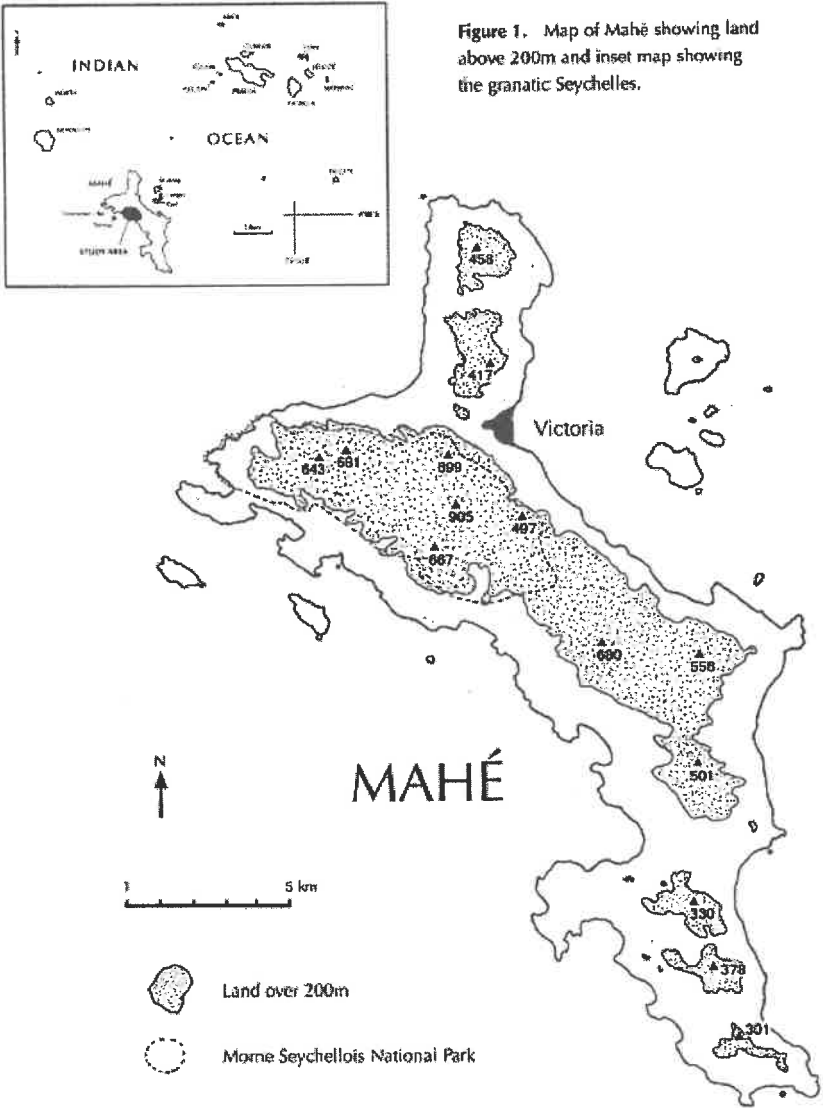
The Seychelles Kestrel is endemic to the remote Indian Ocean archipelago of Seychelles (Fig. 1) where it is the only breeding diurnal raptor (Penny 1974). Early accounts of the Seychelles avifauna described the native landbirds and recorded their distribution throughout the islands (Newton 1867, Oustalet 1878). Gaymer *et al.* (1969) stated that the kestrel was 'territorial, with only one pair in most plateau areas'. Subsequently, Feare *et al.* (1974) used colour-ringed birds to estimate home range size for five pairs of kestrels and used these data to estimate population size on the 145 km² island of Mahé. My work on the species involved intensive research on population ecology, food and conservation during 1975-77 (Watson 1981) with additional data gathered during subsequent visits, including a fairly comprehensive re-survey of dispersion in part of the 1975 study area during February 1998.

With a body weight of 70-80g the Seychelles Kestrel is the smallest member of the genus *Falco*. Adult males and females are indistinguishable by plumage, with both sexes having grey heads, rich chestnut backs and wing-coverts, and black and grey banded tails, all of which are among typically male characteristics of kestrel species in which sexual plumage dimorphism occurs (Village 1990).

Seychelles Kestrels have a distinct breeding season with egg-laying in September/October and the young leave the nest in November/December (Watson 1992). Food is predominantly lizards with arboreal green geckos (*Phelsuma*) captured from branches and trunks of trees, and ground-living skinks (*Mabuya*) that are typically taken on, or close to the ground (Watson 1981).

Past and current distribution of the kestrel is reviewed in Collar & Stuart (1985). Nowadays the main population (c. 370 pairs) is on Mahé with another 35-40 pairs on Silhouette (Fig. 1). Small numbers occur on most of the satellite islands off Mahé (including Conception where presence was confirmed in 1998), and on the island of Praslin to which birds were reintroduced in 1977 (Watson 1989). Kestrel habitat on Mahé comprises variously dense and more open secondary woodland in the mountains, and a range of lowland habitats including coconut plantation, gardens and mixed-woodland as well as agricultural crops and urban areas.

Figure 1 Map of the granitic Seychelles showing the location of the kestrel study area on Mahé.



This paper describes dispersion behaviour and documents the pattern of dispersion in the Seychelles Kestrel. It also reports on kestrel distribution in an area of Mahé in 1998, some 23 years after the same area was first surveyed in 1975.

STUDY AREA AND METHODS

Study Area

An area of 1270 ha in north-west Mahé (Fig. 1) was used for work on dispersion. This included a range of altitudes from the summit ridge around 500 m to sea level. Around 50% of Mahé lies above and below the 200 m contour and proportions within the study area were broadly similar to this. The main vegetation communities of Seychelles are described in Vesey-Fitzgerald (1940), Sauer (1967) and Procter (1984).

Within the study area, four broad habitat types were recognised. In upland areas, above the 200 m contour, *mixed upland forest* was predominant. This is a structurally diverse habitat with a canopy height of 12-15 m. In the highest altitude areas the dominant tree species are the endemic *Northia seychellarum* and *Dillenia ferruginia* but more typically this habitat type comprises secondary woodland dominated by exotic species such as the acacia-like *Albizia falcata* and the shrub *Cinnamom zeylanicum*. The second and more restricted upland habitat of *open scrub woodland* is structurally more simple with a typical maximum height of 5m or less. It is often associated with bare-rock areas, known locally as *glacis* where the dominant species are *Memecylon elaeagni* and *Randia* spp., but also includes the structurally comparable tea plantations that were quite widespread in the study area.

Below the 200 m contour much of the land is covered by *mixed coconut plantation and lowland forest* habitat which is structurally varied and typically reaches a height of 15 m or more. Here coconut palms *Cocos nucifer* are associated with trees such as *Calophyllum inophyllum*, *Terminalia catappa* and *Artocarpus* spp. and a wide range of exotic shrubs. Finally, *open lowland habitat* occurs below 200 m and is characterised by structural simplicity. This includes monoculture coconut plantations with a canopy height of 5-20 m depending on age, as well as areas holding a range of other agricultural crops.

Individually Marked Birds

To provide information on home range use, kestrels were individually colour-ringed. Adult birds were trapped at a range of sites using a bal-chatri (Berger & Mueller 1975) containing a Madagascar Fody (*Foudia madagascariensis*) during the period January - June. During the subsequent breeding season (September - November) a selection of nestlings or dependent young were also marked with colour rings. Sightings of marked adults were recorded over a 12 month period from March on a systematic basis. At least twice each month, all localities where marked adults occurred were searched, with the aid of tape recordings in especially dense forest. Once located, colour-ringed birds were observed for around one hour. The bird's position and subsequent movements were recorded and sightings were transferred to a map with an overlying 1 ha grid. Movements of dependent young were recorded in a similar way from the time they fledged in November/December until they began to disperse in February.

Territorial Boundary Disputes

Boundary disputes between Seychelles Kestrels are characterised by intense and prolonged vocal activity. Individuals in dispute perch conspicuously in the upper layers of the vegetation and all birds present give vent to a loud *keez* call (Willoughby & Cade 1964), repeated at a rate of two notes per second for 20 seconds or so. In prolonged conflicts the interaction sometimes intensifies with birds displacing one another from their prominent perches, and in its most extreme form this displacing behaviour can involve actual contact. During work on home ranges and other fieldwork activity, all territorial disputes were noted and their locations plotted on maps.

Display Flights

Aerial display in the Seychelles Kestrel is distinctive and can be exhibited by either member of

a mated pair. Typically a bird takes to the air and, with a series of flaps and glides, circles up to a height of 50-100 m when calling begins. The call comprises an erratic series of truncated notes, each followed by a distinct but variable pause. A bird may continue circling for as long as 20 minutes, calling intermittently. Based on evidence from territorial disputes, this circling behaviour generally occurred close to territorial boundaries. After circling a bird may descend directly to a prominent perch or may enter a straight, level or slightly descending flight with erratic, forced wing-beats and during the course of the flight it typically gives the truncated call note. These straight flights can cover up to 800 m before the bird perches, or alternatively enters a second bout of ascending, circling flight before finally dropping to a perch. As with boundary disputes, records were kept of the frequency of occurrence of display flights and the location of these was recorded on maps.

Nest Sites and Spacing Analysis

Nest sites were located as described in Watson (1992). Within the study area, most nest sites were in cliffs with smaller numbers in holes in trees and in the crowns of coconut palms. The distribution of sites was plotted on maps and spacing of nest sites was assessed using an analysis of nearest-neighbour-distance. To test for regular nest spacing, the G-statistic (GMSD) was used as recommended by Brown (1975). Values of GMSD range from 0 to 1. Larger values indicate greater regularity of spacing and values less than 0.65 indicate that nest sites are randomly spaced (Nilsson *et al.* 1982).

Re-survey in 1998

During a 10-day period in February 1998 I re-surveyed a substantial part of the kestrel study area in north-west Mahé. In the time available I was able to visit 22 of the original 34 territories, spending a minimum of 3 hours close to the location of the 1975 nest site, sometimes spread over 2 or 3 visits.

RESULTS

Home Range

Individually marked adults and/or dependent young were present among 25 of the 34 pairs of kestrels that nested in the study area in 1975. All 1 ha squares from which marked birds were recorded are shown in Fig. 2. Data for the 12-month period from March 1975 have been pooled. Evidence from sites N and U, where the largest number of records were obtained, indicated no significant difference in the pattern of range use between the non-breeding period (March-August) and the breeding period (September-February). Results for adult males and females (separated on size difference, Watson 1981) have been pooled since no significant difference occurred in the number of 1 ha squares visited by males ($x = 17.43 \pm \text{sd } 4.65, n=7$) compared with females ($x = 18.20 \pm \text{sd } 5.77, n = 15$). For ranges where both marked adults and young were present, all records of adults are shown in Fig. 2 and records of young are shown only for squares where no sightings of marked adults occurred.

Territorial Boundary Disputes

Most data on boundary disputes refer to the 14-month period from January 1975, with some further records from the second half of 1976. A dispute frequency index was calculated based on the amount of time spent by me on fieldwork during each month (Fig. 4). Although some disputes occurred in all months of the year, there was a clear peak in frequency between March and June and dispute frequency was low from September - February (the main breeding period). No data were available for April/May 1976 but otherwise the pattern was similar to 1975. Altogether 107 boundary conflicts were recorded at 64 localities in the study area during the 12-months from March 1975 (the period when home range use was recorded). Disputes are shown on Fig. 3 and each point may refer to more than one conflict as these have been plotted separately only where they occurred more than 100 m from another recorded conflict. Comparison between Figs. 2 and 3 reveals that, where the edges of ranges were known from movements of marked birds, the location of dispute points closely coincided with range boundaries.

Figure 2 Recorded ranges of colour-ringed Seychelles kestrels within the study area on Mahé. Upper-case letters refer to sightings of colour-ringed adult birds and lower-case to dependent young. All records denote occurrence within 1-ha squares.

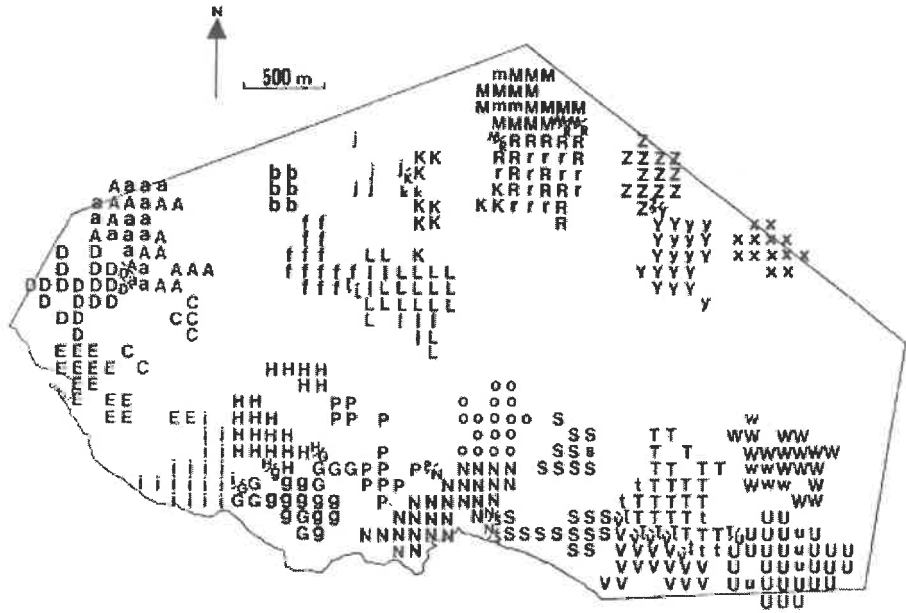
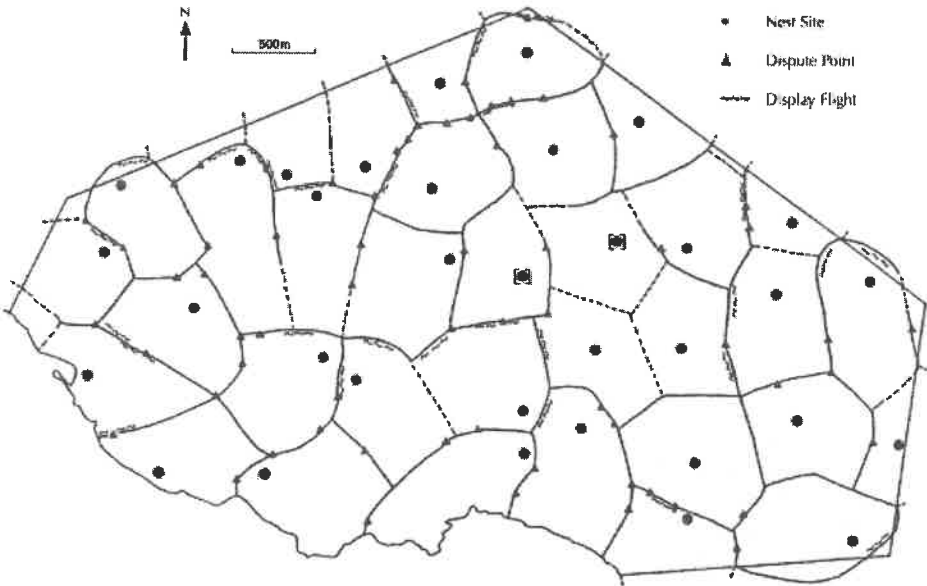


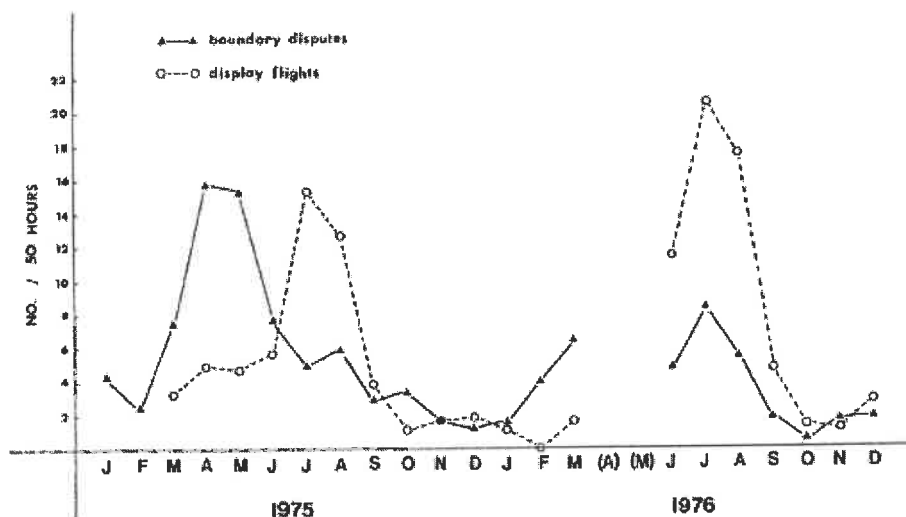
Figure 3. Territorial boundaries of Seychelles kestrels in the Mahé study area. Locations of nest sites (•), dispute points (▲), and display flights (—) are shown. Boundaries were drawn using this information and the range data in Fig. 2. See text for explanation of solid and hatched lines.



Display Flights

The frequency of display flights was highest in July/August 1975 and this pattern was repeated at the same time in 1976 (Fig. 4); in both years this was immediately prior to the onset of breeding. The locations of display flights that were recorded during the 12-month period from March 1975 are shown in Fig. 3.

Figure 4. Frequency of boundary disputes and of display flights by Seychelles kestrels during each month in 1975 and 1976. Frequency data are standardised to number of disputes/display flights per 50 hours fieldwork .



Territory Size

The close agreement between home range boundaries, the location of boundary disputes, and of display flights confirms that Seychelles Kestrels defend an exclusive home range (Type A territory, Hinde 1956). Territorial boundaries are shown as solid lines in Fig. 3 where evidence was available from either marked birds, from boundary disputes or from display flights. Dotted lines are used where boundaries were less certain. In some cases these were determined from the movements of unmarked birds known to be associated with particular nest sites, and in a few cases where no data were available, the dotted lines are arbitrarily placed midway between adjacent nest sites. In the following analysis territories are included only where 75% or more of the boundary was known for certain. There were 22 such territories within the study area.

Territory size was measured to the nearest 0.5 ha using squared paper and a traced map of territorial boundaries. The 22 territories had a mean area of $40.3 \text{ ha} \pm \text{sd } 3.99$ with a range from 33.5 to 46.5 ha. There was no significant difference in territory size above and below the 200 m contour (12 territories centred above 200 m; $\bar{x} = 39.5 \pm \text{sd } 3.77$; 10 territories centred below 200 m; $\bar{x} = 41.2 \pm \text{sd } 4.24$). Habitat differences did explain some of the variation in territory size. The habitat types of *mixed upland forest* and *mixed coconut plantation and lowland forest* are structurally more diverse than *open scrub woodland* and *open lowland habitat*. There was a significant relationship between territory size and the proportion of the territory that contained the structurally more complex habitats ($r = -0.686$, $\text{df} = 20$, $p < 0.001$). Specifically, smaller territories held a higher proportion of structurally more complex vegetation.

Analysis of Spacing

Nest sites were located for 32 of the 34 pairs within the study area in the 1975 breeding season (Fig. 3). Nearest-neighbour-distances ranged from just over 200 m to more than 600 m with a mean of around 450 m. Testing for randomness/regularity of nest spacing gave a G-statistic of 0.94 indicating that nest sites were significantly over-dispersed. A small number of sites in the north-west of the study area showed a more clumped distribution and this was caused by several pairs nesting on a very extensive area of cliff at Morne Blanc. Here it appeared that some of the separation between adjacent pairs was being effected by vertical distances on a particularly large cliff face.

Re-survey in 1998

During survey work in February 1998 kestrels were detected within 100 m of the 1975 nest site at 20 out of 22 territories visited. None of the original marked birds were seen and it is almost certain that all the 1998 birds were different individuals from those of 1975. In eight territories, at least one adult kestrel was seen in association with one or more dependent young, and in the remaining 12 territories the adult pair only was recorded. In the two territories where no kestrels were seen within 100 m of the 1975 nest site this may have been a product of the relatively short time available for the survey, or it may have reflected loss or movement of birds from these sites. Comprehensive survey was not possible throughout the area and it is possible that some pairs of kestrels that had moved their nesting sites were missed. Nor was it possible from this quick survey to be sure that no new pairs had become established in places that had not been occupied in 1975.

DISCUSSION

Pairs of Seychelles Kestrels occupied individual home ranges and these were used throughout the year. Ranges were contiguous and boundaries between pairs were actively defended. Home range in the Seychelles Kestrel is therefore synonymous with territory. Boundary disputes occurred throughout the year but were most frequent between March and June, immediately following the period when fledged young became independent. An aerial display behaviour served to reaffirm territorial boundaries and was most frequent during July/August, just prior to breeding. A re-survey of the study area 23 years after the initial research revealed a highly stable pattern of dispersion over time. More than 90% of localities containing nesting kestrels in 1975 revealed evidence of occupancy by pairs or families of kestrels in 1998.

The majority of non-colonial raptors have nest sites that are spaced out, with a small surrounding area (the nesting territory, Newton 1976) defended against conspecifics. Food is typically obtained from hunting ranges that overlap widely (e.g. European Kestrel *Falco tinnunculus*, Village 1990; Peregrine Falcon *Falco peregrinus*, Cade 1960; Goshawk *Accipiter gentilis*, Kenward 1977; European Sparrowhawk *Accipiter nisus*, Newton 1979). Rather fewer species have exclusive home ranges (e.g. Buzzard *Buteo buteo*, Mebs 1964; Greater Kestrel *Falco rupicoloides*, Kemp 1968 in Newton 1979; Black Eagle *Aquila verreauxii*, Gargett 1975; Galapagos Hawk *Buteo galapagoensis*, de Vries 1975). The dispersion continuum from colonialism, through overlapping home ranges to exclusive defended areas probably reflects progressive adjustment to an increasingly even and predictable food supply (Newton 1979). Factors leading to a more even and predictable food supply include dependence on vertebrate (rather than invertebrate) prey, stability (as opposed to unpredictability) of climate, and structural complexity of habitat (complex woodland as opposed to structurally simply grassland/ tundra). The conditions for the Seychelles Kestrel meet each of the above requirements and it is unsurprising to find that this species has a relatively extreme dispersion pattern (exclusive home ranges).

The mean territory size of Seychelles Kestrels was 40.3 ha with a range of 33.5-46.5 ha among 22 pairs. Range size in raptors is generally positively correlated with the size of the bird (Newton 1979). As the smallest member of the genus *Falco*, it is not surprising that the Seychelles Kestrel has one of the smallest home ranges recorded for any diurnal raptor, only beaten by the Frog Hawk *Accipiter soloensis* (Kwon & Won in Newton 1979). Grant (1966) showed that the numbers and biomass of passerine birds was greater per unit area on islands compared with equivalent mainland

areas. If this is also true for lower vertebrates such as the lizards that are the Seychelles Kestrel's staple diet, then this could be another factor contributing to the exceptionally small home range in the Seychelles Kestrel.

Several raptors have been shown to have smaller ranges in areas where food availability was measurably greater (e.g. Buzzard, Picozzi & Weir 1974; Black Eagle, Gargett 1975; European Sparrowhawk, Newton *et al.* 1986). The relationship between territory size and habitat in the Seychelles Kestrel is probably linked to differences in food availability, since an important prey species, the arboreal gecko *Phelsuma* is likely to be more plentiful in the structurally more complex woodland habitat where Seychelles Kestrels occupied appreciably smaller ranges (Watson 1981).

Significant over-dispersion of nest sites occurred in the Seychelles Kestrel and has been reported for many species of raptor (e.g. European Sparrowhawk, Newton *et al.* 1977; Buzzard, Tubbs 1974; Peregrine Falcon, Ratcliffe 1962; Golden Eagle *Aquila chrysaetos*, Watson 1997). The phenomenon of over-dispersion is consistent with the view that populations are, at least proximately, limited by the territorial behaviour of individual pairs (Newton 1979). Further support for this view comes from the removal experiments of Seychelles Kestrels that were carried out in 1977 (Watson 1981, 1989) and these confirmed the existence of a non-breeding surplus. Finally, the exceptionally stable dispersion pattern that was evident between surveys 23 years apart, in 1975 and 1998, further supports the hypothesis that territorial behaviour is an important factor regulating population size in the Seychelles Kestrel.

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