

Associations of evolutionary & ecological distinctiveness amongst Indian Ocean kestrels

Jim J. Groombridge, Malcolm A. Nicoll, Carl G. Jones
& Jeff Watson

ABSTRACT

The evolutionary relationship between African kestrels, and their radiation across the Indian Ocean islands has attracted much debate from both evolutionary biologists, and conservationists tasked with recovering the endangered island forms. A molecular cytochrome-*b* phylogeny of African kestrels has delivered a novel perspective on the distinctiveness of several mainland and endemic island kestrels. The molecular phylogeny supports an Old World origin for typical kestrels, and indicates a recent radiation of kestrels from Madagascar towards Mauritius and the Seychelles. The earlier arrival of kestrels on Mauritius appears consistent with the cessation of major island-forming volcanic activity there, whereas colonisation of the Seychelles appears compatible with the Pleistocene emergence of smaller islands. The different history of island isolation experienced by the Mauritius and Seychelles forms provides an ideal framework in which to compare morphological and ecological change. The molecular phylogeny reveals the Mauritius Kestrel to be the most evolutionarily distinct of the two island forms, whereas wing morphology and prey choice illustrate parallel forest-dwelling adaptations on both islands for ambush-style hunting of endemic Indian Ocean *Phelsuma* geckos. The molecular study underlines the conservation priority that has ensured the successful recovery of the Mauritius Kestrel, and reveals ecological patterns and processes elsewhere.

INTRODUCTION

Traditionally, the uniqueness - or biodiversity value - of an endangered species has been based upon a culmination of ecological, morphological, and behavioural comparisons with the remaining species in the genus. However,

there is mounting recognition that measurement of the evolutionary distinctiveness of an endangered species should be taken into account when prioritizing cases for conservation. The increasing availability of molecular data and modern methods for reconstruction of phylogenetic histories has enabled evolutionary distinctiveness *per se* to play a role in defining the priority status of endangered species (Caccone *et al.* 1999; Soltis & Gitzendanner 1999). Considerable debate surrounds the application of this tool (Erwin 1991; Vane-Wright *et al.* 1991; Williams *et al.* 1994; Faith 1994; Williams & Humphries 1994); should we favour those lineages that represent a unique evolutionary trajectory, or conserve phylogenetic diversity *per se*? (Bennett & Owens 2000). The need to address this question for endemic island species appears to be particularly important, since islands harbour unique evolutionary processes, and are often species-poor, but rich in endemic forms (Whittaker 1998). In today's climate of 'rapid-response' conservation, the onset of a recovery initiative for an endangered species is rarely a logical consequence of detecting a unique evolutionary history. However, here we apply ecological and morphological data, retrospectively, to a molecular phylogeny to illustrate where the restoration of an endangered raptor on Mauritius has helped to maintain evolutionary and phenotypic diversity.

Recovery of the Mauritius Kestrel

Once the world's rarest bird, with a wild population of four known individuals in 1974 (Temple 1974, 1977), the restoration of the Mauritius Kestrel *Falco punctatus* to 400-500 birds by 1997, and to 600-800 birds by 2003 (Jones *pers. com.*) has been regarded as a dramatic success (Safford & Jones 1997; Groombridge *et al.* 2000). The Mauritius Kestrel is a small Indian Ocean falcon endemic to Mauritius. Formerly distributed throughout the island (McKelvey 1977; Temple 1977; Jones 1987), this species' range was restricted to the island's mountainous areas by early this century, following human colonisation and the intensive cultivation of lowland areas (Jones 1987). Pesticide contamination during an anti-malaria campaign from 1948-70 brought about the catastrophic decline of the kestrel population (Cheke 1987; Safford & Jones 1997). By the 1960s the kestrel was regarded as critically endangered (Brown & Amadon 1968), before the wild population crashed to only four known birds (Temple 1974, 1977). Consequently, the Mauritius Kestrel became the focus of intensive conservation efforts, and from 1974 to 1988 five adult Mauritius Kestrels, seven fledglings and 14 individuals from wild-laid eggs were taken from the wild to initiate a captive population. A ten-year (1984-94) programme of captive-breeding and reintroduction was implemented (Jones *et al.* 1995). By 1994 a total of 331 kestrels had been successfully reintroduced, many of which moved into new areas of habitat. By 1997 the total wild population was thought to be over 400 birds (Safford & Jones 1997), and consisted of the original western population, derived from wild and reintroduced birds, and a separate eastern – and small northern – population established entirely from reintroduced birds.

Alongside the intensive conservation efforts since 1973, ecological studies of the Mauritius Kestrel have revealed considerable specialization for prey choice and morphological differences which have fuelled considerable interest

in the evolutionary relationship of the Mauritius Kestrel to other kestrel species world-wide (Temple 1977; Boyce & White 1987). Temple (1977, 1978) could only imply an African origin for the Mauritius Kestrel, regarding the species as too specialised to enable closer origins to be suggested, but Jones & Owadally (1985) proposed the Seychelles Kestrel *F. araea* and Mauritius Kestrel as sister taxa with relatively recent origins. The relative distributions of the Mauritius, Seychelles, and Madagascar Kestrel *F. newtoni* within the Indian Ocean has suggested an eastern radiation from mainland Africa. However, inferences regarding the phylogenetic origins of these kestrels based on their plumage and morphological comparison has required validation from independent information on their evolutionary history.

History of the Seychelles Kestrel

The Seychelles Kestrel is the only diurnal raptor endemic to the islands of the Seychelles archipelago and was first described by Newton (1867). In contrast to the migratory habits of many typical kestrels, the Seychelles Kestrel is sedentary (Brown & Amadon 1969). Both adult sexes have near-identical plumage, of which diagnostic features include creamy-buff, unspotted underparts, a pure grey-coloured head and rump, a rich reddish-brown back and wing-coverts sparsely spotted with black, and a grey tail with five black bands. The eye is dark brown, and the cere, eye-ring, legs and feet are bright yellow (Watson 1981).

The Seychelles archipelago consists of both granitic and coralline islands, with the largest island (Mahé) being 145 km² in size, and supporting a mixture of upland 'mountain' forest, and open lowland forest, both types being heavily degraded and restructured forms of a historical native forest ecosystem that occurred on the pristine Seychelles islands (Sauer 1967; Vesey-Fitzgerald 1940). The impacts of increasing settlement on the Seychelles since human colonisation in 1770, and subsequent clearance of native forests there for commercial forestry and agriculture during the 18th and 19th centuries, have followed a pattern of historical deforestation similar to that imposed on Mauritius (Cheke 1987). The Seychelles Kestrel population has had to contend with the same negative impacts from introduced mammalian predators and competitive avian species as the Mauritius Kestrel; including rats *Rattus rattus*, feral cats *Felis catus*, and introduced Indian Mynah birds *Acridotheres tristis*. Barn Owls *Tyto alba* were introduced to the Seychelles islands in the 1950s, and are likely to have brought equally serious ecological implications, being both a predator on young and adult Seychelles Kestrels, as well as competing for available nest sites. Several authors believed that the Seychelles Kestrel was at one time close to extinction (Crook 1960; Fischer *et al.* 1969; Gaymer *et al.* 1969), but this historical rarity was not confirmed by systematic population survey. Gaymer *et al.* (1969) suggested a total population size below 30 birds in 1965, whereas later surveys counted 49 pairs (Feare *et al.* 1974). More recently, Watson (1981) used data on home range size and available habitat area to suggest that the largest island of Mahé alone could hold 370 kestrel pairs. Conservation measures for this species have included translocation of individuals from Mahé to unpopulated outer islands in 1977 to form breeding subpopulations there, and these efforts have proved successful (Watson 1989).

The surveys by Watson (1991) suggested a total population size of 420 pairs for the Seychelles Kestrel, and the most recent surveys by Kay (2002) have confirmed that current population size may be similar to estimates made the mid-1970s.

Characteristics of the Indian Ocean island kestrels

Generally, there exists a degree of plumage dimorphism between the sexes of kestrels, but this feature does not always show an identifiable geographic pattern within the typical kestrels. Some kestrel species show a very distinctive plumage pattern for each sex, such as the Common kestrel *F. tinnunculus*, Australian kestrel *F. cenchroides* and Lesser Kestrel *F. naumanni*, but in others, both sexes share a plumage pattern typical of either male (dark morph Madagascar and Seychelles kestrels), or female (light morph Madagascar, Mauritius, Moluccan [*F. moluccensis*], Greater [*F. rupicoloides*] and Fox kestrels [*F. alopex*]; Cade 1982; Village 1990). This tendency observed in some kestrels of a shift towards either typical male- or female (or juvenile)-type plumage is particularly interesting with regard to those kestrels endemic to Madagascar, Mauritius and the Seychelles, where the ancestral route of radiation between these islands may have played a role. Based on morphological comparison alone, the Mauritius and Seychelles kestrels are both thought to be derived from the Madagascar Kestrel (Benson & Penny 1971; Jones & Owadally 1985), but the Seychelles Kestrel is more similar in appearance to that of the Madagascan species than the Mauritius Kestrel (Benson 1967; Benson & Penny 1971; Jones 1987). The Madagascar Kestrel exists as two colour morphs, which are not sex-linked; a dark phase and a light phase (Siegfried & Frost 1970), and plumage comparison implies that the Mauritius Kestrel originated from the pale phase and the Seychelles Kestrel from the dark phase (Watson 1981).

Classically, kestrels are small, long-winged, long-tailed, short-toed falcons, of which the kestrel group comprises 13 species, which together have a global distribution that spans both New and Old Worlds (Boyce & White 1987; Village 1990). Despite the high diversity observed within morphological characters across all typical kestrels, ecological and morphological studies suggest that the Mauritius Kestrel appears to be more highly adapted to forest-dwelling compared to other typical kestrels. Two morphological characters serve to illustrate the most distinctive differences of the Mauritius form in comparison to other kestrels and falcons; wing shape and tarsus length. The Mauritius Kestrel is a medium-sized kestrel, and possesses shorter, broader, more rounded wings and longer tarsi and toes than those of other kestrel species. Short, rounded wings are a characteristic most commonly associated with hawks of the genus *Accipiter*, a genus widely-recognised as containing typical forest-hunting specialists, but this trait is also evident in both the Mauritius and Seychelles island forms, as well as in the New Zealand Falcon *F. novaeseelandiae*. The particular wing-shapes of the Mauritius and Seychelles forms are unusual in kestrels but typical of other forest raptors (Jones 1987), and would suggest an adaptation for heightened agility when pursuing prey through thick forest canopy. The tarsus of the Mauritius Kestrel is long, being approximately 32% longer than that of the European kestrel, and only 6%

shorter than that of the forest-hunting *Accipitrines* (Jones 1987). The increase in tarsus length (and an associated leg length) is assumed to be an adaptation for snatching prey off exposed branches, or extracting captured prey from thick vegetation. The Seychelles Kestrel is approximately 25% smaller than the Mauritius form (Jones 1987), but also displays these adaptations for forest-living to varying extents. Behavioural studies, and surveys of prey type and density by Watson (1981) indicate that this island kestrel hunts predominantly *Phelsuma* and *Mabuya* lizards, which are relatively common on the Seychelles.

In this paper, we summarize our knowledge of the evolutionary history of the Mauritius and Seychelles kestrels inferred from a recent molecular study by Groombridge *et al.* (2002); we combine morphological data from Jones (1987) and Watson (1981) with more recent data to point out characteristics of the ecology and morphology of these two island kestrel forms, and draw parallels between their biological differences, and their respective ancestral origins, in the context of the evolution and conservation of the Indian Ocean kestrels.

METHODS

Phylogeny reconstruction

Briefly, DNA was extracted from fresh blood and feather material obtained from the following species; Mauritius, Seychelles, Madagascar, Greater, Lesser, Australian, and Common kestrels, as well as from the South African Rock Kestrel *F. t. rupicolus*, and Canary Islands subspecies *F. t. canariensis* and *F. t. daconiae* (see Figure 1: *can*, *d1* and *d2* respectively). Appropriate portions of the mtDNA cytochrome-*b* gene were amplified using the avian cytochrome-*b* primers L-14990 and H-16065 for most kestrel taxa (Desjardins & Morais 1990). However, species-specific PCR primers based on conserved sequence alignment were designed for the Seychelles and Madagascar kestrels (Groombridge *et al.* 2002). Internal sequencing primers used for all species in this study were as follows; L-14996 (5' AACATCTCAGCATGATGAAAYTTYGG 3'; R. Thomas, *pers. comm.*); L-15212 (Baker *et al.* 1995); L-15656 and H-15914 (Helm-Bychowski & Cracraft 1993). Additional species-specific internal sequencing primers were designed for the Seychelles and Madagascar kestrels (Groombridge *et al.* 2002). The products were analysed by gel electrophoresis on an automated DNA sequencer (Applied Biosystems 377). Accuracy of gene sequence was confirmed by aligning multiple over-lapping fragments from forward and reverse sequencing reactions, such that each position of the gene was sequenced 3-4 times. Positioning for correct reading frame was verified by alignment with chicken *Gallus gallus* mtDNA sequence positions 14995-16020 (Desjardins & Morais 1990). Suitable candidates for outgroups within the family Falconidae were chosen from Genbank; western Redfooted Falcon *Falco vespertinus* (FVU83311), and American Kestrel (FSU83306). Phylogenetic analyses were carried out using PAUP* (Swofford 1997), and involved distance, parsimony and maximum likelihood analyses. A more detailed description of DNA extraction methods, details of PCR amplification and sequencing, and phylogenetic reconstruction are given in Groombridge *et al.* (2002).

Ecological and morphometric data

Wing profiles were taken from live adult kestrels on Mauritius and the Seychelles between 1982-98. Profiles shown are from female Mauritius Kestrel IRN-591786 (captured Stoneman, 3rd December 1993), female Seychelles Kestrel D-26165 (captured L'Eglise Baie Laizaire, January 1998), female Common Kestrel 84-White (obtained from captive stock held as part of the captive-breeding programme on Mauritius), and a male Lesser Kestrel found dead in Istanbul in August 1998 (Jones, *pers. comm.*). Morphometric measurements were taken from live and museum specimens of Mauritius Kestrels between 1992-98, and from live specimens of the Seychelles Kestrel captured on the Seychelles by Watson (1981). Comparative data were obtained from specimens at the Natural History Museum, Tring, UK., and from published sources (details given in Table 1).

Hunting behaviour and prey items for the Mauritius Kestrel were compiled from field observations and prey items delivered to nest sites of the east coast population on Mauritius between 1991-2001. Where possible, prey items were identified to genus or species. Bird prey items included adults, nestlings and fledglings. Comparative prey item data for the Seychelles Kestrel were extracted from similar field observations collated between 1974-77 by Watson (1981).

Table 1. Morphometric measurements of different kestrel species

Species	(n)	Sex	Tarsus	Wing	Tail	Weight (g)	Source
Lesser	(26)	M	30.8±1.0	239±5.4	144±5.2	90-172	Cramp & Simmons 1980;
	(16)	F	29.9±1.5	237±7.3	149±3.4	160±16.1	This study*
Common	(37)	M	39.6±0.1	246±1.0	163±0.9	202.2±2.8	Cramp & Simmons 1980;
	(44)	F	39.6±0.2	256±1.2	171±1.0	214.8±4.3	Kirkwood 1981
Madagascar						105±5.8	Brown & Amadon 1968
	(22)	?	31.1±3.7	191.8±9.6	119.8±8.1	145±4.0	Benson & Penny 1971; Seigried & Frost 1970
Seychelles	(15)	M	27.7±3.3(17)	148.2±1.7	102.1±6.0(17)	72.4±4.3	Watson 1981
	(33)	F		158.2±1.8		87.9±4.7	
Mauritius	(15)	M	40.0±1.3	173.1±3.5	128.4±4.3	118.5±8.0	This study
	(13)	F	41.0±1.0	187.6±2.0	138.5±5.4	158.0±9.9	

*data from specimens held at Natural History Museum, Tring, UK.

RESULTS

A summary of the molecular findings of Groombridge *et al.* (2002) are given in Figure 1, which aligns a cytochrome-*b* molecular phylogeny to geological events. Branch length and molecular divergence times indicate that the Mauritius Kestrel has experienced a longer period of island isolation relative to the Seychelles Kestrel. Although some phylogenetic analyses were inconsistent in their placement of the Mauritius Kestrel, it seems likely that

both island forms share the Madagascar Kestrel as their most recent common ancestor.

Figure 1. Molecular phylogeny from cytochrome-*b* sequence data with reference to geological events (summarized from Groombridge *et al.* 2002). Inset illustrates application of different substitution rates obtained from other avian cytochrome-*b* studies to calculate estimates of divergence time for particular nodes. Can, *F. t. canariensis*; d1, d2, *F. t. dacotiae*.

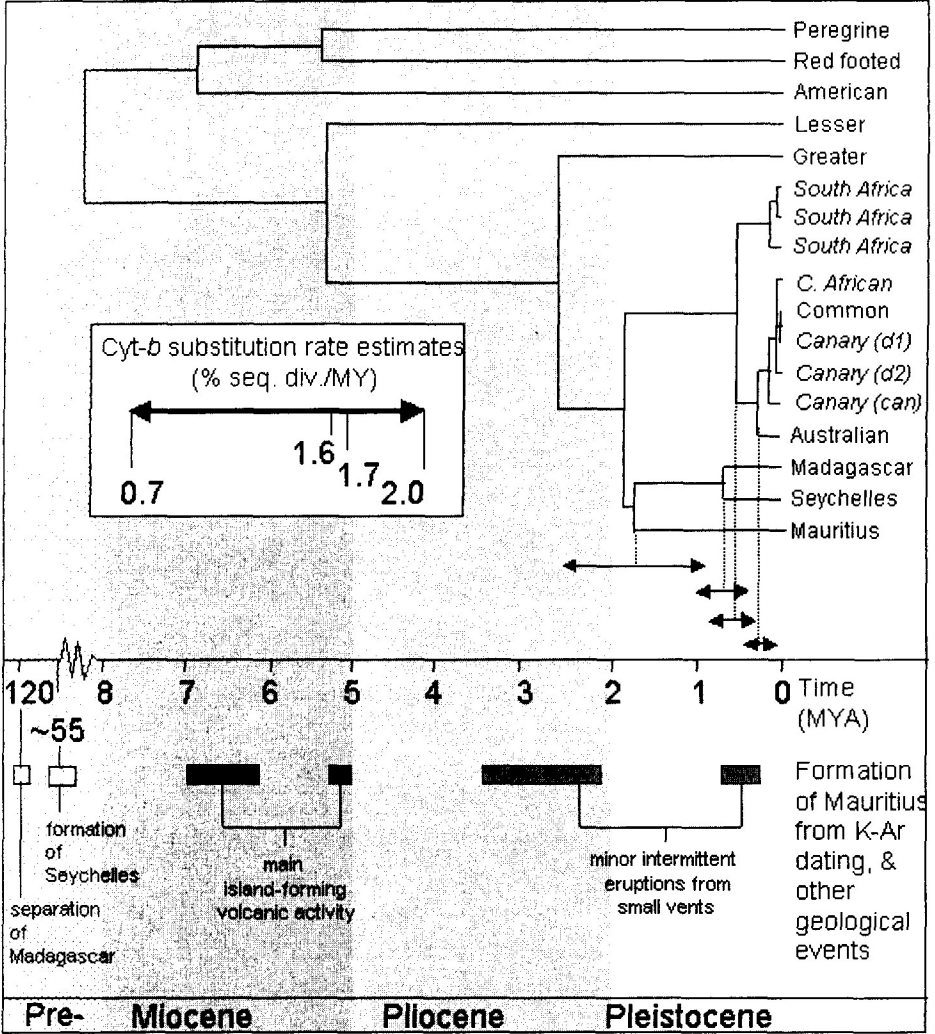


Figure 2 gives scale-drawn wing-profiles for the Mauritius, Seychelles, Common, and Lesser kestrels for a comparison of wing-shape. The two island forms show a markedly smaller wing size, relative to the Common Kestrel, and a comparison of length and width illustrates the shorter, but more rounded wings of the Mauritius and Seychelles forms.

Figure 2. Wing-profiles of the Lesser, Common, Mauritius and Seychelles kestrels. Profiles are drawn from live adult females; (a) Lesser, (b) Common, (c) Mauritius, (d) Seychelles kestrel.

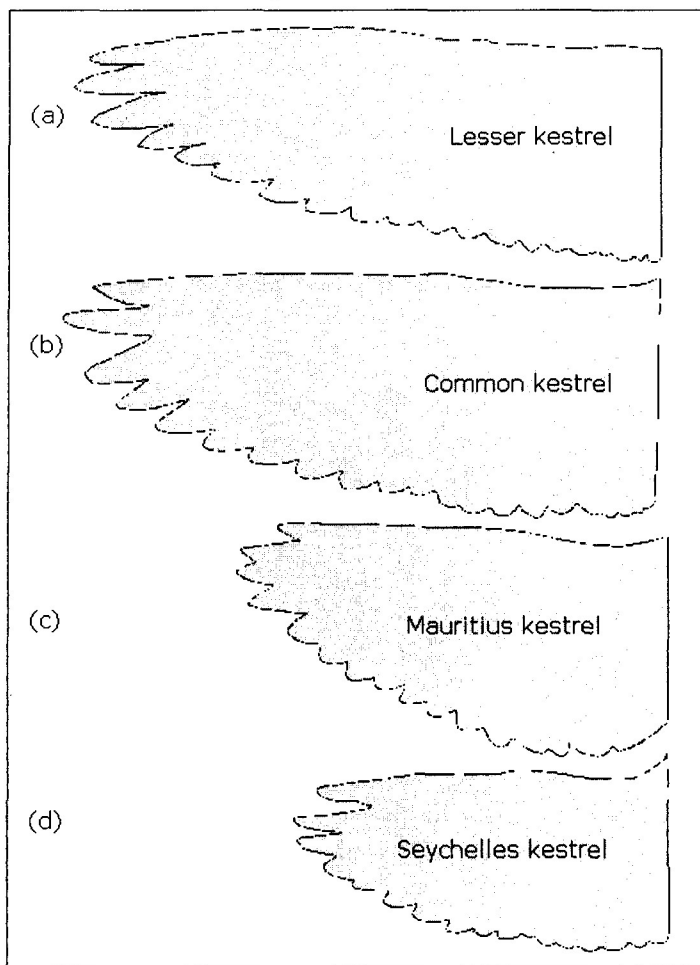
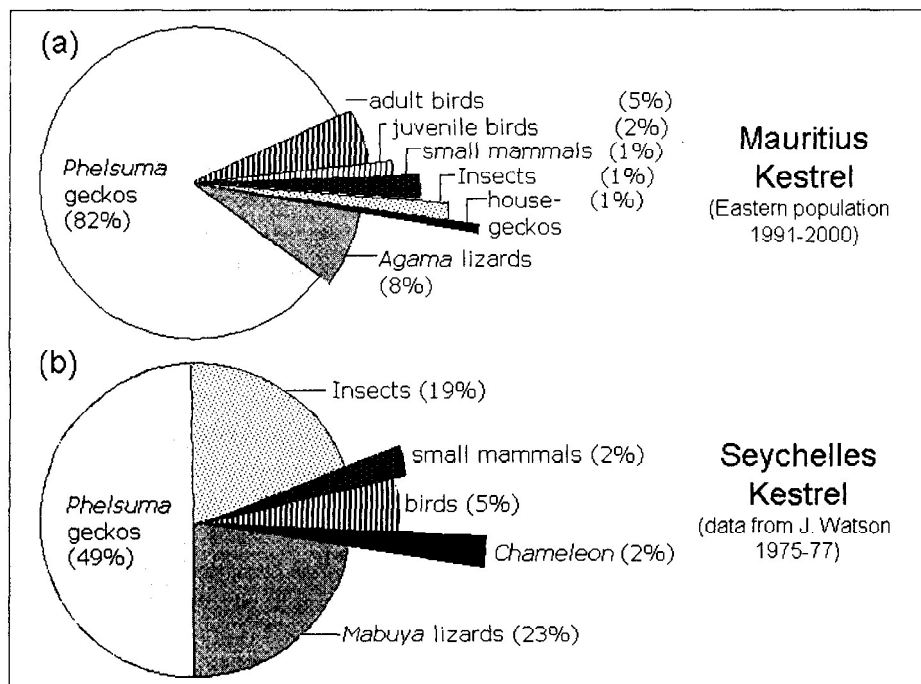


Figure 3 gives proportions of prey items caught by Mauritius and Seychelles kestrels, which were observed to be brought back to active nests between 1991-2001 and 1974-77 respectively. On Mauritius, *Phelsuma* geckos and *Agama* lizards make up 90% of all prey captures (82% and 8% respectively), whereas non-reptile prey comprises only 9%, including adult and juvenile birds (5%), insects (1-2%), and small mammals (1-2%). Adult and juvenile birds comprised several introduced species, including the Red-whiskered Bulbul *Pycnonotus jocosus*, Waxbill *Estrilda astrild*, Spice Finch *Lonchura punctulata*, Madagascar Fody *Foudia madagascariensis* and Barred Ground Dove *Geopelia striata*, as well as the endemic Grey White-eye *Zosterops borbonicus mauritanus*. The majority of mammal prey items were of the introduced House Shrew *Suncus murinus*, as well as the common black rat. Together, insect prey items formed a diverse assemblage, including native and introduced locusts, dragon-flies, cock-roaches, and praying mantis. A more complete breakdown of prey items taken by the Mauritius Kestrel is given by

Jones (1987). In comparison to Mauritius, the Seychelles Kestrel shows a lower proportion of *Phelsuma* prey items (49%), but a higher proportion of insects (19%). Endemic *Mabuya* lizards form a considerable portion of the Seychelles Kestrel diet, and surveys of their distribution indicate that this species is predominantly ground-dwelling (Watson 1981).

Figure 3. The proportion of prey items delivered to the nest for Indian Ocean kestrels; (a) Mauritius Kestrels between 1991-2001, (b) Seychelles Kestrels between 1974-77 (Watson 1981).



DISCUSSION

Correlates of evolutionary history & plumage pattern

The molecular results of Groombridge *et al.* (2002) are summarized in Figure 1. The phylogeny supports our hypothesis of a logical 'stepping-stone' model of kestrel radiation across the Indian Ocean, and is consistent with some differences in plumage. Some kestrels show strong colour dimorphism between the sexes, giving rise to a 'male-type' and 'female-type' pattern in kestrels (Cade 1982). In contrast, colour dimorphism is negligible in all three of the Indian Ocean kestrel species (Jones 1987). However, both sexes of the Seychelles Kestrel and dark morph Madagascar Kestrel closely resemble the 'male-type' plumage of typical kestrels, whereas those of the Mauritius Kestrel and light morph Madagascar Kestrel resemble the 'female-type' plumage. These different affinities are supported by the molecular phylogeny (Groombridge *et al.* 2002). The existence of two plumage morphs of the Madagascar Kestrel, a light morph and a dark morph (and a rarer, intermediate morph), invites an additional tentative comparison between them and the

Mauritius and Seychelles forms. The Mauritius Kestrel most closely resembles the light morph of the Madagascar Kestrel, and the Seychelles Kestrel the dark morph. The similarity between the two colour phases and the two island kestrel forms may be the consequence of chance characteristics imported from an ancestral Madagascar population. Although this hypothesis is difficult to test, the molecular phylogeny indicates some support for the ancestral role of the Madagascar Kestrel, a view supported by parsimony.

Factors affecting routes of radiation

The divergence time estimated from molecular data for the Mauritius Kestrel coincides with the geological history of Mauritius calculated from potassium-argon (K-Ar) dating (see Figure 1; Groombridge *et al.* 2002). Analysis of volcanic rocks on the island indicates that the major island-forming activity took place between 5.0-7.0 MYA (McDougall & Chamalaun 1969). The arrival of kestrels on Mauritius seems to have coincided with the end of the minor volcanic activity on the island, which ceased at around 2.0 MYA. Younger lavas have been found on Mauritius, but are attributed to low volume extrusions from small vents (McDougall & Chamalaun 1969), and appear not to have adversely affected the island's earlier colonisation.

The molecular history suggests that kestrels did not reach the Seychelles from Madagascar until around 0.3-1.0 MYA, despite the ancient origin of the Seychelles archipelago, estimated at 55-65 MYA (Norton & Sclater 1979). However, the numerous small islands en route, such as Aldabra and the Farquhar and Amirante Islands, could have aided kestrel dispersal. The precise timing may have been made possible by a fall in sea level, and the occurrence of such events is consistent with glacial cycles during the Pleistocene era (Berger 1984; Rohling *et al.* 1998). Braithwaite (1984) estimated that sea level changes of Pleistocene magnitude would have sufficiently exposed the submerged platforms in the western Indian Ocean to increase the total land area of the islands by 125,000 km². Support for such island-mediated dispersal is provided by the Aldabran Kestrel *F. newtoni aldabranus*, a subspecies of the Madagascar Kestrel (Benson 1967; Benson & Penny 1971), which may be a relict of recent dispersal during the Pleistocene or later.

Morphological change & ecological specialization

The Seychelles and Mauritius kestrels are the two species that most closely occupy closed habitat – all other typical kestrels occupy predominantly open habitats. In contrast to open habitat, where an absence of perches may ultimately have driven the hovering behaviour of typical kestrels, the Seychelles and Mauritius kestrels hunt mainly beneath the forest canopy. The shorter wings of both island species relative to the predominantly open-country-dwelling Common and Lesser kestrels, suggests a convergence towards an Accipitrine wing shape (Table 1; Watson 1981). The high proportion of *Phelsuma* geckos that make up the hunting prey-base of both Mauritius and Seychelles kestrels indicate a preference for small, agile lizards in the diet of both species. Field studies confirmed they exist in high densities on both islands (Jones 1987; Watson 1981). The *Phelsuma* geckos have undergone a wide radiation across many of the islands of the Indian Ocean, and

as a consequence many endemic forms have evolved that differ markedly in body size and appearance. Both Mauritius and the Seychelles archipelago are home to several endemic *Phelsuma*. On Mauritius, endemic species differ in their habitat preference; *P. gambeaui* and *P. ornata* are found exclusively in lowland forests, whereas *P. rosagularis* inhabits upland forests, and *P. cepedianae* is common throughout. On the Seychelles archipelago two endemic forms exist, *P. astovei* and *P. semicarinata*, and further endemic forms exist on Aldabra (*P. abbotti*) and the Amirante Islands (*P. astriata semicarinata*). The relative proportion of the exotic agamid lizard prey items (8%) on Mauritius and endemic *Mabuya* lizards (23%) on Seychelles indicates an ability by both kestrel species to take larger lizard prey. In particular, the large proportion of *Mabuya* prey items taken by Seychelles Kestrels is similar to the prevalence of insects caught, which forms a larger share of the prey base in comparison to that of the Mauritius Kestrel. This more insectivorous prey-base of the Seychelles Kestrel may be a consequence of the smaller size of this species relative to the Mauritius form.

Two morphological features of the Mauritius and Seychelles kestrels appear to maximise their hunting success for small lizards. To pursue and successfully snatch and extract these small, agile lizards from dense vegetation requires a high level of aerodynamic agility during the pursuit, and a lengthening of the feet to enable them to reach into the vegetation cover to grab their prey. Both the Mauritius and Seychelles kestrels possess short, rounded wings that are very different in profile to the Common Kestrel and the similarly-sized Lesser Kestrel (Table 1; Figure 2), and are similar to that of an accipiter. Broadly, we can hypothesize that the histories of island isolation of both these kestrel species (Figure 1) have witnessed a shift in hunting strategy from a generalist open country hunting strategy, typified by the Common and Lesser kestrels' longer, thinner wing-shape designed for hovering flight, to a 'surprise' hunting strategy, where shorter, more rounded wings can enable more rapid in-flight turns to pounce and snatch small, agile prey from shorter distances. A 'surprise' hunting strategy would seem to be the most efficient method for capturing *Phelsuma* geckos, whose escape response is to dart into cover or dense vegetation. In contrast to most open-country kestrels, whose prey is generally captured on the ground, both Seychelles and Mauritius kestrels are able to take prey throughout the full range of vertical vegetation, which illustrates the broader niche of these species. There is often a tendency for island species to exhibit broader ecological requirements in terms of food and feeding methods, relative to mainland taxa (Grant 1965).

Conserving phenotypic and evolutionary diversity

The Mauritius Kestrel and Seychelles Kestrel are the only two surviving endemic island species in the Indian Ocean. A third species, the Réunion Island Kestrel *F. duboisi* became extinct during the 1600s (Cheke 1987; Cowles 1987, 1994). The molecular phylogeny has identified the Mauritius Kestrel as the most phylogenetically distinct of the surviving island kestrel forms, which serves to underline its significance regarding the need to conserve evolutionary diversity. From a phenotypic perspective, the two surviving island species have been isolated on their respective islands for different periods of time, providing

an environment for evolutionary change driven by isolating mechanisms and selection for endemic prey biota. This isolation has fostered morphological differences in both species, and has produced novel hunting strategies in comparison to mainland kestrel forms, as a result of behavioural adaptations for hunting *Phelsuma* prey. These features, that have arisen from island evolutionary processes, identify the Seychelles and Mauritius kestrels as components worthy of conservation efforts for continued evolutionary change. The similar morphological and ecological adaptations shown by both endemic island kestrels, relative to their mainland counterparts, illustrates how the evolutionary trajectories of the Mauritius and Seychelles kestrels have converged towards a kestrel form that is suitably adapted to forest-dwelling, and which has become specialized for hunting lizards. At the same time however, both island kestrels have retained a degree of ecological flexibility regarding their diet (see Figure 3), a factor which has benefited the reintroduction programme for the Mauritius Kestrel (Jones *et al.* 1995), and enables the Seychelles Kestrel population to take advantage of altered landscapes across the Seychelles islands (Vesey-Fitzgerald 1940).

The future of the Mauritius Kestrel appears to be relatively secure, and surveys of the wild population will continue to monitor reproductive success. The historical and current status of the Seychelles Kestrel is uncertain; this island form was formerly described as rare (Gaymer *et al.* 1969), but the most recent estimate of total population size suggests around 420 breeding pairs (Watson 1991). No population bottleneck has been described for the Seychelles Kestrel, but this disparity between recent and historical population estimates over the last 50 years appears to suggest otherwise, that perhaps the Seychelles Kestrel has suffered a population bottleneck across a timeframe similar to that of the severe bottleneck experienced by the Mauritius Kestrel. Evidence to support this claim, that the Seychelles Kestrel may be equally compromised by the effects of a historical bottleneck, comes from a population genetic study that used microsatellite markers to quantify levels of genetic variation (Groombridge *et al.* 2000). This study revealed that the current Seychelles Kestrel population appears to be as genetically impoverished as the recovered population of the Mauritius Kestrel. Alongside the endangered status of the Mauritius Kestrel, the evolutionary distinctiveness of the Seychelles Kestrel, revealed by phylogenetic, ecological and morphological comparison, presents a worthy argument for ensuring that it too remains within the remit of conservation.

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Jim J. Groombridge
 Durrell Institute of Conservation &
 Ecology, Department of Anthropology,
 University of Kent, Canterbury, Kent
 CT2 7NS, UK
 Email: J.Groombridge@kent.ac.uk

Malcolm A. Nicoll
 School of Biological Sciences,
 University of Reading
 Reading, UK.

Carl G. Jones
 Durrell Wildlife Conservation Trust,
 Les Augres Manor, Trinity, Jersey
 JE3 5BP, UK.

Jeff Watson
 Scottish Natural Heritage, 9 Culduthel
 Road, Inverness IV2 4AG
 Scotland.