Responses of raptors to habitat fragmentation: from individual responses to population susceptibility

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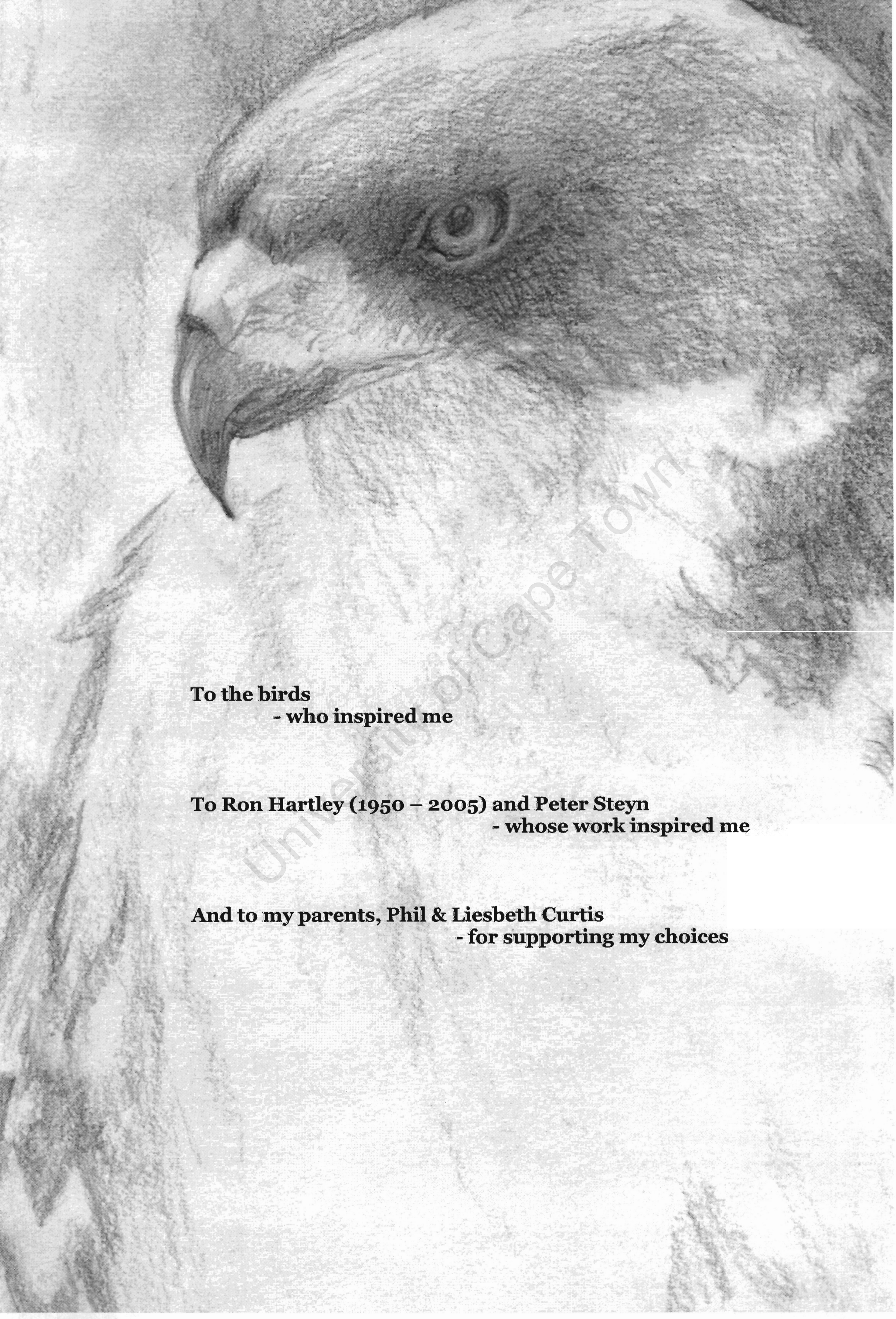
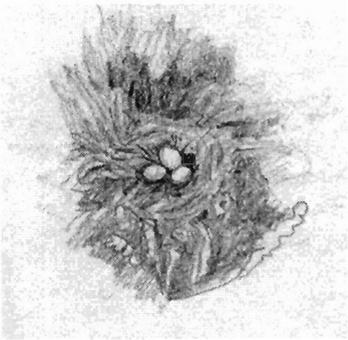


To the birds
- who inspired me

To Ron Hartley (1950 – 2005) and Peter Steyn
- whose work inspired me

And to my parents, Phil & Liesbeth Curtis
- for supporting my choices



"The library of life is burning, and we don't even know the titles of the books"

- Gro Harlem In: David Brackett 2004

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GENERAL SUMMARY

"... species loss from patches is only one way in which the biota changes, and the ability to persist in patches is no guarantee of long-term survival."

R. T. Corlett 2000

Habitat fragmentation has different effects on species and communities, depending on a suite of life-history and population traits: some species are more vulnerable to the effects of fragmentation than others. Contrasting responses suggest there are particular species' attributes that make an organism more or less susceptible to the effects of fragmentation. Much research has focused on identifying which of these traits are the most useful indicators of a species' fragmentation-linked extinction risk. For example, body size, rarity, ecological specialization, matrix use, range size and turnover rate have all been linked with species extinction risk. Few studies have, however, attempted to explore the traits that predispose raptors to vulnerability from fragmentation. In this study, I compare the responses of two near-sympatric raptors (the Black Harrier *Circus maurus* and the Black Sparrowhawk *Accipiter melanoleucus*) to habitat fragmentation. On a broader scale, I use a simple model of susceptibility to fragmentation effects, and a sample of hawks (*Accipiter* spp) and harriers (*Circus* spp) in the family Accipitridae, to predict which species attributes are most likely to produce a negative response to habitat fragmentation. I then compare these predictions with the current global threat status of each species to test whether the model can predict threat status with acceptable accuracy.

The Black Harrier is a globally *Vulnerable* species, near-endemic to South Africa, with its core breeding range centred on the Fynbos Biome of the

Western Cape. Lowland habitats within this region, especially Renosterveld have been severely fragmented and degraded by activities associated primarily with agriculture, and I hypothesise that the Black Harrier has lost a significant proportion of its preferred natural habitat as a result. To test this hypothesis, I examine i) the distribution of breeding pairs of harriers in relation to patches of varying size and quality, ii) the foraging range and habitat use of two provisioning males in a large lowland patch and iii) the productivity of harriers breeding in different habitat types.

The Black Sparrowhawk has responded positively to the creation of forest patches through the introduction and spread of alien trees. Also, previous work has demonstrated the benefits of habitat fragmentation for sparrowhawks, where the fragmentation of large forest tracts creates opportunities for local increases in breeding densities, through the provision of more forest edges (Malan & Robinson 2001). I hypothesise that, in contrast to Black Harriers, Black Sparrowhawks can persist in small habitat patches, as they only use the patch for breeding, while they forage in the adjacent, open matrix. Thus, sparrowhawks will be less selective with respect to patch size and will select patches closer to suburbia than to the indigenous Fynbos vegetation, as the former provide superior foraging opportunities. To test these ideas, I examine the distribution of Black Sparrowhawks within and across forest patches on the Cape Peninsula, South Africa and attempt to identify which factors are most likely to influence their breeding success.

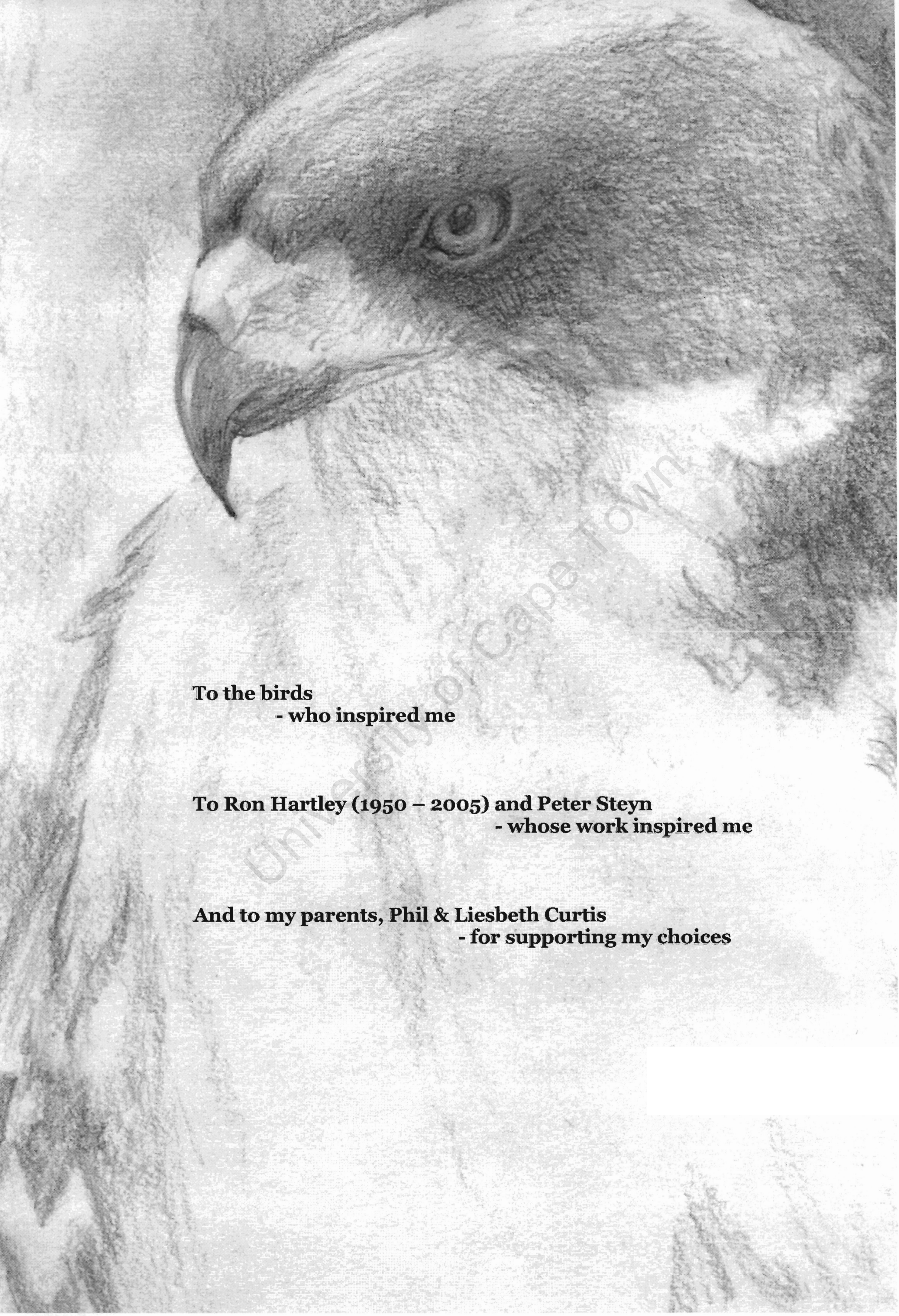
Key findings:

- Black Harriers are highly sensitive to fragmentation and are unable to persist in small, isolated patches.
- Black Harriers forage within patches of natural habitat and avoid the agricultural matrix, reinforcing the premise that this species is highly dependent on natural habitat patches.
- Black Sparrowhawks select nest sites closer to modified than to natural habitats.
- Black Sparrowhawks select strongly for large patches over smaller ones. However, in contrast to harriers, they can breed in small patches, suggesting they are tolerant of fairly high levels of fragmentation.
- There are performance-linked benefits for sparrowhawks that breed in large patches, denoted by higher breeding success. This is probably because 1) larger patches provide more buffering from severe winter weather (as birds can, and do, breed further from the edge in large patches) and 2) larger patches provide more opportunity for pairs to build multiple nests, reducing their chances of having all their nest sites usurped by Egyptian Geese *Alopochen aegyptiaca*.
- Black Harriers and Black Sparrowhawks respond differently to fragmentation, primarily because of the different ways in which they use habitat patches: harriers rely patches for both breeding and foraging, while sparrowhawks rely on patches for breeding only.
- In the Fragmention Susceptibility Model, a single parameter, such as body mass, is not a useful indicator of a species' extinction risk as a result of fragmentation.

- By using an index combining life-history traits (habitat and dietary specialisation) and an index of range, the Fragmention Susceptibility Model was able to make fairly accurate predictions of threat status for the majority of globally threatened taxa, and further identified a handful of species that may warrant conservation consideration (species not currently listed in the International Red Data Book).

Conclusions

Species dependent on remnant patches for all aspects of their existence may be those most prone to local extinction, whereas species dependent on the patch for only a limited suite of their requirements may be able to persist, or even thrive - in much smaller patches. Even fairly crude biological data can assist in raising warning flags about species susceptible to fragmentation. If scientists are to achieve greater accuracy in predicting the relative responses of species to habitat fragmentation, it is of vital importance not only to recognise that a species indeed uses such patches, but also to understand those elements of the species' life history for which it requires the patch. At least in the case of raptors, it appears that use of the popular surrogate of body size to predict susceptibility to habitat fragmentation is unreliable, whereas a combination of degrees of habitat and dietary specialisation and range size provides more robust threat predictions.



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GENERAL INTRODUCTION

> *"Human activity is the primary agent for habitat destruction on earth… The effects of natural agents of biological control, physical and biological, are now dwarfed by our activities."*
>
> C. Dytham 2000

BACKGROUND & RATIONALE

The development and spread of agriculture has resulted in substantial landscape modification on every continent except Antarctica (Saunders *et al.* 1991). Land clearance and consequent degradation, transformation and fragmentation of natural systems continue to accelerate in many parts of the world (Saunders et al. 1991). South Africa is no exception (Low & Rebelo 1996, Biggs & Scholes 2002) and, increasingly, natural landscapes are making way for housing development, agriculture and forestry. The result is a series of isolated patches or 'remnants' of natural habitat. These vary in size, quality and conservation potential, and are dispersed within an otherwise transformed matrix.

The impacts of such habitat loss differ substantially between species and communities. For example, negative effects have been measured for insects (Didham 1996), fish (Fagan *et al.* 2005), primates (Estrada *et al.* 2002, Chiarcello & de Melo 2001) and birds (Diamond *et al.* 1987, Kattan *et al.* 1994, Herket 1994) (reviewed by Turner 1996). In contrast, other studies have found weak responses to habitat fragmentation, in for example, plant communities (Kemper *et al.* 1999), birds (Schmiegelow *et al.* 1997) and other small vertebrates (McCoy & Mushinsky 1994). These contrasting responses suggest that there are particular species' attributes that make an organism more or less susceptible to the effects of fragmentation of their preferred habitat.

Among birds, sensitivity to fragmentation has been linked to body size (with contrasting results - Bennett & Owens 2002, Gaston & Blackburn 1995) and habitat specialisation (Bennett & Owens 2002). In general, ecological generalists are predicted to respond less to fragmentation, while those with specialised requirements are likely to have a limited capacity to adapt to habitat changes.

Although many raptor population decreases and local extinctions can be attributed to habitat fragmentation (BirdLife International 2004), there is also significant variation in the way in which species respond and adapt to man-altered environments. Even within families, as in the case of the Accipitridae, some taxa are affected negatively by fragmentation (e.g. Madagascan Serpent-Eagle *Eutriorchis astur* - Langrand & Meyburg 1984), while others, at least up to a point, may benefit or be relatively unaffected by it (e.g. Northern Goshawk *Accipiter gentilis* - Woodbridge & Dietrich 1994).

In this study, I compare the responses of two near-sympatric species (the Black Harrier *Circus maurus* and the Black Sparrowhawk) to habitat fragmentation. On a broader scale, I use a simple model of susceptibility to fragmentation effects, and a sample of hawks (*Accipiter* spp) and harriers (*Circus* spp) in the family Accipitridae, to predict which attributes predispose species to a negative response to habitat fragmentation.

1) INDIVIDUAL RESPONSES TO FRAGMENTATION: COMPARISONS BETWEEN A HARRIER AND A HAWK

Two types of fragmented habitats occur in the Western Cape, South Africa: one a shrubland habitat, the other, a 'forest' habitat. Historically, the Cape lowlands were covered in low, shrubby vegetation (primarily Fynbos, Strandveld and Renosterveld); much of this habitat has now been lost to agriculture, primarily crop and stock farming (Low & Rebelo 1996, Kemper *et al.* 1999). These anthropogenic habitats are more seasonally variable, and structurally shorter and simpler than the habitats they have replaced, resulting in decreased physical habitat complexity. The Black Harrier is dependent on Fynbos habitats, but the extent to which fragmentation has affected the species is unknown. By contrast, on the Cape Peninsula, shrubby fynbos vegetation has, in places, been replaced by plantations of alien trees, mostly pines (*Pinus* spp.) and eucalypts (*Eucalyptus* spp.) (Cowling *et al.* 1996). These forest patches mimic 'natural' forest habitats, in terms of their patchiness and their suitability for tree-nesting raptors, and so provide an ideal opportunity to study the responses of forest-dependent raptors (such as the Black Sparrowhawk) to a fragmented landscape.

Superficially, it appears that the responses of these two raptor species to such significant habitat changes have been very different. On the one hand, the Black Harrier, a species apparently closely tied to 'pristine' Fynbos habitats (Van der Merwe 1981, Steyn 1982), may have been negatively impacted by extensive loss of shrubby vegetation (Curtis *et al.* 2004). On the other hand, the Black Sparrowhawk, a species entirely dependent on forest habitats (Steyn 1982, Allan & Tarboton 1985), but which responds well to fragmentation (Malan & Robinson 2001), has almost certainly expanded its range as a direct result of increased availability of alien forest patches (Allan & Tarboton 1985).

Habitat fragmentation and Black Harriers

The Black Harrier is the world's most range-restricted continental harrier species (Simmons 2000; Fig. 2). It is near-endemic as a breeding species to the Fynbos biome of south-western South Africa, with peripheral populations in the southern reaches of the Karoo and Grassland biomes of the Free State and KwaZulu-Natal (Van der Merwe 1981, Simmons 1997). Opinions on the historical and present conservation status of the Black Harrier differ (van der Merwe 1981). It was included in the 'supplementary list' (a list which includes species that may qualify for inclusion in a revised Red Data Book (RDB)) in the first South African RDB (Siegfried *et al*. 1976). In the second RDB (Brooke 1984) it was classified as 'neither rare nor vulnerable', but worthy of monitoring. In the third and most recent RDB (Barnes 2000), it is classified as *Vulnerable.* It is also classified globally as *Vulnerable* (Birdlife International 2004), because of its small population size of 1000-2000 birds (Siegfried 1992, van der Merwe 1981).

The Black Harrier may have lost as much as 50% of its natural habitat to the spread of cereal agriculture and viticulture, alien vegetation and urbanisation. For example, in the fertile, lowlands of the western and south-western plains of South Africa, more than 90% of the indigenous Renosterveld vegetation has been transformed by agriculture in the last 100-150 years (Kemper *et al.* 1999, Low & Rebelo 1996, Figs. 1a & 1b). Because there are no reliable data on pre-transformation harrier populations, and the habitat affinities of the species are poorly understood, the true effects of anthropogenic landscape change remain unclear (Curtis *et al.* 2004). There are a few documented cases of local extinctions of Black Harriers (e.g. on the Cape Flats) as a direct result of habitat change (Starke & Sclater 1903, Boshoff *et al.* 1983). However, there are also some areas (particularly on the west coast) where breeding density is unusually high (Curtis *et al.* 2004). This may be because of the semi-colonial nature of some harriers (Simmons 2000), or it may reflect a spatial 'retreat' of local populations.

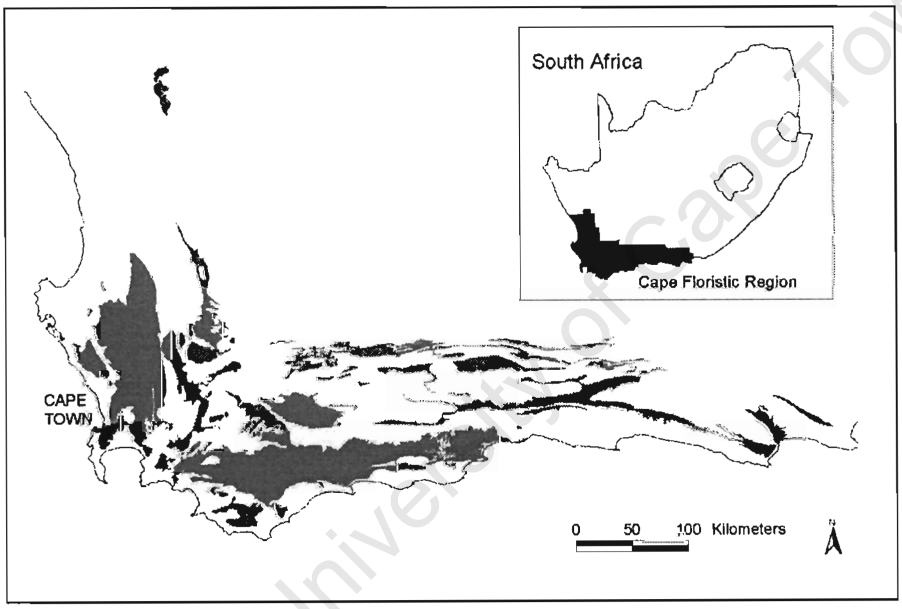

Figure 1a Map showing the original extent of Renosterveld in the Western Cape, South Africa

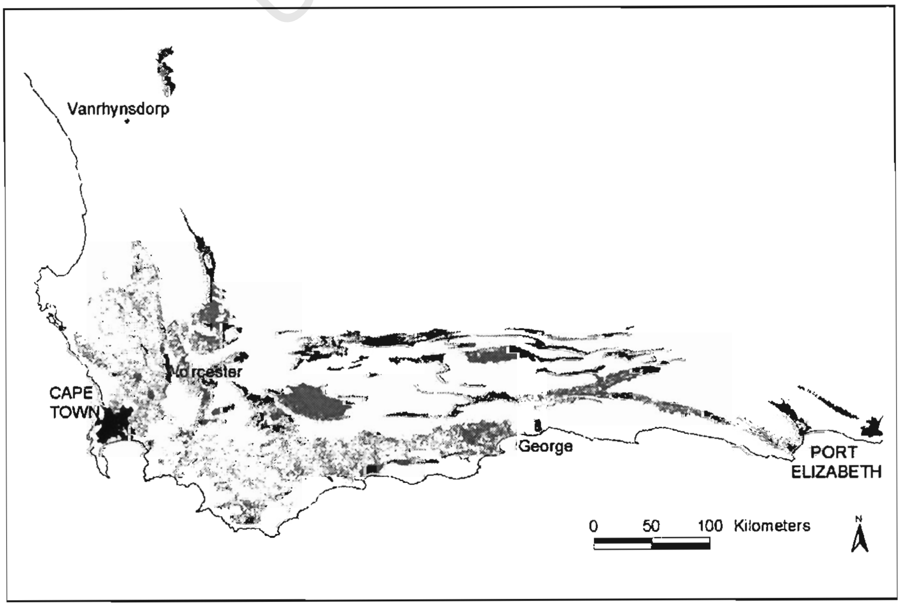

Figure 1b Map showing the current extent of Renosterveld in the Western Cape, South Africa

*Maps obtained with kind permission from the South African National Biodiversity Institute.

Patches and Black Sparrowhawks

Like the Black Harrier, the Black Sparrowhawk has been both included in and excluded from the various South African RDBs. (Siegfried *et al.* 1976, Barnes 2000). In contrast to the Black Harrier, habitat change, in the form of introduced alien trees, has facilitated a range expansion by this species (Hockey 2003, Allan & Tarboton 1985, Tarboton & Allan 1984, Tarboton *et al.* 1978), to the point where it is considered 'common, and of little conservation concern' (Barnes 2000). Also, previous work has demonstrated the benefits of habitat fragmentation for sparrowhawks, where the fragmentation of large forest tracts creates opportunities for local increases in breeding densities, through the provision of more forest edges (Malan & Robinson 2001).

On the Peninsula, Pine trees (in particular *Pinus pinaster* and *P. radiata)*, among others, are cultivated and harvested for commercial use. As a result, large, continuous tracts of plantations of pines cover a significant proportion of the Peninsula (Cowling *et al.* 1996). Because of their invasive nature and the suitability of the local climate, many of these species have spread into other areas on the Peninsula, creating a mosaic of small, 'naturalised' forest patches. The Black Sparrowhawk was almost unknown on the Cape Peninsula until the 1990s (Oettlé 1994, Hockey *et al.* 1989, Smith 1830), but, as elsewhere, has exploited man-made opportunities, created by the introduction of alien trees. Currently almost 30 breeding pairs have been located on the Peninsula (Curtis *et al.* 2005).

Although the Cape Peninsula's resident Black Sparrowhawk population is not a 'natural' one, the dispersion of patches of alien trees, which effectively mimic a fragmented forest habitat, offer a unique opportunity to study the responses of this forest hawk, to fragmented habitats.

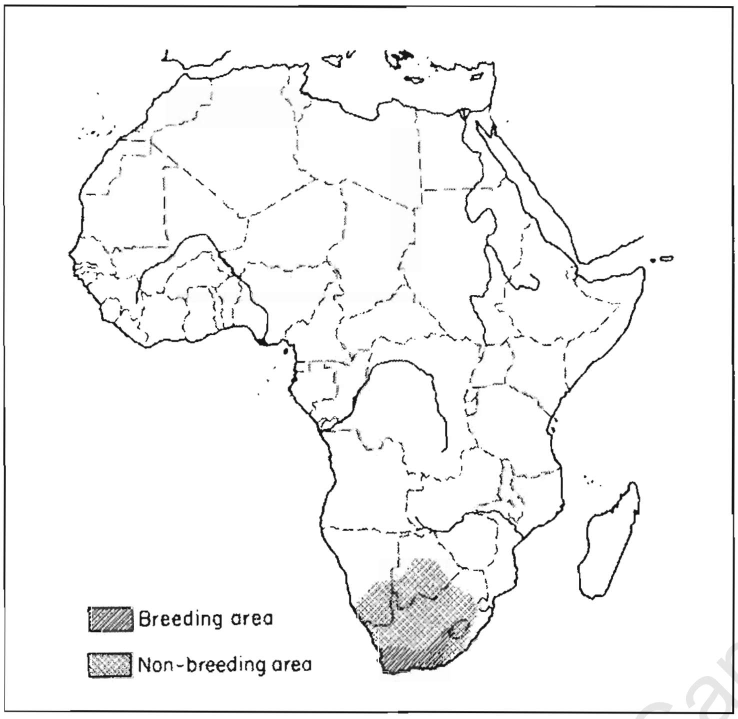

Figure 2 Map showing the range of the Black Harrier (Brown *et al.* 1982)

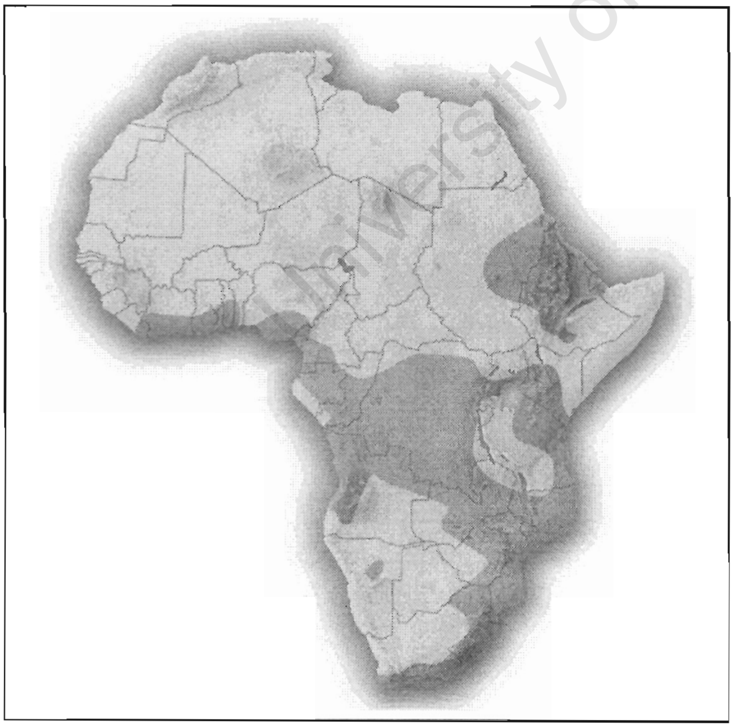

Figure 3 Map showing the range of the Black Sparrowhawk (Curtis & Koeslag 2004)

Life-history traits of Black Harriers and Black Sparrowhawks

To determine how the two species might differ in their responses to fragmented habitats, it is necessary to compare basic life-history trait differences between them (Table 1). Black Harriers nest on the ground and lay larger clutches than tree-nesting Black Sparrowhawks (Steyn 1982, Curtis *et al.* 2005, Table 1). Black Harriers are smaller and less sexually dimorphic (although females are larger in both species) (O. Curtis unpubl. data, Table 1). Black Harriers have a shorter breeding season than Black Sparrowhawks, which have an unusually long breeding season in the Western Cape (Curtis *et al.* 2005, Curtis *et al.* 2004, Curtis & Koeslag 2004, Table 1).

Harriers hunt a wider variety of prey, while sparrowhawks are bird-hunting specialists (Curtis *et al.* 2005, Malan & Robinson 1999, Kemp & Kemp 1998, Table 1), thus the hunting methods of the two birds differ substantially (Table 1), The Black Harrier has a much more restricted range (Simmons 1997, Kemp & Kemp 1998, Fig. 2) than the Black Sparrowhawk (Allan 1997, Kemp & Kemp 1998, Fig. 3) (Table 1).

Black Sparrowhawks breed in forested habitats, but hunt in adjacent, open country (Malan & Robinson 1999, Ferguson-Lees & Christie 2001). Detailed information on where Black Harriers hunt in relation to where they breed is scant, but it is generally accepted that they hunt and breed in similarly structured habitats (Curtis *et al.* 2004).

Table 1 Summary table of some basic life-history traits of Black Sparrowhawks and Black Harriers

Attribute	**Black Sparrowhawk**	**Black Harrier**
Clutch size	2–3	2-5
Body mass	450–1040g	350–540g
Breeding season	March–October	June–October
Diet	Birds (doves, pigeons, gamebirds)	Small mammals, small birds & lizards
Hunting method	Sit and wait and ambush	Search (long distance quartering) and pounce
Distribution and habitat	Forested habitats across sub-Saharan Africa	Endemic to South Africa (particularly the Fynbos Biome); small population in Namibia
Nest and Nesting habitat	Large stick nest in tree	Bowl-shaped nest on ground.
Hunting habitat	Open suburban/natural areas	Open Fynbos, Renosterveld, grassland and croplands

Objectives and hypotheses

I examine the distributional and performance-linked consequences of habitat fragmentation for two raptor species, and how these species use natural and modified habitats for both breeding and foraging. Specifically, I test the following hypotheses:

- *Use of the patch.* Black Harriers obtain the majority of their resource requirements from within remnant habitat patches, while Black Sparrowhawks are able to use the matrix between forest patches for hunting and are thus not entirely reliant on patches.

- *Importance of patch size.* Harriers use only the larger, resource-rich patches for breeding, while sparrowhawks breed in a variety of patch sizes.
- *Breeding dispersion across patches.* Harrier pairs are clumped in the larger, resource-rich patches only, while sparrowhawk pairs are dispersed relatively evenly across an array of patches.
- *Breeding dispersion within patches*. Harriers place their nests more centrally in patches (to gain ready access to resources within the patch), while sparrowhawks place their nests closer to the edges than to the middle of the patch (to gain ready access to resources outside the patch).
- *Fragmentation and breeding success*. All other things being equal, breeding success by harriers is more directly affected by patch attributes and location within and across patches than breeding success by sparrowhawks.

2) SPECIES' ATTRIBUTES AND FRAGMENTATION: CONSEQUENCES FOR SPECIES' VULNERABILITY

After making comparisons between the two species, I broaden my approach and attempt to make predications about raptor responses to fragmentation and the consequences thereof. I generate a Fragmentation Susceptibility Model, designed to predict a species' response to habitat fragmentation, and then test the viability of the model. In order to do this I:

- Assign an index of susceptibility to each species (for which there is sufficient data) in the genera *Accipiter* and *Circus*, using simple indices of range and ecological specialization.
- Enter the data into the model which predicts the susceptibility of each species to fragmentation-linked extinction risk, ranked as either high-, medium- or low risk.
- Test the predictions of the model against the real/current threat status of the birds (using published threat categories - Birdlife International 2004).

GENERAL METHODS & STUDY AREAS

Black Harriers

Black Harriers were studied in two main areas, the Swartland and the Overberg regions of the Western Cape, from 2000–2004. Rigorous surveys were carried out, across a suite of habitat patches of varying quality and size, and in different vegetation types. Data (i.e. breeding parameters, nest site selection and diet) were collected from 131 breeding attempts and 70 nest sites. A radio-telemetry study was conducted in 2004 to determine the spatial foraging patterns of adult male harriers when provisioning females and young at nests.

The West Coast and Swartland area (Fig. 4) extends along the south-west coast of the Western Cape Province, from the city and suburbs of Cape Town (33°56'S; 18°25'E) in the south-west to the rural towns of Velddrif, Piketberg and Paarl in the north-west, north-east and south-east respectively (Fig. 4). Vegetation varies from Dune Thicket on the coast, to Sand Plain

Fynbos and West Coast Renosterveld in the lowlands, and Mountain Fynbos inland and at higher altitudes (Low & Rebelo 1996). Altitude ranges from sea level to about 900 m asl, and the climate is warm temperate, with a mean annual rainfall of 430 mm, falling mostly in winter, and mean minimum and maximum annual temperatures of about 12°C and 24°C (South African Weather Service). Cereal agriculture and viticulture are the main forms of land use. Large stretches of the coastal strip are contained in private and state-owned conservation areas. In the inland-lowlands, more than 95% of the natural environment has been transformed by agriculture, leaving only small, isolated patches of natural vegetation along drainage lines and in higher-lying areas, while coastal and montane areas remain fairly 'intact', being highly unsuitable for agriculture (Kemper *et al.* 2000).

The Overberg area extends along the south coast of the Western Cape Province, from approximately Caledon (34°13'S; 19°21'E) in the west to Albertinia (34°13'S; 21°33'E) in the east, and south to the Agulhas Plain (Fig. 4). However, my study area did not include the areas east of Swellendam (Fig. 4). Vegetation of the lower-lying areas comprises mainly East Coast Dune Thicket, Limestone Fynbos and South Coast Renosterveld; higher altitudes are dominated by Mountain Fynbos (Low & Rebelo 1996). About 90% of the lower-lying areas have been transformed into tracts of cereal agriculture and pastures (Kemper *et al.* 2000, Low & Rebelo 1996), while some extensive coastal and montane areas remain largely intact. Rainfall patterns vary from west to east, with winter rainfall in the west and a bimodal spring-autumn rainfall regime in the east (Kemper *et al.* 2000, Low and Rebelo 1996). Average rainfall ranges from 350 – 600 mm per annum

(Kemper *et al.* 2000), with mean minimum and maximum annual temperatures of about 12°C and 24°C (SAWS).

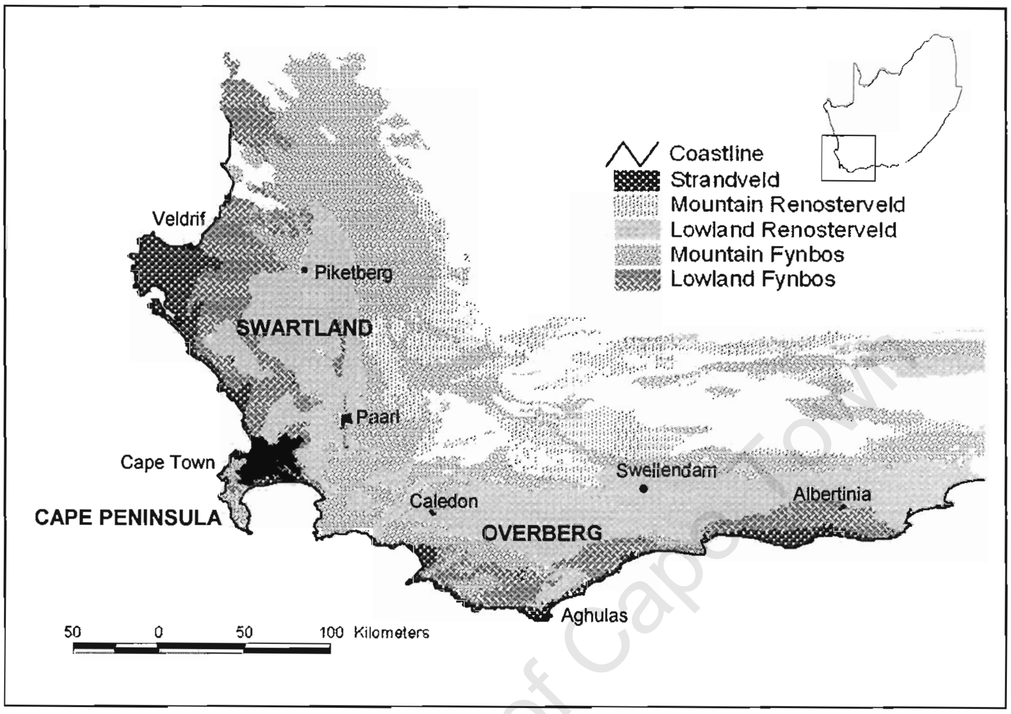

Figure 4 Map showing the general study areas for the Black Sparrowhawk (Cape Peninsula) and the Black Harrier (Overberg and Swartland), Western Cape, South Africa.

Black Sparrowhawks

The breeding biology of the Black Sparrowhawk was studied in an area of *ca* 70 km^2 along the eastern slopes of the Table Mountain range, Cape Peninsula (34°00'S 18°26'E), from 2000 - 2004. Data (breeding parameters, nest site selection and diet) were collected from 72 breeding attempts and 25 pairs (at a total of 38 nest sites).

The study area contains a matrix of habitats, including heathland (Fynbos), urban gardens, and exotic Pine (*Pinus* spp) and Eucalyptus (*Eucalyptus* spp.)) plantations. Altitude ranges from about sea level to 300 m a.s.l., and the climate is temperate, with locally variable winter rainfall (Cowling *et al.* 1996). Mean annual rainfall is about 1250 mm, with average minimum and maximum temperatures of 12°C and 21°C respectively (SAWS).

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CHAPTER 1

Black Harrier *Circus maurus* distribution and productivity in relation to habitat type and fragmentation in the Western Cape, South Africa

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Abstract

The Black Harrier is an endemic, globally *Vulnerable* species with its core breeding range centered on the Fynbos Biome of the Western Cape, South Africa. Lowland habitats within this region, especially Renosterveld, a fertile vegetation type characterised by the shrub *Dicerothamnus rhinocerotis*, have been severely fragmented and degraded by activities associated primarily with agriculture. I hypothesise that the Black Harrier has lost a significant proportion of its preferred natural habitat due to this degradation. In order to test this hypothesis, I examine i) the dispersion of breeding pairs of harriers in relation to patches of varying size and quality, ii) the foraging range and habitat use of two provisioning males in a large lowland renosterveld patch and iii) the productivity of harriers breeding in different habitat types. I surveyed 79 lowland Renosterveld patches of varying size and quality in the Swartland and Overberg plains of south-western South Africa. No breeding harriers were found in 36 patches in the lowlands of the Swartland, and only seven (16%) of 43 surveyed patches in the Overberg contained breeding pairs of harriers. Harriers selected large patches (minimum patch size ±100 ha) for breeding: these tended to be the more ecologically intact ones. Within the range of patch sizes used by breeding Black Harriers, there was no evidence that patch size influenced breeding success, however, on a larger scale, breeding success was significantly higher in coastal habitats than in montane and lowland areas. Two radio-tracked provisioning males foraged 2.3-2.9 km from their nests. Although these foraging radii included substantial amounts of transformed habitat, the birds foraged almost exclusively in natural habitats, indicating a strong dependence on untransformed habitats. In terms of these results, out of almost 17 000 patches remaining in the Overberg, only ca 2.6% are of sufficient size to support a breeding pair of harriers; in addition, many of the smaller patches (< 100ha) are likely to have a low degree of connectivity and are therefore unsuitable for harriers. Extrapolations suggest that before land transformation, the lowlands of the Overberg region alone may have supported about 390-1570 pairs of Black Harriers, of which perhaps no more than 60 pairs (15%) remain in the region. I conclude that Black Harriers have been severely impacted by habitat fragmentation and that historically the species was dependent on, and probably abundant in, lowland habitats. Conservation of the Black Harrier, with a world population currently estimated at 500–1000 pairs, depends on the preservation of large, ecologically intact patches of natural Fynbos vegetation.

Introduction

The development and spread of agriculture has resulted in substantial landscape modification on every continent except Antarctica, and this transformation of natural systems continues to accelerate in many parts of the world (Saunders *et al.* 1991). One consequence of this is the formation of a series of isolated patches, or 'remnants' of natural habitat. These vary in size, quality and conservation potential, and are dispersed within an otherwise transformed matrix. Responses to habitat fragmentation vary between taxa and species (Corlett 2000), but the process of fragmentation is generally corrosive and destructive, resulting in a decrease in diversity and abundance at both the species and the community levels (Cameron 1999, Sekercioglu 2002*a*, b). Among raptors, some species respond positively to fragmentation processes, e.g. Black Sparrowhawk *Accipiter melanoleucus* (Malan & Robinson 2001, Chapter 2) and Great Horned Owl *Bubo virginianus* (Johnson 1993 in Woodbridge & Detrich 1994), while others are severely impacted by habitat loss and degradation (e.g. Madagascar Serpent-Eagle *Eutriorchis astur*, Red Goshawk *Erythrotriorchis radiatus* and Wallace's Hawk-Eagle *Spizaetus nanus* (BirdLife International 2004)).

Even among the harriers (*Circus* spp.), the effects of habitat fragmentation vary between species and the relative impacts depend primarily on the nature of the habitats that replace the original habitat. The degree of impact also depends on whether the species is able to utilise the 'matrix' created by fragmentation or whether it is dependent solely on the remaining natural habitat. For example, Montagu's Harrier *C. pygargus* (Arroyo *et al.* 2002) and Cinereous Harrier *C. cinereous* (Figueroa & Corales 1999) breed and forage in open, scrub habitat, but can adapt to, or even exploit, 'new' habitats created by croplands.

The Black Harrier *Circus maurus* is a ground-nesting raptor, endemic to South Africa and Namibia (Simmons 1997). It is listed as *Vulnerable* both globally (BirdLife International 2004) and in South Africa (Barnes 2000), with a world population estimated at 500-1000 pairs (van der Merwe 1985, Siegfried 1992). Its core breeding range is centred on the Cape Floristic Region (CFR) of the Western Cape, South Africa (Simmons 1997). Lowland- and coastal-breeding birds feed primarily on rodents, and to a lesser extent on small birds, reptiles and insects (Simmons *et al.* 2005, O Curtis unpubl. data). Montane breeders divide their diet more evenly between rodents and birds (Simmons *et al.* 2005). The CFR has been heavily impacted by agriculture and to a lesser extent, by development and by the spread of alien vegetation (Kemper *et al.* 2000, Low & Rebelo 1996). For example, in the lowlands of the CFR, less than 10% of the indigenous vegetation type 'Renosterveld', characterised by the shrub Renosterbos *Dicerothamnus rhinocerotis*, remains throughout the region (Kemper *et al.* 2000, Low & Rebelo 1996). Negative effects of this habitat loss and fragmentation on the Black Harrier have been suggested (Hockey *et al.* 1989), but there is conflicting evidence as to whether numbers have decreased, increased, or remained stable in recent decades (van der Merwe 1981, Curtis *et al.* 2004). There are, however, a few documented cases of local extinctions of Black Harriers (e.g. on the Cape Flats) as a direct result of habitat change (Starke & Sclater 1903, Van der Merwe 1981, Boshoff *et al.* 1983).

Unlike some of its northern congeners (e.g. Montagu's Harrier – Arroyo *et al.* 2002, Corbacho *et al.* 1997), Black Harriers do not habitually breed in croplands, favouring more 'pristine' habitats (Steyn 1982, Curtis *et al.* 2004). It is possible that the species has lost as much as 50% of its preferred natural habitat in the Western Cape to ongoing fragmentation processes (Curtis *et al.* 2004). To test the hypothesis that habitat fragmentation has negatively affected Black Harriers, I examine the breeding dispersion and breeding performance of harriers in relation to various habitats and habitat patches, with the following predictions: i) harriers are associated with 'pristine' habitats for both breeding and foraging; as a result, habitat fragmentation has negatively impacted their breeding population. Thus they will favour larger habitat patches over small ones, and patches which are in close proximity to other patches (i.e. areas with a high degree of connectivity); ii) the patches used will be in relatively 'pristine' condition; iii) harriers will place their nests close to the centre of habitat patches in order to maximize foraging opportunities in natural vegetation around the nest; and iv) birds occupying 'superior' habitats will display fitness-linked benefits by having greater breeding success than birds breeding in degraded habitats. There may, however, be overriding factors (e.g. weather, predation, food availability) that influence nest site selection and the performance-linked consequences thereof (Nielsen & Drachmann 2003, McClaren *et al.* 2002, Redpath *et al*. 2002, Selås 1997, Kruger 2002). Thus, the final prediction tested is that v) harrier breeding success and/or breeding frequency will be affected by either the amount of rainfall, or the timing of rain in relation to the breeding season, because of the role that rainfall patterns play in influencing the abundance of the birds' prey, as has been shown for Montagu's Harrier (Garcia & Arroyo 2001).

Study areas

The study was conducted in two regions of the Western Cape Province, South Africa: the west coast, including the Swartland, and the south coast (Overberg) (Fig. 1).

The West Coast and Swartland area extends along the south-west coast of the Western Cape Province, from the city and suburbs of Cape Town (33°56'S; 18°25'E) in the south-west to the rural towns of Velddrif, Piketberg and Paarl in the north-west, north-east and south-east respectively (Fig. 1). Vegetation varies from Dune Thicket on the coast, to Sand Plain Fynbos and West Coast Renosterveld in the lowlands, and Mountain Fynbos inland and at higher altitudes (Low and Rebelo 1996). Altitude ranges from sea level to about 900 m asl, and the climate is warm temperate, with a mean annual rainfall of 430 mm, falling mostly in winter, and mean minimum and maximum annual temperatures of about 12°C and 24°C (South African Weather Service (SAWS)). Cereal agriculture and viticulture are the main forms of land-use. Large stretches of the coastal strip are contained in private and state-owned conservation areas. Inland, over 90% of the natural environment has been transformed by agriculture, leaving only small, isolated patches of natural vegetation along drainage lines and in higher-lying areas.

The Overberg extends along the south coast of the Western Cape Province, from approximately Caledon (34°15'S; 19°20'E) in the west to Albertinia in the east (34°13'S; 21°33'E), and south to the Agulhas Plain (Fig. 1). However, my study area did not include the areas east of Swellendam (34°03'S; 19°25'E; Fig. 1). Vegetation of the lower-lying areas comprises mainly East Coast Dune Thicket, Limestone Fynbos and South Coast Renosterveld; higher altitudes are dominated by Mountain Fynbos (Low and Rebelo 1996). About 90% of the lower-lying areas have been transformed into tracts of cereal agriculture and pastures (Kemper *et al.* 2000), while some extensive coastal and montane areas remain largely intact. Rainfall patterns vary from west to east, with winter rainfall in the west and a bimodal spring-autumn rainfall regime in the east (Kemper *et al.* 2000, Low and Rebelo 1996). Average rainfall ranges from 350 – 600 mm per annum (Kemper *et* *al.* 2000), with mean minimum and maximum annual temperatures of about 12°C and 24°C (SAWS).

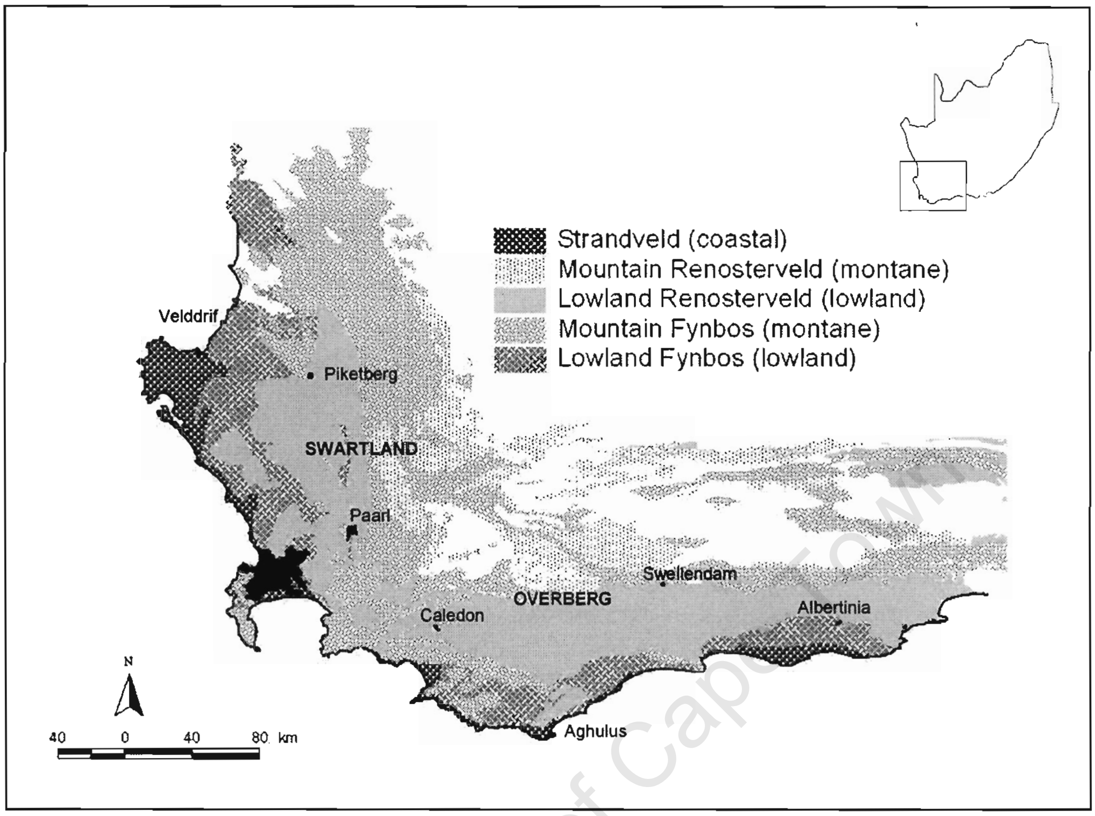

Figure 1 Map showing study areas for Black Harriers in the Swartland and Overberg , Western Cape, South Africa.

Methods

Harrier dispersion across and within lowland habitat patches

In 2003 and 2004, I conducted a survey to record the presence or absence of breeding Black Harriers in the lowlands of the Swartland and the Overberg. I used the South African National Biodiversity Institute's (SANBI) GIS database of lowland natural habitat patches (comprising a sub-sample of about 200 patches, out of a total of almost 17000 remnants) in the Overberg and Swartland combined) to select, on a random basis (using Microsoft Excel's random selection) a sub-sample of 36 and 43 patches of varying size and quality in the Swartland and Overberg respectively. Each lowland patch was surveyed for a minimum of three hours, from an elevated point inside the fragment. Where a pair of harriers was observed, the area was further monitored until the presence or absence of breeding activity was confirmed.

Information extracted from the SANBI database was used to calculate patch sizes, using Arcview GIS 3.3 (2002): data were projected in Transverse Mercator, WGS 84, Central Meridian 19. The available sample of lowland habitat patches was subjectively divided into three size categories - small (<100ha), medium (100–500ha) and large (>500-6100ha), based on the distribution of patch sizes - and the proportion of patches containing breeding harriers was calculated for each category. Each patch was also allocated a habitat 'quality' score of either poor, moderate or good. This was done using the SANBI's existing data and was based mostly on grazing and trampling pressure, botanical diversity and alien vegetation density. In order to test whether harrier nests were placed randomly or non-randomly with respect to the edges of patches, I compared the distance of each nest from the nearest edge of the patch (measured in the field) with the maximum theoretical distance that a nest could be sited from any edge of the patch (measured using the SANBI's digital maps). Once the 'minimum patch size' for a breeding pair of harriers was established, a 'connectivity measure' was calculated using the SANBI's GIS database for each patch on or above this limit. To determine the area over which 'connectivity' should be measured, two provisioning male harriers were trapped in the Bontebok National Park in October 2004 and were fitted with radio-tracking devices (Biotrack transmitters, weighing 3.5 g). Each bird was followed over 3-5 days to determine 1) the maximum distance that they foraged away from their nests, and 2) the proportion of time spent foraging in natural and transformed habitats relative to the availability of these two habitat types within the birds' maximum foraging ranges.

A conservation organization in the Western Cape, known as the Cape Conservation Unit (CCU), has recently identified and mapped the most important lowland Renosterveld patches in the region, for conservation planning purposes. This assessment has been based primarily on the biodiversity value and connectivity of the patches and has identified 'core sites' (key Renosterveld patches with a high biodiversity value) and 'critical habitats' (other threatened and important habitats adjacent to core sites) for the lowlands in the Western Cape. This 'biodiversity value' was assessed through a combination of surveys and research on different taxa in parts of the Cape Floristic Region (CFR) (Von Hase *et al.* 2003). Harrier nest locations were overlaid on this map to assess whether or not harrier dispersion mirrored the distribution of important, 'ecologically intact' habitats (*sensu* Von Hase *et al.* 2003). Rainfall data were obtained from the SAWS.

Productivity and breeding frequency across all habitats

Data from five harrier breeding seasons (2000–2004) were combined for analyses of various breeding parameters. Fieldwork was generally conducted from June to November across the five-year study period. Although harriers do not make use of the same nest structure from year to year, where pairs bred in the same general area, I considered this to be a single nesting site (Curtis *et al.* 2004). Due to the extent of the study areas, it was not possible to follow every nest through the entire breeding cycle, thus many of the breeding data were collected on an opportunistic basis.

Three distinct topographical categories were recognized (coastal, lowland and montane), with several vegetation types spread across these categories

(Appendix 1, Fig. 1). 'Coastal' sites included the coastal strip of Strandveld or Dune Thicket along the west and south-west coasts of the study areas. 'Lowlands' were defined as the low-lying areas between the coastal and mountainous areas, and included mostly Renosterveld vegetation, while the 'montane' sites were higher-altitude (>300 m asl), mountainous areas, primarily supporting Mountain Fynbos vegetation. Because some breeding areas were large, contiguous tracts of land (i.e. they were not habitat 'patches' *sensu stricto*) and thus, their total area was difficult to define and calculate, nest sites were divided into two categories: i) those that were within large, continuous patches (LCPs) (defined as being greater than 1000 ha, as well as well-connected with adjacent natural habitats) and ii) those in small, isolated patches (SIPs), (defined as being less than 1000 ha and surrounded by a matrix of transformed habitats). Thus, the division by LCPs and SIPs places more emphasis on connectivity, while patch size categories within the Renosterveld remnants are based purely on the area of the patch.

Comparisons of clutch size, breeding success and nest success were made between four habitat divisions: a) topographical categories (coastal, lowland or montane), b) vegetation types (fynbos, Renosterveld or strandveld), c) Swartland and Overberg sites and d) LCPs and SIPs. I tested for correlations between breeding frequency (the proportion of the maximum known number of nest sites occupied in any one season) and rainfall patterns for the west coast sub-sample of nests, as this was the most comprehensive dataset for the five-year period. Limited data on rodent populations and breeding frequency for two reserves on the west coast were available (R. E. Simmons unpubl. data), and I tested for a relationship between fluctuating mouse populations and fluctuating harrier breeding frequency at these two sites. In addition, to compare rodent densities between south coast Renosterveld and adjacent agricultural lands, rodent trap-lines were set at

Bontebok National Park. Due to logistical constraints, two trap-lines were set within the Park, each containing 20 traps, and only a single line of 20 traps was set in the old lands (abandoned fields) adjoining the Park. Locations for these lines were selected randomly, but within the general foraging areas available to the radio-tagged individuals. All traps were spaced 10 m apart and were baited with a mixture of peanut butter and bread. Each trap-line was set for eight days and traps were emptied twice daily; proportional trapping success was assumed to represent proportional rodent abundance.

Statistical analyses

Data were all non-normally distributed, thus, non-parametric statistical tests were used for analyses. Kruskal-Wallis ANOVA and/or Mann-Whitney U-tests were used to analyse variation in clutch size and breeding success (the number of young fledged per breeding attempt - Postupalsky 1973) between years, between LCPs and SIPs, between vegetation types and across the three topographical categories. Mann-Whitney U-tests were also used to examine differences in patch size between the Overberg and Swartland and patch connectivity within Overberg lowland patches. Chi-squared tests were used to determine whether breeding harriers favoured larger lowland patches over smaller ones and to test for variation in breeding frequency and nest success (the proportion of nests that fledged at least one young – Postupalsky 1973) between years and between habitats. Spearman's Rank Correlation was used to test the relationship between distances of nests from the edge of a patch and patch size, as well as the relationship between patch size and the number of nests in the fragment. For the foraging data, only the time spent actually watching the hunting individuals was used for analysis (i.e. a total of 8 hrs, 21 mins and 13 secs). The home range was calculated from furthest point a radio-tagged male was observed hunting from the nest and assuming this to be the maximum radius of the foraging range.

Results

By the end of 2004, 70 nest sites had been located and 131 breeding attempts monitored (Appendix 1).

Spatial requirements and habitat use of harriers

One of the radio-tracked males (provisioning an incubating female) foraged a maximum of 2.3 km from the nest (potentially covering an area of 1662 ha). Within this area, 62% of the habitat was natural, the remainder transformed. The bird spent 99.2% of its foraging time in natural vegetation; i.e. it foraged within an area of 1030 ha. The second bird (provisioning a female and three young) foraged up to 2.9 km from the nest (potentially covering an area of 2642 ha). Sixty-eight percent of the habitat within this radius was natural, and this bird spent all of its foraging time in natural habitats (1797 ha). For calculating connectivity (the proportion of natural habitat surrounding the nest), a radius of 3 km from the nest was used.

Limited data suggest a preference for natural habitats reflected in substantial differences in rodent trapping rates between natural and transformed habitats. The two trap-lines within natural vegetation had catch rates of 48-52%, whereas in old lands, capture rate was 3% ($\chi^2 = 68.5$, $p << 0.001$, df = 2).

Dispersion in relation to lowland habitat patches

Of the 36 Swartland patches, none held a breeding pair of Black Harriers, while in the Overberg, 13 pairs of harriers (for three of which no actual nest was located) were located in seven (16%) of the 43 patches surveyed. Patches used by nesting

Black Harriers in the Overberg ranged in size from 104–6100 ha, and the sizes of only three patches exceeded the minimum foraging area of 1030 ha. Harriers selected large patches for breeding ($\chi^2 = 17.5$, $p < 0.005$, $n = 43$, df = 2) (Fig. 2). However, three additional nests were located incidentally in lowland (Overberg) patches that were not part of the randomized sampling. Two of these nests were in small patches; the smallest being 22 ha. Thus, percentage connectivity was calculated for all patches of 22 ha and larger. Harriers selected patches with a higher than average degree of connectivity (Mann Whitney U = 19.5, $p = 0.0003$, $n = 31$) and only bred in small patches with connectivity values in excess of 450 ha (and ranging up to 1979 ha - Appendix 2). The number of nests in a single patch increased with increasing patch size ($r = 0.77$, $p = 0.01$, $n = 9$). Patch O98 was a large, extensive patch (Appendix 2), bordering a large nature reserve and was not surveyed extensively, thus it was excluded from this analysis.

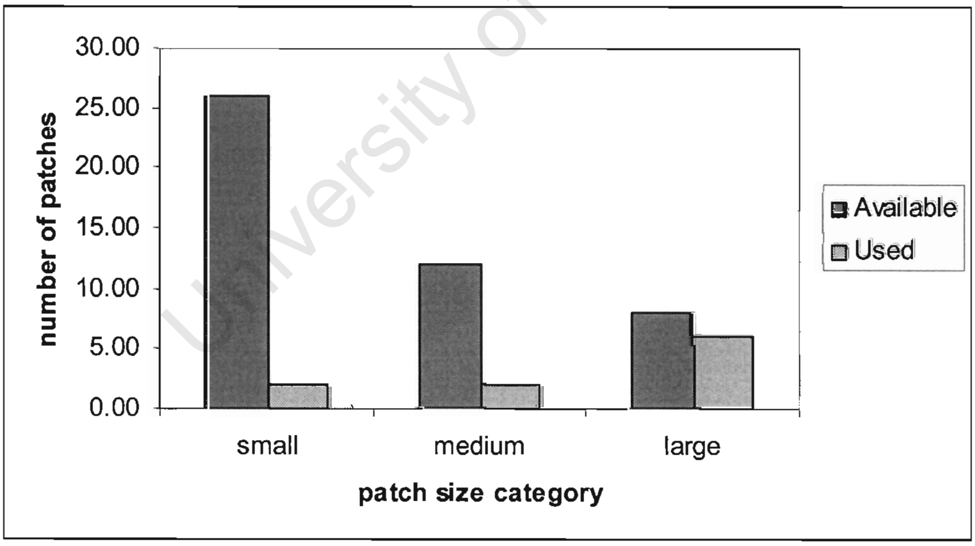

Figure 2 Patch size selection by Black Harriers in the Overberg lowlands, Western Cape, South Africa, according to size categories: small (< 100ha), Medium (100-500 ha) and large (>500-6100 ha).

Table 1 Patch quality selection by Black Harriers in the Overberg, Western Cape, South Africa

	PATCH QUALITY					
	poor		**moderate**		**good**	
PATCH SIZE	total	occupied	total	occupied	total	occupied
small	6	0	5	0	13	0
medium	0	0	5	0	7	2
large	0	0	2	2	5	3

*Greyed areas indicate where breeding harriers were located

Superficially, it appears that harriers avoided poor-quality patches, and preferred medium- to good-quality habitats (Table 1), although the sample is too small to subject the data to any rigorous statistical analyses. All harrier nests in the lowlands located in this study fell into the areas identified as 'core sites' (i.e. Renosterveld patches with a high biodiversity value) (Fig. 3).

The distance that harrier nests were placed from the edge of a patch varied from 100 – 1400m (n = 14 nests, 7 patches), and although not statistically testable, it appears that harriers do not target the centres of patches as nest sites (Fig. 4).

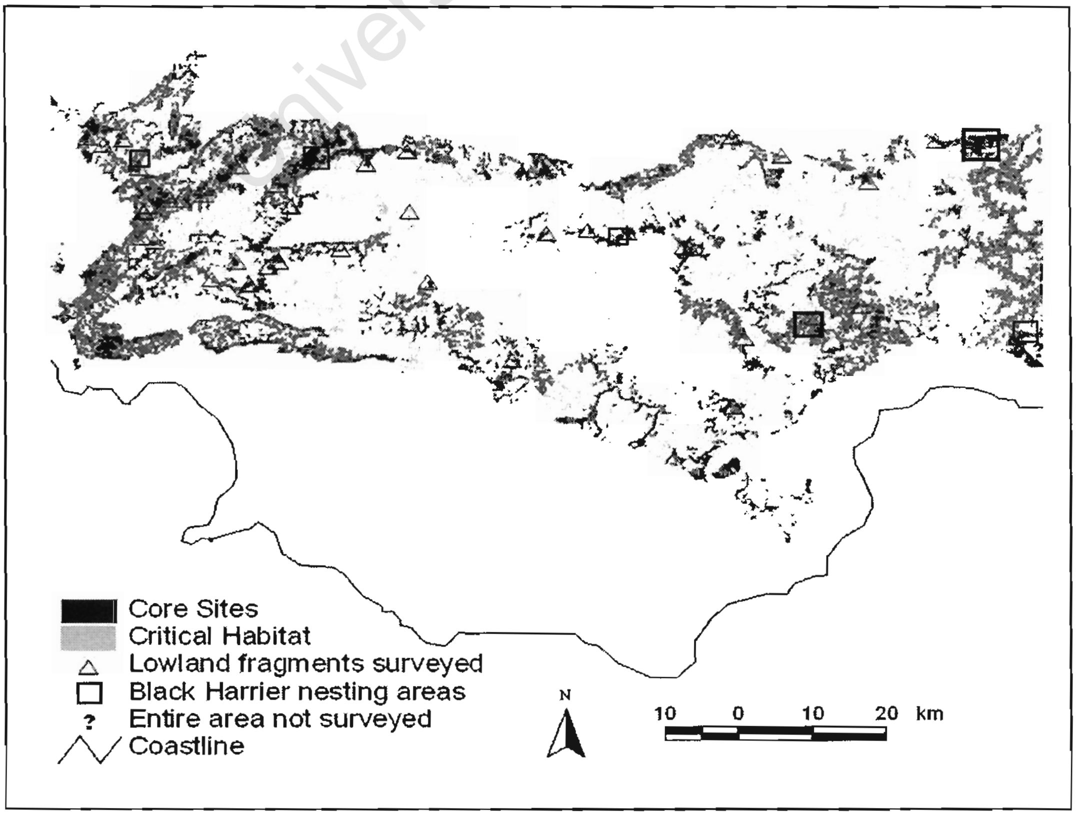

Figure 3 Map showing the dispersion of Black Harrier breeding sites in relation to the distribution of conservation priority habitat sites (the size of the squares denoting harrier nest sites are proportional to the actual number of harrier nests) (adapted with permission from the SANBI).

Within the sub-sample of patches surveyed in this study, neither patch size (Mann-Whitney U = 744.5, p = 0.88, n = 79), or patch quality ($\chi^2 = 0.64$, $p > 0.05$, df = 2) varied between Overberg and Swartland sites. However, when the entire SANBI patch dataset (for 18 711 patches) was analysed, Swartland patches were, on average, significantly larger than those in the Overberg (Mann-Whitney U = 12.4 x 10^6, p << 0.01, n = 18 711) (Table 2), but the number of Overberg patches far exceeds the number in the Swartland and collectively have a larger total area (Table 2). There are also more patches that fall above the minimum size threshold for breeding harriers in the Overberg than in the Swartland (Table 2).

Table 2 Lowland habitat patch attributes for the Swartland and the Overberg regions of the Western Cape, South Africa

	Swartland	**Overberg**	**Total**
Sub-sample of lowland patches			
Total number of patches	36	45	81
Total area of patches combined (ha)	12417	19848	32265
Average size of a patch (ha)	345	376	
Largest patch size (ha)	4318	6101	
Smallest patch size (ha)	0.94	0.06	
% good quality patches	53	58	
% medium quality patches	36	28	
% poor quality patches	11	14	
Number of patches above the minimum size threshold (100 ha) for breeding harriers	15	19	34
Number of patches occupied by breeding harriers	0	7	7
All lowland patches			
Total number of patches	1900	16811	18711
Total area of patches combined (ha)	46156	70850	117006

Average size of a patch (ha)	24	4	
Largest patch size (ha)	4318	6101	
Smallest patch size (ha)	0.06	0.06	
Number of patches above the minimum size threshold (100 ha) for breeding harriers	226	433	659

Dispersion across breeding habitats

In some breeding areas, harriers were semi-colonial, with nests as close as 100 m apart, such as at Koeberg Nature Reserve on the west coast (Curtis *et al.* 2004). Within other large breeding areas, such as Ertjies Dam (Appendix 1), nests were as much as 4 km apart, while small, isolated patches, such as Boix's nest (Appendix 1) contained only one breeding pair of harriers and were >30 km from the nearest known nest.

Productivity and breeding frequency

Average clutch size for the entire study population across all years was 3.4 ± 0.9 ($n = 77$), while fledged brood size averaged 1.7 ± 1.3 ($n = 98$).

Average clutch size varied significantly across years for the entire study population (Kruskal-Wallis $H = 21$, $p = 0.0003$, $n = 77$, $df = 4$). Sample sizes were largest in 2003 and 2004 and clutch size did not vary between these years (Mann-Whitney $U = 90$, $p = 0.7$, $n = 28$); data from these two years were thus pooled for further analyses. Clutch size did not vary between Overberg and Swartland sites, between vegetation types, LCPs and SIPs, or between coastal, lowland and montane sites (Table 3). Breeding frequency varied between years for all sites combined ($\chi^2 = 28.1$, $p << 0.001$, $n = 169$), as well as for the west coast sub-sample ($\chi^2 = 17.8$, $p << 0.001$, $n = 111$).

Nest success did not vary between years ($\chi^2 = 3.4$, $p > 0.05$, $df = 4$), thus data were pooled. There was also no variation in nest success between Overberg and Swartland sites, between vegetation types, or SIPs and LCPs. Nest success did, however, vary significantly between coastal, lowland and montane sites, with coastal sites being the most productive (Table 3).

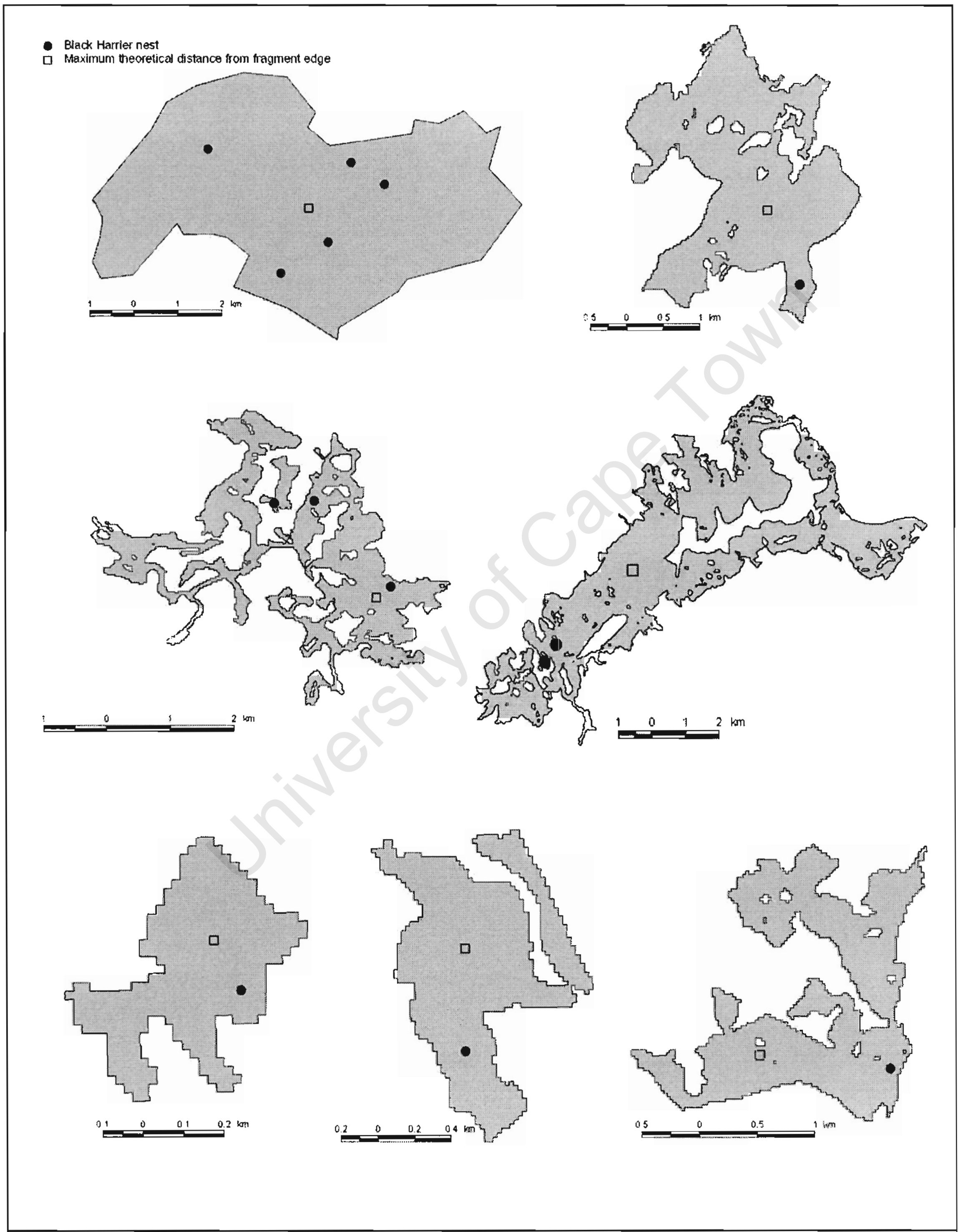

Figure 4 Black Harrier nests in relation to patch edges and theoretical maximum distance from the edge of the habitat fragment

Average annual breeding success did not vary across years (Kruskal-Wallis ANOVA H = 4.8, p = 0.3, n = 98, df = 4), therefore these data were pooled for analysis. Breeding success also did not vary between Overberg and Swartland sites, between vegetation types or between SIPs and LCPs. However, breeding success did vary significantly between coastal, lowland and montane sites (Table 3), with the greatest difference being between coastal (mean brood size = 2.0) and montane sites (mean brood size = 1.1) (Mann-Whitney U = 338.0, p = 0.02, n = 81).

There was no link between breeding success and average rainfall during the breeding season (r = 0.08, p = 0.9, n = 5), nor do there appear to be any correlations between other breeding parameters and the amount or timing of rainfall (Table 4). However, in 2003 and 2004 (the poorest breeding years), the onset of the rains was fairly late relative to the previous three years (Table 4).

Table 3 Black Harrier productivity in the Overberg and Swartland, Western Cape, South Africa in a) three topographical regions, b) three broad vegetation types, c) the Overberg and Swartland and d) large, continuous patches and small, isolated patches.

a	Coastal	Lowland	Montane	Test statistic	P - value
Clutch size	2.9 ±1.2 (17)	3.3 ±0.8 (7)	3.3 ±0.5 (4)	H = 0.52	0.78
Fledging success	2.0 ±1.27 (65)	1.4 ±1.2 (17)	1.1 ±1.3 (16)	H = 7.1	0.02 *
% successful nests	77% (65)	65% (17)	44% (16)	$\chi^2 = 6.7$	<0.05 *

b	Strandveld	Renosterveld	Fynbos	Test statistic	P - value
Clutch size	3.5 ±0.6 (16)	3.3 ±0.7 (8)	3.5 ±0.6 (4)	H = 2.01	0.37
Fledging success	1.9 ±1.3 (58)	1.3 ±1.2 (16)	1.6 ±1.3 (24)	H = 3.25	0.20
% successful nests	74% (58)	57% (16)	67% (24)	$\chi^2 = 2.0$	>0.05

c	Swartland	Overberg	Test statistic	P - value
Clutch size	3.4 ±0.8 (14)	2.7 ±1.1 (14)	U = 72.5	0.19
Fledging success	1.8 ±1.2 (64)	1.6 ±1.4 (34)	U = 993.5	0.46
% successful nests	73% (64)	62% (34)	χ^2 = 1.42	>0.05

d	LCP	SIP	Test statistic	P - value
Clutch size	3.0 ±1.1 (23)	3.2 ±0.4 (5)	U = 52	0.71
Fledging success	1.8 ±1.3 (86)	1.4 ±1.2 (12)	U = 424.5	0.30
% successful nests	70% (86)	67 (12)	χ^2 = 0.05	>0.05

Table 4 The effects of rainfall on Black Harrier productivity and breeding frequency at west coast breeding sites, Western Cape, South Africa.

ear	Ave rainfall	Total rainfall	Ave rainfall Jun - Nov	Ave clutch size	Ave fledged brood per attempt	Ave fledged brood per successful attempt	Ave nest success (%)	Breeding Frequency (%)	Month when cumulative rainfall exceeded 75mm	Peak rainfall month	Ave lay date	Month of first laying
000	14.0	165.6	24.2	3.0	2.1	2.3	90	83	July	Sep	07-Sep	July
001	31.1	372.0	45.7	3.4	2.0	2.5	79	87	May	Jul	23-Aug	June
002	26.5	313.0	32.3	4.0	2.5	2.7	92	79	April	Jul	14-Jul	July
003	20.2	228.8	30.7	2.8	1.4	2.5	50	52	Aug	Aug	28-Aug	Aug
004	22.8	272.8	35.9	2.6	1.3	2.1	58	42	June	Oct	22-Sep	Aug

Breeding commenced later than in previous years, and the breeding season was correspondingly short. The most successful breeding took place in the year with the earliest rainfall (2002).

Although the data for mouse population sizes and breeding frequency for the two west coast reserves were too small for any rigorous analysis, it appears that numbers of breeding harriers are positively linked to rodent abundance, although the latter does not appear to be linked with rainfall (Table 5).

Table 5 Small mammal trapping success compared with rainfall and the number of active Black Harrier nests at two study sites on west coast (Koeberg and the West Coast National Park), Western Cape, South Africa.

Study site	Year	no. of nests	% mice	Average annual rainfall
Koeberg	2000	6	40	14

	2001	4	22	31.1
	2002	1	15	26.5
	2004	1	21	22.8
WCNP	2002	11	63	26.5
	2003	6	33	20.2
	2004	6	35	22.8

Discussion

Harriers and patch size

Black Harriers do occasionally hunt in agricultural habitats (Curtis *et al.* 2004, Van der Merwe 1981), but they rarely, if ever, breed in them. Based on the rodent trapping at Bontebok National Park, it seems likely that relative prey abundance could partly explain this choice, if similar differences are found everywhere among habitats. Also, agricultural habitats are more open and may not provide the necessary microclimate for breeding (pers. obs). Throughout the breeding cycle, Black Harriers are Central Place Foragers, which presumably constrains (for energetic reasons) their foraging range from the nest. When nesting in natural vegetation, Black Harriers are sensitive to patch size, but patch suitability is strongly influenced by the connectivity of the area surrounding the nest – no birds were found breeding in patches with connectivity values less than 450 ha, suggesting that this might be the minimum area of natural habitat required in proximity to the nest. This observation supports the hypothesis that the species has been negatively affected by habitat fragmentation. Small, isolated patches are unlikely to support the foraging requirements of a provisioning adult harrier. Larger patches should contain more food (based on the Bontebok NP rodent trapping) and also provide more choice in terms of availability of microhabitats for nest site selection (Wiens 2000). It has been suggested that large patches provide some refuge from predation (relative to smaller patches) (Chalfoun *et al.* 2002), but in this study, several nests in even the largest patches failed due to predation (unpubl. data).

Based on the radio-tracking at Bontebok National Park, an area of extensive natural habitat, a pair of Black Harriers breeding in the lowlands requires a foraging area of ca 1000-1800 ha, although pairs breeding in smaller patches in some cases have as little as 450 ha of natural habitat within 3 km of the nest. This suggests that some hunting may occur in the matrix and/or that prey abundance and availability varies among patches. The current area of natural lowland vegetation in the Overberg (70 850 ha – Table 2) is about 10% of its original extent (Kemper *et al.* 2000 & Low & Rebelo 1996). If the original extent of lowland habitat in the Overberg was 708 500 ha, assuming equal opportunities for harriers throughout the habitat, and conservatively assuming that territories are non-overlapping (which is not the case), historically there was enough habitat for ca 390-1570 pairs of Black Harriers in the Overberg lowlands alone. The upper limit of this estimate may be artificially high, as it is likely that there are certain micro-habitat features of nest sites which limit the amount of breeding habitat available to them (Redpath *et al.* 1998). During patch surveys conducted in this study, 16 pairs of Black Harriers were located in a total area of 19 847 ha (Table 2). Given the total area of Renosterveld remaining in the Overberg (70 850 ha – Table 2), it seems unlikely that the total remaining harrier population in this habitat exceeds 60 pairs, 15% of the minimum historical estimate (of 390 pairs).

Harriers and patch quality

The small numbers of harriers breeding in lowland patches made drawing a meaningful relationship between harrier presence or absence and habitat quality difficult. The limited data (Table 1) suggest that harriers are sensitive to patch quality. Harrier breeding dispersion in the lowlands of the Overberg is closely linked to the distribution of 'core' habitats (as defined by biodiversity and connectivity values), supporting the idea that harriers are strongly associated with 'ecologically intact' habitats. However, because most of the larger patches are 'core' habitats, as yet it is difficult to separate the relative influences of patch size and patch quality on harrier dispersion.

Harriers do not seem to be sensitive to where, in relation to the fragment's edge, they place their nests. This suggests that the birds select a micro-habitat within a patch (e.g. a watercourse, a certain slope aspect or a certain type or height of vegetation - Redpath *et al.* 1998), rather than placing the nest in an optimal position to maximize foraging opportunities.

The lack of breeding harriers in the Swartland's lowland Renosterveld patches was unexpected, as there are large, seemingly good-quality patches available to the birds. However, the Swartland experienced drought from 2003–2004, when the lowlands survey was conducted: this appeared to affect breeding frequency in other parts of the Swartland, where far fewer pairs bred than in 2000-2002 (Appendix 1). It cannot be concluded, therefore, that Black Harriers never breed in Swartland patches: they may, however, only do so in years of average or better than average rainfall.

The dispersion of breeding Black Harriers is either clumped, as on the west coast, or over-dispersed, as in fragmented Renosterveld habitats. On the west coast, breeding microhabitats were aggregated. Harriers bred in semi-colonial situations centered on these 'patches' and hunted away from the nest (unpubl. data). In contrast, harrier nests in Renosterveld patches, were further apart and provisioning adults hunted in the vicinity of the nest. Thus, although Black Harriers are capable of semi-colonial breeding, they do not do so in all habitats/situations, because where food is scarce, and nesting microhabitats widely dispersed, territoriality prevents 'clumped' breeding. A similar comparison between two sympatric harriers has been made by Garcia & Arroyo (2005), who demonstrated that Hen Harriers *C. cyaneus* defend territories because they forage close to their nests, while Montagu's Harriers are able to breed colonially as they generally forage away from the nest. For Black Harriers, there are several Renosterveld patches which, according to the results in this study, are of sufficient size to support a breeding pair of harriers, yet few actually do. This suggests that the primary limiting factor for harriers breeding in habitat patches is either i) predation pressure, ii) nesting microhabitat availability, or iii) the abundance and/or availability of prey, or a combination of these. Predation is unlikely to be the primary limiting factor, because birds breeding in large patches still experience high levels of nest predation (unpubl. data). Nesting microhabitat availability may be important in some areas, however, even where suitable nesting habitats were present, there was seldom more than one pair of harriers occupying a patch. Thus, food abundance and/or availability is likely to be the main driving force that determines where harriers can and cannot breed: areas with high food availability and scarce, localized nesting habitats are likely to hold more breeding pairs of harriers than those where both food and nesting habitat is scarce. Food availability, in turn, is likely to be influenced by the management of the vegetation – for example, poorly managed, overgrazed vegetation would have negative implications for rodent prey species' populations. Ninety percent of the nests located in this study were on formally conserved, private- or state-owned land, i.e. areas with no livestock. This reinforces the premise that harriers are sensitive to the way in which habitats are managed, which presumably affects the spectrum of nesting microhabitats available, and, most importantly, the food supply during the breeding season.

Harriers and breeding productivity in different habitats

Breeding success and nest success varied across the three topographical areas, suggesting that there are inherent qualities within these areas that render them of good or poor quality for harriers. The 'quality' of a nesting area may be determined primarily by predation pressure and the abundance and/or availability of prey (Cody 1981). Birds breeding in montane areas, where diet is least strongly biased towards rodents, and where predation rates are high (Curtis *et al.* 2004), had the lowest breeding success. In the lowlands, rodent capture rates and harrier foraging patterns at Bontebok National Park strongly suggest that the food supply is of overriding importance, especially given that there is no clear pattern linking predation risk and patch size. Patch quality is probably affected by past and present management actions (e.g. livestock presence) within and around the patch (Newton & Knight 2004, Saunders *et al.* 1991).

The reasons why Black Harriers are most successful in coastal habitats are not clear. Compared with lowland habitats, coastal habitats are of minimal value for agriculture; as a result, they are far less fragmented and degraded and thus, by default, relatively well conserved (Low & Rebelo 1996). Coastal habitats may have always been superior for harriers, and the species' current dispersion and performance across the three topographical types is simply a reflection of its historical distribution - i.e. harriers were always rare in the lowlands. Alternatively, the current relatively high densities and performance of coastally breeding harriers may reflect displacement of birds from the more fragmented lowlands into what are presently better-quality nesting habitats. Resolving this dichotomy is problematic partly because of a real paucity of information about the historical distribution of harriers and partly because of the history of the lowland vegetation. A little over 100 years ago, the lowlands resembled a grassland, rather than a heathland (Newton & Knight 2004). It is hypothesised that overgrazing by livestock pre-1900 caused a major depletion of the indigenous grasses (e.g. *Themeda triandra*) and a concomitant increase in shrub cover, resulting in a complete change in vegetation structure (Newton & Knight 2004). Given that grassland habitats in other parts of the species' range are used for breeding (e.g. Eastern Cape - K. Webster, R. Streton, pers. comm., SAFRING Nest Record Card Scheme), it is possible that grassy, lowland habitats of the 19th Century were at least as suitable for Black Harriers as Renosterveld is today.

Due to relatively small sample sizes, I could not detect an obvious close relationship between rainfall and breeding frequency or any measure of breeding success. However, Black Harriers bred at the highest frequency and produced most fledglings in the year with the highest rainfall, suggesting rainfall could be important in determining productivity. Black Harriers, especially in the lowlands and on the coast, are primarily rodent-eaters (Simmons *et al.* 2005, unpubl. data). Fluctuations in breeding numbers and performance of other harrier species are hypothesised to be linked to fluctuations in rodent populations (Amar *et al.* 2005, Arroyo *et al.* 2002, Butet & Leroux 2001, Redpath *et al.* 2002). The link between rodent abundance and Black Harrier breeding frequency seems well established. Breeding performance may also be linked to rainfall (greatest in wet years), but in the temperate climate of the Western Cape, the link between fluctuations in rodent numbers and rainfall is less well established (David & Jarvis 1985).

Conclusions

Fragmentation processes in the Western Cape are ongoing and continue to threaten native ecosystems (Rouget *et al.* 2003). Despite the introduction of laws designed to restrict/regulate certain agricultural activities (e.g. the ploughing of 'virgin' lands without a permit), many farmers continue to plough up remnant patches (pers. obs.). Almost 10% of the Overberg sites surveyed in this study were ploughed by landowners immediately before, or soon after, the survey (pers. obs.).

The Black Harrier appears to be highly sensitive to habitat fragmentation, at least in relation to its breeding dispersion: its population has decreased - perhaps by 85% or more in Renosterveld habitats - as a result of landscape-level agricultural disturbance. Black Harriers are sensitive to both patch size and connectivity, and at least to some extent to the quality of 'natural' habitats. If ongoing fragmentation and loss of lowland heathlands is not addressed at a management level, there is a real possibility that the threat status of this habitat specialist will escalate from *Vulnerable* to *Threatened*.

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Appendix 1 Breeding parameters for Black Harrier nests in the Western Cape Province, South Africa

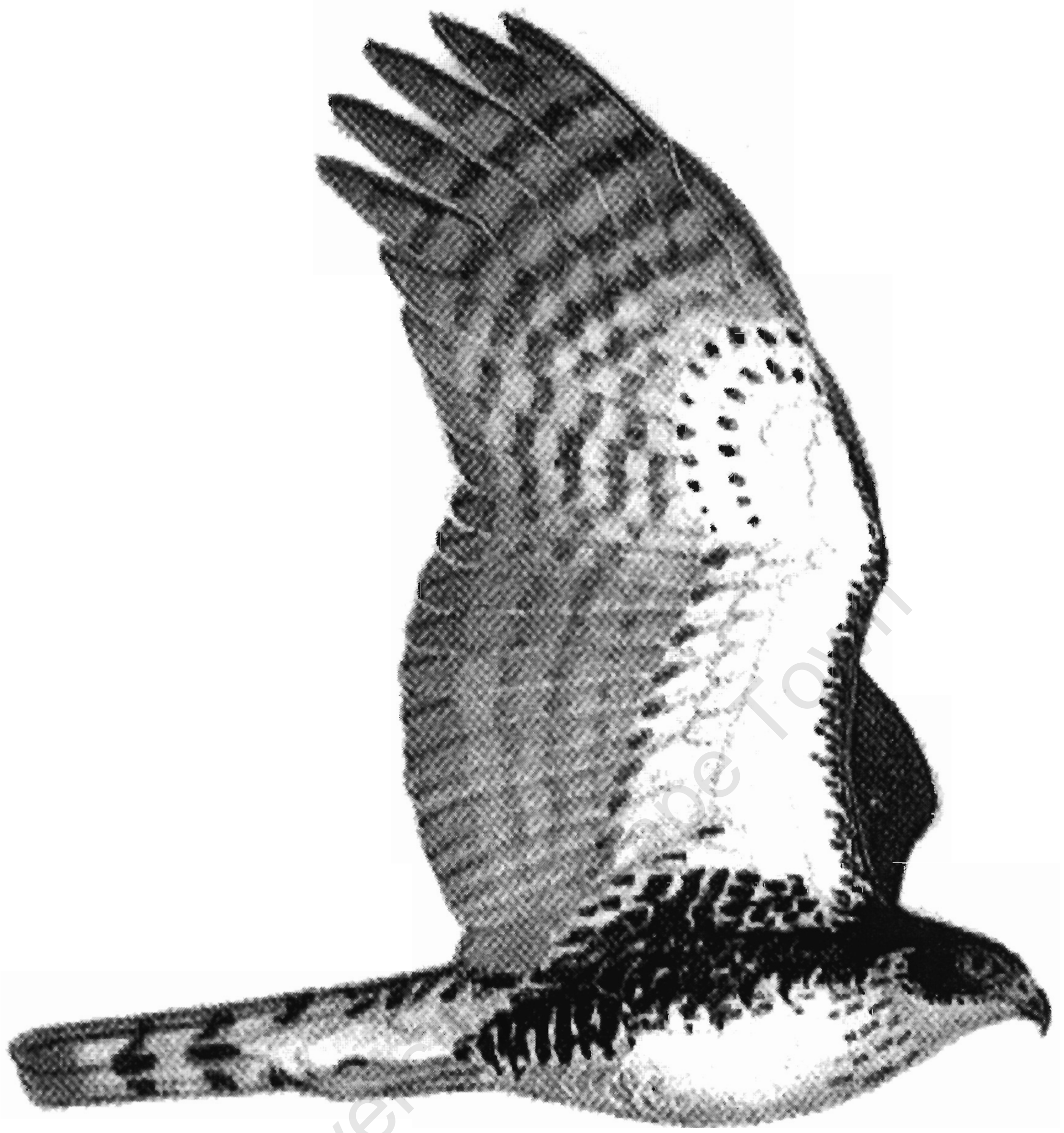
Locality	Protected?	Latitude	Longitude	Overberg or Swartland	Topography (c, l, m)	Vegetation type	LCF, SIF	Clutch Size 2000	Fledged Brood 2000	Clutch Size 2001	Fledged Brood 2001	Clutch Size 2002	Fledged Brood 2002	Clutch Size 2003	Fledged Brood 2003	Clutch Size 2004	Fledged Brood 2004	Average clutch size	Average fledged brood
Andrew's Field #1	y	-34.759133	20.043783	Overberg	coastal	Fynbos	LCF						1						1.0
Andrew's Field #2	y			Overberg	coastal	Fynbos	LCF												
De Hoop #1	y	-34.473700	20.490517	Overberg	coastal	Fynbos	LCF		3										3.0
De Hoop #2	y	-34.397580	20.419480	Overberg	coastal	Fynbos	LCF										3		3.0
De Hoop #3	y	-34.380000	20.533310	Overberg	coastal	Fynbos	LCF										3		3.0
De Hoop #4	y	-34.406680	20.576940	Overberg	coastal	Fynbos	LCF									4		4.0	
De Hoop #5	y	-34.405450	20.573310	Overberg	coastal	Fynbos	LCF										2		2.0
De Hoop #6	y			Overberg	coastal	Fynbos	LCF												
OTB #1	y			Overberg	coastal	Fynbos	LCF										3		3.0
De Mond #1	y	-34.703300	20.132000	Overberg	coastal	Strandveld	LCF					4	0					4.0	0.0
De Mond #2	y	-34.708450	20.129417	Overberg	coastal	Strandveld	LCF					5		2	0			3.5	0.0
De Mond #3	y	-34.717750	20.104383	Overberg	coastal	Strandveld	LCF					5	3					5.0	3.0
De Mond #4	y	-34.717750	20.104383	Overberg	coastal	Strandveld	LCF					4						4.0	
De Mond #5	y			Overberg	coastal	Strandveld	LCF												
De Mond #6	y			Overberg	coastal	Strandveld	LCF												
De Mond #7	y	-34.706944	20.124722	Overberg	coastal	Strandveld	LCF							5	5			5.0	5.0
D'alton's farm	n	-34.581780	19.889170	Overberg	lowland	Fynbos	SIF									3	0	3.0	0.0
Boix's nest	n	-34.024200	20.827320	Overberg	lowland	Renosterveld	SIF									3	2	3.0	2.0
Bontebok NP #1	y	-34.058600	20.435830	Overberg	lowland	Renosterveld	LCF				2	3		3	2	5	3	3.7	2.3
Bontebok NP #2	y	-34.077528	20.468944	Overberg	lowland	Renosterveld	LCF										0		0.0
Bontebok NP #3	y	-34.056611	20.486000	Overberg	lowland	Renosterveld	LCF										0		0.0
Bontebok NP #4	y	-34.056200	20.487033	Overberg	lowland	Renosterveld	LCF									3	0	3.0	0.0
Bontebok NP #5	y	-34.067100	20.473100	Overberg	lowland	Renosterveld	LCF										3		3.0
Nysty #1	n	-34.321830	20.264030	Overberg	lowland	Renosterveld	SIF										2		2.0
Nysty #2	n	-34.344639	20.237944	Overberg	lowland	Renosterveld	SIF										0		0.0
Porcupine Hill	y	-34.106420	19.239220	Overberg	lowland	Renosterveld	SIF										2		2.0
Sans Souci #1	n	-34.332900	20.223300	Overberg	lowland	Renosterveld	SIF							3	0			3.0	0.0
Sans Souci #2	n	-34.332840	20.218070	Overberg	lowland	Renosterveld	SIF										1		1.0
Theewaterskloof	y	-34.081850	19.309070	Overberg	lowland	Renosterveld	LCF										3		3.0
Verdwaalskloof	n	-34.209778	19.956816	Overberg	lowland	Renosterveld	SIF							3				3.0	
Boskloof #1	y	-34.416667	19.660417	Overberg	montane	Fynbos	LCF	3	0	4	0	4	3			3		3.5	1.0
Boskloof #2	y			Overberg	montane	Fynbos	LCF								2				2.0
Stanford #1	y	-34.433983	19.573983	Overberg	montane	Fynbos	SIF	3		4	0							3.5	0.0
Stanford #2	y	-34.434050	19.575067	Overberg	montane	Fynbos	SIF	3										3.0	
Stanford #3	y	-34.428900	19.571050	Overberg	montane	Fynbos	SIF					4	3	4	3			4.0	3.0
Ertjies Dam #3	y	-34.105333	19.498700	Overberg	montane	Renosterveld	LCF												
Ertjies Dam #1	y	-34.118910	19.457310	Overberg	montane	Renosterveld	LCF									3	0	3.0	0.0
Ertjies Dam #2	y	-34.122280	19.456640	Overberg	montane	Renosterveld	LCF									3	0	3.0	0.0
Grotto Bay	y	-33.504567	18.339133	Swartland	coastal	Fynbos	LCF			4	3							4.0	3.0
Jakkalsfontein#1 (pan nest)	y	-33.406083	18.260167	Swartland	coastal	Strandveld	LCF	3	3	3	1	4	2					3.3	2.0
Jakkalsfontein#2 (Cliffortia)	y	-33.411183	18.241617	Swartland	coastal	Strandveld	LCF		3	4	3		3			3	3	3.5	3.0
Jakkalsfontein#3 (Nursery nest)	y	-33.410167	18.263233	Swartland	coastal	Strandveld	LCF		2		2	4	3	3	3	2	0	3.0	2.0
Jakkalsfontein#4 (Gavin's Rock)	y	-33.415250	18.247717	Swartland	coastal	Strandveld	LCF		2	3	3	4	2		3			3.5	2.5
Jakkalsfontein#5 (Dune nest)	y	-33.424650	18.257467	Swartland	coastal	Strandveld	LCF			3	3		3					3.0	3.0
Jakkalsfontein#6 (Banana Vlei)	y			Swartland	coastal	Strandveld	LCF					4	0					4.0	0.0
Koeberg #1	y	-33.659050	18.434233	Swartland	coastal	Strandveld	LCF	3	2	4	2	4	3					3.7	2.3
Koeberg #2	y	-33.662417	18.432383	Swartland	coastal	Strandveld	LCF	3	2	4	0							3.5	1.0

Koeberg #3	y	-33.659500	18.434517	Swartland	coastal	Strandveld	LCF	3	2	4	3		3			4	3	3.7	2.8
Koeberg #4	y	-33.660783	18.432333	Swartland	coastal	Strandveld	LCF		3										3.0
Koeberg #5	y	-33.660217	18.435533	Swartland	coastal	Strandveld	LCF	3	0									3.0	0.0
Koeberg #6	y			Swartland	coastal	Strandveld	LCF	3	2	4	0							3.5	1.0
Rondeberg #1 (pan)	y	-33.486183	18.477350	Swartland	coastal	Strandveld	LCF								0	4	3	4.0	1.5
Rondeberg #2 (Lang vlei)	y	-33.426750	18.268017	Swartland	coastal	Strandveld	LCF								0		0		0.0
West Coast NP #1	y	-33.136150	18.100800	Swartland	coastal	Strandveld	LCF			2	0	4					1	3.0	0.5
West Coast NP #10	y	-33.155883	18.100717	Swartland	coastal	Strandveld	LCF			3								3.0	
West Coast NP #11	y	-33.157100	18.112533	Swartland	coastal	Strandveld	LCF												
West Coast NP #2	y	-33.151750	18.105567	Swartland	coastal	Strandveld	LCF			3						3	0	3.0	0.0
West Coast NP #3	y	-33.152450	18.107600	Swartland	coastal	Strandveld	LCF			4	3			2	0	4	2	3.3	1.7
West Coast NP #4	y	-33.152433	18.109050	Swartland	coastal	Strandveld	LCF			4			2	3				3.5	2.0
West Coast NP #5	y	-33.157300	18.113867	Swartland	coastal	Strandveld	LCF			3	2	4	3	3				3.3	2.5
West Coast NP #6	y	-33.159367	18.113900	Swartland	coastal	Strandveld	LCF			4	3		3	3		0	0	2.3	2.0
West Coast NP #7	y	-33.157750	18.105667	Swartland	coastal	Strandveld	LCF			3			3				2	3.0	2.5
West Coast NP #8	y	-33.150983	18.166100	Swartland	coastal	Strandveld	LCF			3				3			1	3.0	1.0
West Coast NP #9	y	-33.151633	18.101717	Swartland	coastal	Strandveld	LCF			3					3			3.0	3.0
Grotto Bay #2	y	-33.497900	18.326367	Swartland	coastal	Strandveld	LCF									1	0	1.0	0.0
Riverlands	y	-33.495717	18.572633	Swartland	lowland	Fynbos	SIF						2		2				2.0
Perdeberg #1 (Slent)	y	-33.608217	18.815183	Swartland	montane	Fynbos	LCF	4	3				0					4.0	1.5
Perdeberg #2	y	-33.606533	18.816450	Swartland	montane	Fynbos	LCF	3	0	2	2							2.5	1.0
Perdeberg #3	y	-33.602133	18.816917	Swartland	montane	Fynbos	LCF	1	0		0							1.0	0.0
Perdeberg #4	y	-33.595583	18.806300	Swartland	montane	Fynbos	LCF	3	1									3.0	1.0

Appendix 2 Attributes of Overberg Renosterveld fragments and the presence/absence of Black Harriers, Western Cape Province, South Africa

SITE	Connectivity: % natural habitat area within 3km radius	Connectivity (ha)	Breeding / not breeding	No. harriers breeding	Nest name	Fragment area (ha)	Area category
O65			not breeding	0		0.06	small
O40			not breeding	0		0.88	small
O122			not breeding	0		1.25	small
O41			not breeding	0		2.13	small
O67			not breeding	0		2.38	small
O3			not breeding	0		3.00	small
O110			not breeding	0		3.19	small
O29			not breeding	0		4.13	small
O2			not breeding	0		6.31	small
O129			not breeding	0		6.94	small
O82			not breeding	0		8.38	small
O119			not breeding	0		11.31	small
O36			not breeding	0		11.50	small
O114			not breeding	0		16.44	small
O152			not breeding	0		19.81	small
SS2	25	707	breeding	1	Sans Souci1	21.56	small
NY1	90	2545	breeding	1	Nysty2	24.06	small
O62	10	283	not breeding	0		24.81	small
O77	10	283	not breeding	0		29.81	small
O5	10	283	not breeding	0		32.00	small
O138	10	283	not breeding	0		41.25	small
O79	10	283	not breeding	0		51.31	small
O111	12	339	not breeding	0		65.31	small
O68	9	254	not breeding	0		72.44	small
O55	8	226	not breeding	0		72.63	small
O86	10	283	not breeding	0		82.13	small
O120	7	198	not breeding	0		104.25	medium

O71	16	452	breeding	1	Verdwaalskloof	104.44	medium
O136	12	339	not breeding	0		120.19	medium
O144	10	283	not breeding	0		159.37	medium
O44	21	594	not breeding	0		161.94	medium
O8	12	339	not breeding	0		166.94	medium
O47	23	650	not breeding	0		169.94	medium
O80	8	226	not breeding	0		183.19	medium
O45	20	565	not breeding	0		197.87	medium
O33	20	565	breeding	1	Porcupine Hill	238.31	medium
O89	13	368	not breeding	0		264.56	medium
O108	26	735	not breeding	0		306.19	medium
TW	32	905	breeding	1	Theewaterskloof	590.19	large
O94	25	707	breeding	2	Sans Souci1	596.25	large
O63	23	650	not breeding	0		653.25	large
O95	23	650	breeding	1 (nest not located)	Plaatjies Kraal	835.25	large
O105	38	1074	not breeding	0		836.87	large
O13	70	1979	breeding	5	Bontebok1-5 (4 prs)	4000.00	large
O124	40	1131	breeding	3 (nest #3 not located)	Ertjies Dam1-3	3442.87	large
O98	70	1979	breeding	1 (entire area not suveyed)	De Hoop	6100.81	large



Kemp & Kemp 1998

CHAPTER 2

Responses of Black Sparrowhawks *Accipiter melanoleucus* to fragmented habitats on the Cape Peninsula, South Africa

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Abstract

Habitat patches can occur naturally or as a result of anthropogenic processes. The latter typically result in a matrix of transformed habitats, affecting species differently, depending on their respective biologies. Throughout its range, the Black Sparrowhawk *Accipiter melanoleucus* has responded positively to the creation of forest patches through the introduction and spread of alien trees. I studied a population of 26 pairs of Black Sparrowhawks on the Cape Peninsula, South Africa, from 2000–2004 and examined their breeding distribution within and across habitat patches and attempted to identify the factors most likely to influence their productivity. Black Sparrowhawks on the Cape Peninsula follow a despotic distribution pattern, in which birds breeding in superior habitats breed more successfully, despite being more closely spaced. Nearest neighbour distances ranged from 593–5023m (n = 26), and density within the study area was 38 breeding pairs/100km^2, one of the highest densities recorded for any *Accipiter* of equivalent size. For spatial analysis, habitat patches were divided into large, continuous patches (LCPs) and small, isolated patches (SIPs). Birds in LCPs were evenly dispersed (as a function of territoriality), while birds in SIPs were more randomly distributed (in response to habitat availability). Sparrowhawks in LCPs were also more productive than those in SIPs. Sparrowhawks showed a preference for large, mature stands of exotic pine (*Pinus* spp) trees and breeding success increased significantly with increasing patch size. There appear to be two main advantages to Black Sparrowhawks that use larger habitat patches for breeding: 1) birds in larger patches breed further from the edge of the patch and are thus possibly afforded better buffering from severe weather conditions, and 2) birds in larger patches are able to build more alternative nests, possibly decreasing their chances of nest parasitism by Egyptian Geese *Alopochen aegyptiaca*. Parasitism of sparrowhawk nests by Egyptian Geese occurred in 60% of territories; it appears that the threat of having a nest parasitized by geese is the main motivation for building alternative nests. Throughout the remainder of their southern African range, Black Sparrowhawks breed in winter (the dry season). On the Cape Peninsula (a winter-rainfall area), and independently of patch size, average annual breeding success was negatively correlated with average rainfall during the breeding season (March – November). This probably reflects a failure of the (recently colonising) birds to adjust their breeding season to avoid winter rains.

Introduction

Disjunct habitat patches occur naturally in heterogeneous environments, but can also result from anthropogenic processes affecting more homogeneous environments. For example, patches of forest may either occur naturally (e.g. Afromontane forest), or along drainage lines in areas of more open habitat. They may also be formed as by-products of extensive logging and clearing operations in what was previously a larger tract of forest, or as scattered invasions of alien trees in an otherwise treeless matrix. Although small habitat patches are generally associated with low levels of biodiversity (Castelletta *et al.* 2005, Watson *et al.* 2004), and habitat fragmentation often has negative implications for the maintenance of biotic communities (Cameron 1999, Sekercioglu 2002a, b), some species/communities may be relatively unaffected by patch size (Kemper *et al.* 1999), and can even thrive in environments where preferred habitats are highly fragmented (Johnson 1993 in Woodbridge & Detrich 1994, Moore & Henny 1983).

The value a patch holds for a particular species is determined not only by properties of the landscape, but also by properties of the species (Ovaskainen & Hanski 2003). Important factors that influence how a species responds to habitat patches include i) whether the species is solely dependent on the habitat fragments, or whether it also relies on the habitat matrix (Sekercioglu 2002), ii) its ability to move freely between patches (Sekercioglu 2002), iii) its dependence on edges or ecotones, which often increase in availability during the fragmentation process (Malan & Robinson 2001), and iv) whether the species is able to survive in a single patch, or whether it requires a network of patches (Banks *et al.* 2005). Thus, if a species utilises the habitat matrix (rather than depending on one particular habitat for all its requirements), is able to move freely between fragments, or relies on ecotones, it may adapt to, or even exploit, fragmented habitats successfully.

Raptors are large, mobile birds, varying in their responses to habitat change and in their ability to make use of habitat matrices. The larger Accipitrine hawks generally use patches of large, mature trees for nesting (e.g. Northern Goshawk *Accipiter gentilis* (Penteriani 2002) and Grey Goshawk *A. novaehollandiae* (Mooney & Holdsworth 1988)). However, the success with which a hawk is able to make use of a patch of trees depends on its overall habitat requirements, its principal prey base and its hunting techniques (Allan & Tarboton 1983). Thus, the importance of, for example, patch size, the quality of the patch, and the overlap between hunting and breeding habitats, will determine how the species responds to fragmented patches of trees.

The Black Sparrowhawk *A. melanoleucus* is a large hawk that preys primarily on birds and occurs in forested habitats across much of sub-Saharan Africa (Malan & Robinson 1999, 2001). The species has expanded its range and population size significantly (Hockey 2003), primarily due to the provision of two important resources provided by man-altered landscapes, namely fragmented stands of alien trees, which provide suitable nesting opportunities (Allan & Tarboton 1983), and an urban prey base, which the birds exploit, almost exclusively in some areas (Malan & Robinson 1999, Curtis *et al.* in prep). In addition to its ability to exploit modified habitat matrices, it is highly mobile, requires a single patch of trees in which to nest, and has an affinity for patch edges (Malan & Robinson 2001).

Black Sparrowhawks have responded positively to the spread of alien trees and, in some parts of their range (where habitat choice is limited), they seem to have been highly unselective in terms of the fragment's attributes. For example, Black Sparrowhawks along the Breede River, Western Cape, breed in small clusters of small eucalypt trees, where nothing else is available to them (A. Welz & A. Jenkins pers. comm.). The Cape Peninsula has a wide array of nesting habitats available to sparrowhawks and thus presents a good opportunity to examine which habitat patches are preferred for breeding purposes, given free choice. Using current knowledge of the species (Curtis *et al.* 2005, Curtis & Koeslag 2004, Hartley & Hough 2004, Malan & Robinson 1999, Malan & Robinson 2001, Steyn 1982, Tarboton & Allan 1984, Tarboton *et al.* 1978), I predict the following: 1) patch size will be relatively unimportant for sparrowhawks, because they only use the patch for nesting purposes and hunt in adjacent, more open habitats. There will, however, be a lower limit to this size, because sparrowhawks seek a compromise between breeding close enough to the edge of the patch to allow easy access to their hunting grounds, but far enough inside the patch to be adequately buffered against severe weather (Malan & Robinson 2001); 2) larger patches will hold more nests and more territories than smaller ones; 3) nests will be closer to suburban habitats (e.g. gardens and green belts) than to indigenous (Fynbos) habitats, because the former provide superior hunting opportunities; 4) because most pairs on the Peninsula breed in winter (Curtis & Koeslag 2004), birds will avoid nesting close to north/north-west-facing edges, in order to avoid the adverse effects of the prevailing strong north-westerly winter winds and heavy rainfall; and, 5) within large, continuous fragments, the population will be evenly dispersed (controlled by territoriality), but will be more scattered among the smaller, isolated patches (controlled by habitat availability).

If certain attributes render a patch 'high quality' habitat for sparrowhawks on the Cape Peninsula (e.g. medium-sized patches close to suburbia), pairs occupying such territories are predicted to reflect these benefits in their breeding performance. However, there are other (possibly overriding) factors that may influence nest-site selection and its performance-linked consequences. These include the effects of local environmental conditions (e.g. weather), fluctuating prey populations (McClaren *et al.* 2002), age or experience of the breeding pair (Nielsen & Drachmann 2003) and the presence of competitors and/or predators in the nest vicinity (Selås 1997, Kruger 2002).

This study examines the spatial distribution of Black Sparrowhawk nests in relation to the available habitat patches on the Cape Peninsula and identifies the factors most likely to impact productivity.

Study area

The breeding biology of the Black Sparrowhawk was studied in an area of *ca* 70 km^2 along the eastern slopes of the Table Mountain range, Cape Peninsula (34°00'S 18°26'E) (Curtis 1998). The study area features a matrix of habitats, including urban gardens, pine (*Pinus* spp) and eucalyptus (*Eucalyptus* spp.)) (both exotic to Africa) plantations, small pockets of indigenous Afromontane forest and heathlands (Fynbos). Altitude ranges from sea level to about 300 m a.s.l., and the climate is temperate, with locally variable winter rainfall (Cowling *et al.* 1996). Mean annual rainfall is about

1250 mm, with average minimum and maximum temperatures of 12°C and 21°C respectively (SAWS).

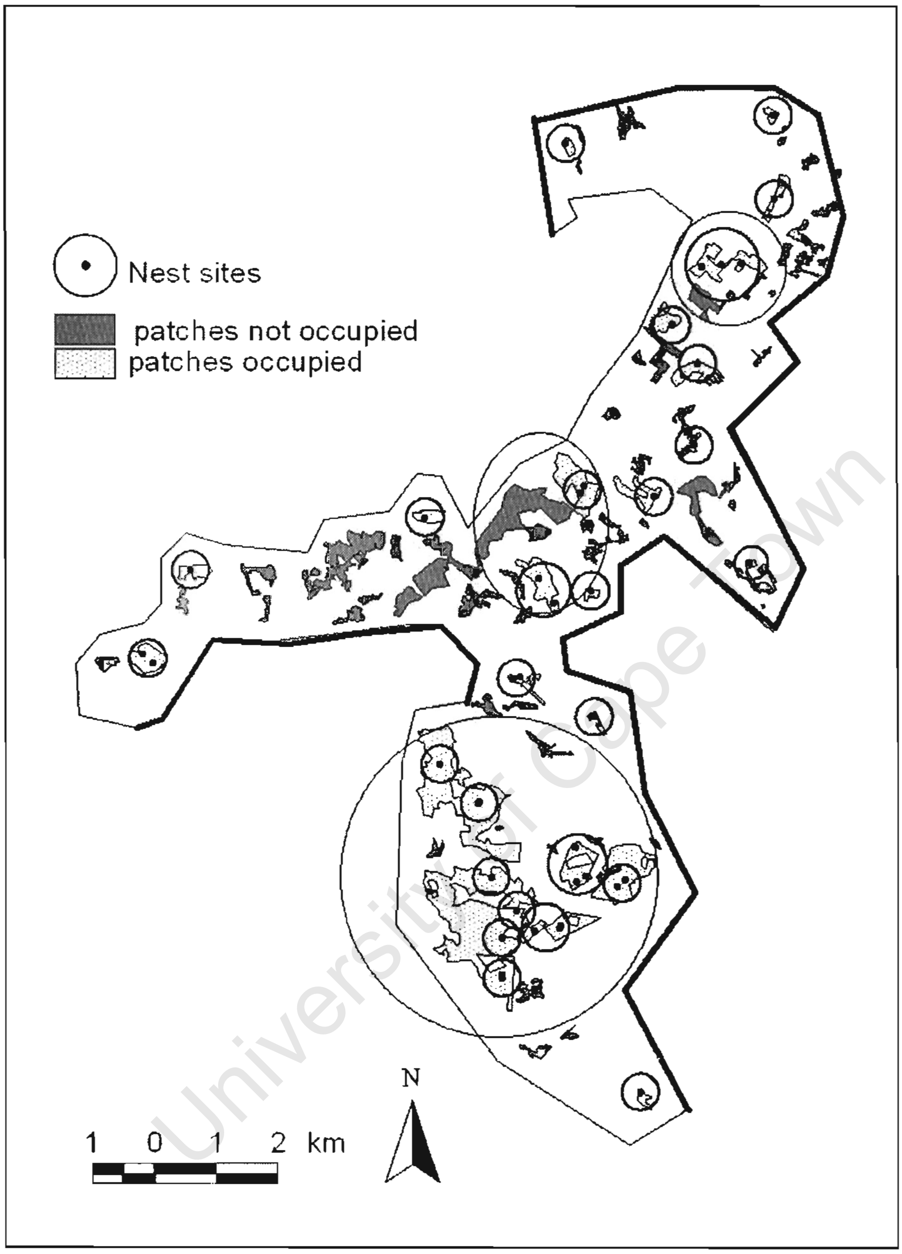

Figure 1 Map showing the study area for Black Sparrowhawks along the eastern slope of Table Mountain, Cape Peninsula, South Africa. The three large circles/ellipses denote the Large Continuous Patches and the dark edges of the study area indicate edges facing suburbia (as opposed to Fynbos).

Methods

Fieldwork was conducted from March to November from 2001-2004, with a few nests having been monitored from 2000. Black Sparrowhawk nests were located by surveying suitable stands of trees during the breeding season for calling sparrowhawks, prey remains, whitewash and nest structures. I used Malan and Robinson's (2001) minimum stand and tree size guidelines for defining and identifying 'suitable' stands of pine, eucalypt and mixed pine, poplar (*Populus* spp), eucalypt and Black Wood *Acacia melanoxylon* trees.

Distribution of nests within and across patches

'Nests' were defined as individual nest sites, while 'breeding areas' were defined by a group of nests, in close proximity, used by the same territorial pair (Speiser & Bosakowski 1987). Individuals were recognised by colour-rings or their unique black and white plumage patterns. Nests (up to four per breeding area) were plotted by overlaying GPS waypoints on aerial photographs using Arcview GIS 3.3 (2002), projected in Transverse Mercator, WGS 84, Central Meridian 19. Patch edges were defined by abrupt changes in vegetation structure (Sisk & Margules 1993) and, where a nest-stand was positioned inside a planted forest, the edge was taken as the edge of the same-aged stand (Malan & Robinson 2001). Arcview was used to calculate i) patch areas, ii) distance from the nest to the nearest edge of the patch, iii) maximum theoretical distance of a nest from the edge of the patch, and iv) the nearest distances to suburbia and to Fynbos respectively, from each nest site. The compass bearing of each nest to the nearest edge was measured from aerial photographs. Where territorial pairs had used more than one nest, these measurements were combined and averaged to give a single measurement for each breeding area.

Nests were divided into two categories for the purposes of nest-spacing analyses: i) those that were within large, continuous patches (LCPs) and ii) those in small, isolated patches (SIPs). Three areas of extensive plantation define the boundaries of the LCPs (the three largest, most connected plantations in the study area) (Fig. 1), while all other territories were regarded as being in SIPs (the small patches, ranging in area from 1–26 ha, generally isolated and not part of a contiguous tract of forest).

Each patch of available habitat was given a score of either 1 (used by sparrowhawks for nesting) or 0 (not used). Available patches were divided into three size categories, small (<5 ha), medium (5-20 ha) and large (>20 ha), and the frequency of patches used vs not used calculated for each category. Thus LCPs and SIFs emphasise the connectivity of the patches, while patch size is simply a measure of the area of an individual patch.

Breeding parameters

Productivity was measured as fledged brood size because nests were generally inaccessible and no clutch or brood size data were obtainable. Parasitism of Black Sparrowhawk nests by Egyptian Geese *Alopochen aegyptiaca* was recorded, either where a goose was seen sitting on the nest, or where there was evidence that a goose had occupied the nest during the season (broken goose eggshells below the nest, or a lining of goose down on the nest).

Analysis

Breeding data over the 5-year study period were analysed by breeding area, because many pairs made use of more than one nest site within the same patch; i.e. an average was calculated for each breeding area over the 5-year period. Where a pair moved to another patch, data for these patches were considered separately. Data were initially subjected to tests for normality (Kolmogorov-Smirnov). Biological data were tested using non-parametric statistical tests, while rainfall data was log-transformed for parametric testing. Correlation matrices were generated using Spearman's Rank coefficients. Non-parametric Kruskal-Wallis, Mann-Whitney and Wilcoxon's Matched-pairs Tests were used to test for significant differences among breeding and patch parameters. A Chi-squared test was used to test for differences in the sizes of patches that did or did not contain sparrowhawk nests. The G-stat was used to calculate the randomness of nest spacing (Brown 1975). This statistic is the ratio of the geometric mean to the arithmetic mean, taken from the squares of the nearest neighbour distances for each breeding area. A ratio with a value of greater than 0.65 suggests that the population is distributed nonrandomly (Brown 1975).

Results

By the end of 2004, a total of 25 breeding pairs (with 41 nest sites) in 27 patches were known in the study area and 72 breeding attempts had been monitored (Appendix 1). An additional breeding area (1 patch) with one fledgling was located at the end of the 2004 breeding season, but because the precise location of the nest was unknown and insufficient data were gathered, the nest could not be included in all analyses. However, the nest was included in the mapping process and density analyses. Almost all nests were in pine trees, with only two in poplars (both of which were eventually abandoned in favour of alternative nests in pines). Average annual breeding success did not vary significantly over the five-year study period (Kruskal-Wallis ANOVA, $H = 7.70$, $n = 73$, $p = 0.103$), so data were pooled across years for analysis.

Distribution within and across patches

Patches used for nesting by sparrowhawks ranged in size from 1-190 ha ($n = 23$), and distance from the nest to the nearest edge of the patch ranged from 0–243 m ($n = 27$). Nearest-neighbour distance ranged from 593-5023 m ($n=28$) and average density was 38 breeding pairs/100km^2. The minimum nearest-neighbour distance (593 m) was used to calculate a minimum breeding area size (= 28 ha), assuming breeding areas to be circular (Fig. 1).

Nearest-neighbour distance was negatively correlated with patch size ($r = -0.49$, $n = 28$, $p = 0.009$) and nearest-neighbour distances were smaller in LCP's than in SIP's (Mann-Whitney $U = 37$, $n = 28$, $p = 0.005$). The population as a whole had a G-stat value of 0.57, suggesting a random distribution. However, dispersion within LCPs was even (G-stat = 0.85), while dispersion of nests in SIPs was random (G-stat = 0.63).

Breeding sparrowhawks selected strongly for the larger patches (χ^2 = 17.9, df = 2, p <<0.01; Fig. 2). Larger patches contained more alternative nests per breeding area (r= 0.41, n = 27, p = 0.03). A graphical representation of the comparison between observed distance to the nearest edge and theoretical distance to the nearest edge of the patch suggests that sparrowhawks do, in some instances breed far from the edges of patches (Fig. 3). This finding is reinforced by the positive correlation between distance to the nearest edge and patch size (r = 0.67, n = 27, p <<0.001). However, many of the nests located deeper in the forest were close to access routes (e.g. forestry roads) that allow the birds an open approach to the nest, within the patch, under the canopy. Birds selected strongly for north-westerly facing edges (χ^2 = 23.3, df = 2, p <<0.01) (Fig. 4), but this had no impact on breeding success (Kruskal-Wallis ANOVA, H = 5.56, n = 70, p = 0.47). Sparrowhawks also selected for nest patches closer to suburbia than to indigenous Fynbos habitats (Wilcoxon Matched-pairs T = 75, n = 28, p = 0.003).

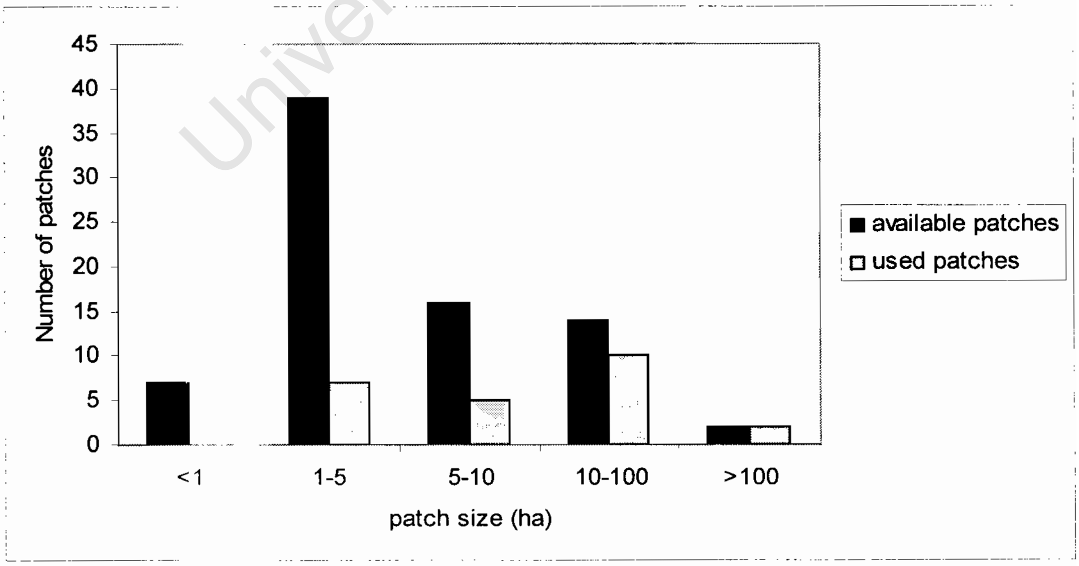

Figure 2 Patch size selection by Black Sparrowhawks on the Cape Peninsula, South Africa.

Productivity

Average breeding success for the population over the 5-year study period was 1.23 ± 0.96 fledglings per breeding attempt (n = 73, range = 0-3). Breeding success of individual pairs increased with increasing patch size (r = 0.42, n = 28, p = 0.03), was weakly correlated with distance from the nest to the edge of the patch (r = 0.36, n = 27, p = 0.06), but was not correlated with nearest-neighbour distance (r = -0.20, n = 28, p = 0.30). Although not significant (p<0.1), the influence of patch size on breeding performance was further emphasised when comparing LCPs and SIPs, productivity being higher in LCPs (Mann-Whitney U = 59, n = 28, p = 0.07).

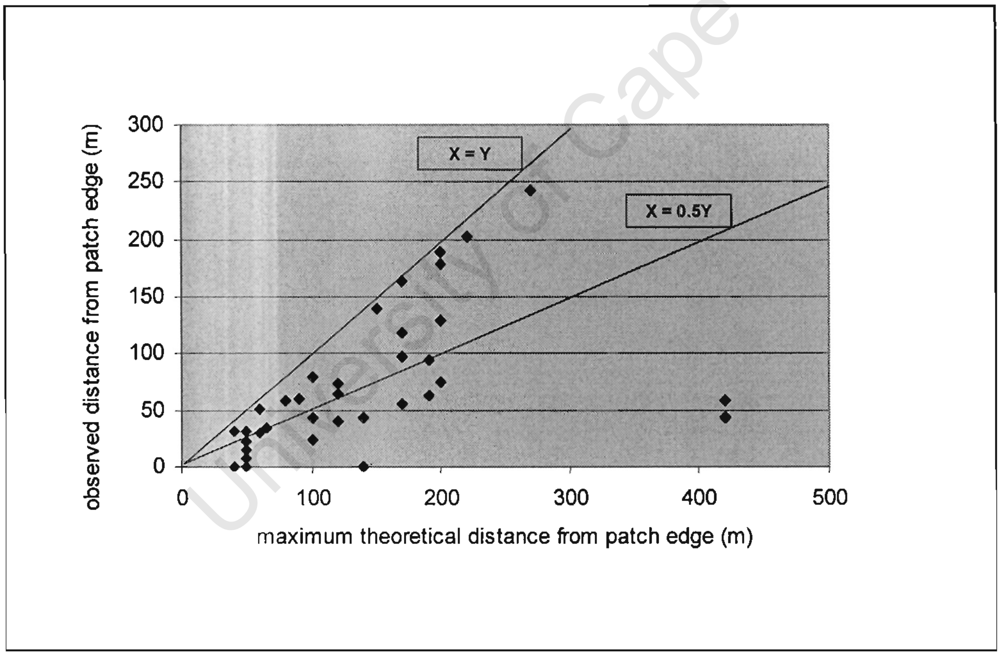

Figure 3 Maximum theoretical distance from the edge of the patch vs observed distance from the edge of Black Sparrowhawk nests on the Cape Peninsula, South Africa (n = 71 nests)

There was no significant difference in breeding performance between birds that bred closer to suburbia and those that bred closer to Fynbos (Mann Whitney U = 67, n = 28, p = 0.45), nor was variation in breeding success linked to the distance of the breeding area from the nearest suburban habitat (r = 0.22, n = 28, p = 0.26).

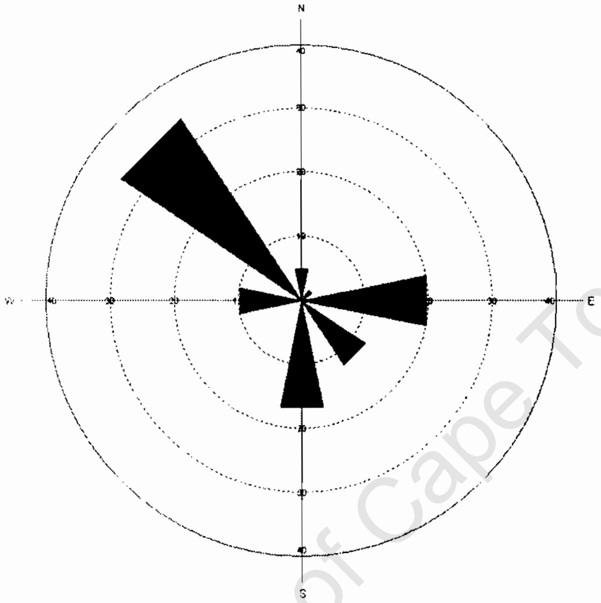

Figure 4 Orientation of Black Sparrowhawk nests (n=41) on the Cape Peninsula, South Africa.

Average annual breeding success was negatively correlated with average rainfall between March and November (r = -0.88, n = 5, p < 0.025) Fig. 5). However, this dataset included data from 2000 - a very dry year with only three known nests, each of which resulted in two fledglings. If this data point is removed, the trend remains unchanged, but loses significance (r = -0.84, n = 4, p > 0.1). Although the datasets were too small for any rigorous statistical testing, birds in larger patches appear to breed more successfully in drier years, while birds breeding in smaller patches do not appear to follow the equivalent pattern (Fig. 6).

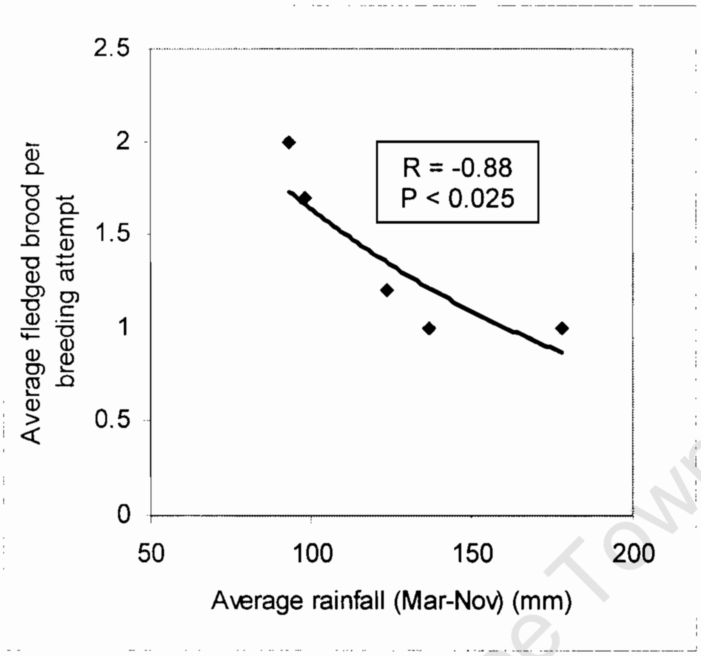

Figure 5 The effect of mean rainfall during the breeding season, on Black Sparrowhawk average annual breeding success on the Cape Peninsula, South Africa.

Egyptian Geese were present in 60% of territories. The siting of a sparrowhawk nest had no influence on its risk of goose parasitism in terms of either distance of the nest to the nearest edge (Mann Whitney U = 59, n = 25, p = 0.37), the size of the patch (Mann Whitney U = 54.5, n = 25, p = 0.25), or the distance to suburbia (Mann Whitney U = 66, n = 25, p = 0.62) vs Fynbos (Mann Whitney U = 59, n = 25, p = 0.37). However, the presence of a breeding pair of geese at the nest site in a given year did have a statistically significant negative impact on sparrowhawk productivity (Mann-Whitney U = 149.5, n = 43, p = 0.04). Of the 15 territories in which nests were parasitized by geese at any time during the study period, 12 (80%) already had or constructed alternative nest sites, while none of the birds in territories without geese made alternative nests. The distance between alternative nests within a breeding area ranged from 30 – 470 m (n = 31).

There was no difference in breeding success between sparrowhawk pairs that had alternative nests and those that did not (Mann-Whitney U = 63, n = 25, p = 0.5).

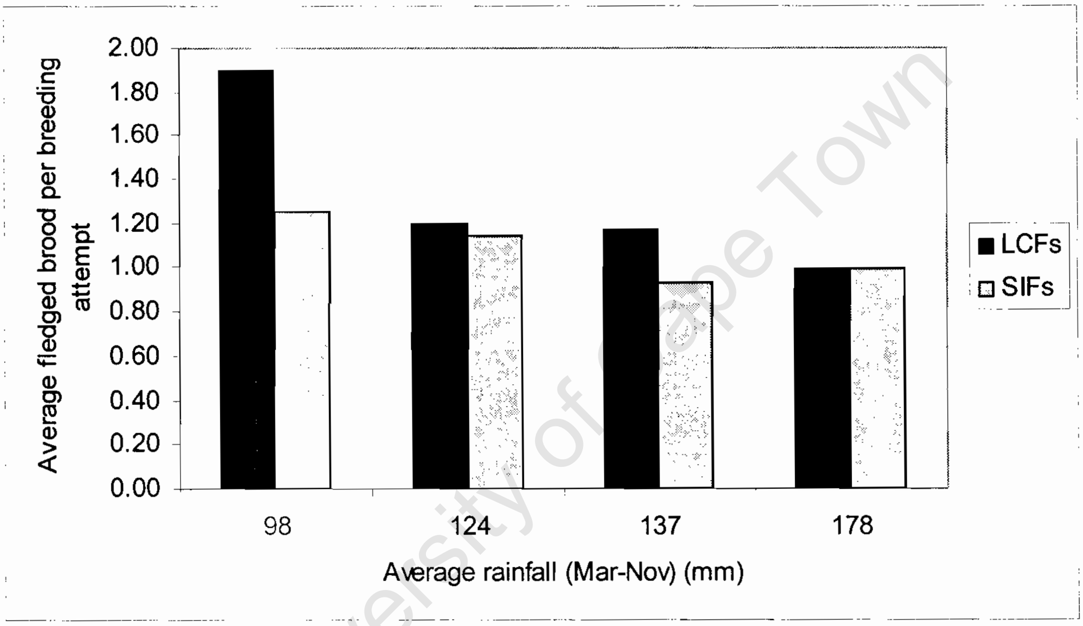

Figure 6 The effect of rainfall on Black Sparrowhawk breeding success in Large Continuous Patches (LCPs) vs. Small Isolated Patches (SIPs) on the Cape Peninsula, South Africa.

Discussion

Distribution of territories across patches

The Black Sparrowhawk is probably a fairly recent arrival on the Cape Peninsula (Curtis & Koeslag 2004, Hockey *et al.* 1999). The first nest was found in 1994 (Oettlé 1994), six years before the start of this study. Other nests were located subsequent to this one and most of these were found in the largest patch of continuous planted forest on the Peninsula (A. Jenkins & G. Malan pers. comm.), and it is very likely that this is where the colonisation process started (Fig. 1). The current distribution of the hawks supports this interpretation. The spatial arrangement of territories suggests that they accord to a despotic distribution (*sensu* Fretwell and Lucas 1970, Newton 1998), whereby the first arrivals settled in the highest quality patches, filling these territories first, with later arrivals or offspring being forced (because of territoriality by established pairs) to settle in suboptimal habitat patches. That the distribution is despotic rather than ideal free (Fretwell and Lucas 1970, Ferrer & Donazar 1996) is further supported by birds in large patches having a greater breeding success than those in small patches, despite being more closely spaced.

Distribution of nests within patches

The preference by Black Sparrowhawks for the largest available patches of forest was not predicted, although this is not unusual for the larger members of the genus *Accipiter* (e.g. Northern Goshawk - Woodbridge & Detrich 1994) and there appear to be certain benefits accruing to Black Sparrowhawks that use larger patches. Firstly, birds in larger patches bred further from the edge. One advantage of this is likely to be increased buffering from severe weather conditions (relative to pairs breeding in SIPs). The negative relationship between rainfall and productivity suggests that selecting nest sites with sufficient protection from weather may be all-important for sparrowhawks (Newton 1986). Sparrowhawk breeding on the Peninsula is unusual in that most pairs commence breeding during the winter rainfall period (Curtis & Koeslag 2004). In other parts of their range, which fall in summer-rainfall areas, Black Sparrowhawks start breeding during the dry winter months (typically July – Allan *et al.* in press). Thus, the Peninsula population encounters problems associated with weather that the birds do not necessarily experience in other parts of the species' range. Other nest-site parameters not measured in this study, such as canopy depth, may also play a role in providing a buffer for nests (Finn *et al.* 2002, Malan & Shultz 2002, Moore & Henny 1983). The second advantage in using a larger patch is that it affords the opportunities to build multiple (alternative) nests, simply because there is a greater selection of nest trees to choose from. Sparrowhawks select the largest trees within a stand in which to nest, probably because the taller leaf canopies of such trees offer a wider choice of nest positions (Malan & Robinson 2001). Despite the fact that pine plantations appear very uniform in terms of their component trees, large trees with a suitable nest-supporting branch structure may be fairly uncommon in a stand (pers. obs., Malan & Robinson 2001). Given the pressure from Egyptian Geese attempting to take over sparrowhawk nests, options for multiple nest sites may be the only means for sparrowhawks to avoid breeding failure due to goose parasitism.

Some sparrowhawk pairs, particularly those in large patches, bred closer to the centre of the patch than to the edge (Fig. 3). This was unexpected, and contrasts with Malan & Robinson's (2001) findings. However, in this study, I defined patch edges slightly differently to Malan & Robinson, who considered access roads within the forest as sufficient for defining the edges of patches. I did not recognise tracks or paths as edges for the purposes of this study, but all nests that were far from the edges of forest patches were close to tracks or paths, which can act as flyways for the hawks (Malan & Robinson 2001).

As predicted, sparrowhawks selected patches closer to suburbia than to indigenous Fynbos (Fig. 1). Black Sparrowhawk diet on the Peninsula, as elsewhere, is dominated by *Streptopelia* doves, columbids and, to a lesser extent, gamebirds (Malan & Robinson 1999, unpubl. data). These species are more abundant in man-altered environments than in Fynbos (Kemp 1993, Colahan 1997, Colahan & Harrison 1997, Rowan 1983), explaining the sparrowhawks' affinity for human settlements. It appears that individuals are selecting, above all, to breed close to their hunting grounds, and that orientation of the nest is of less importance. Therefore, although sparrowhawks may be buffered against bad weather by nesting far from the patch edge, they do not appear to make any effort to avoid winter storms by avoiding north-facing edges. Winter breeding is unique to this population (Curtis & Koeslag 2004), and may simply be the legacy of a recent colonisation; birds may not have had time to adapt to unusual breeding conditions (caused by different local weather conditions). Of importance in this scenario is that it is not yet known whether rainfall affects productivity directly, through chicks dying from cold and wet exposure (Newton 1986, Kostrzewa & Kostrzewa 1990), or indirectly, by impacting on adult hunting time, resulting in lower provisioning rates and an increased risk of chicks dying of starvation (Simmons 1986, Kostrzewa & Kostrzewa 1990). Thus, if rainfall affects productivity indirectly, orientation within the patch will be unimportant. If weather affects the hawks directly, however, orientation will be more important, but could be influenced by local geography (e.g. slope aspect) (Penteriani 2002).

In contrast to their northern hemisphere counterparts, the Northern Goshawk (which tends to range over a wider area and may have alternative nests up to 2.1 km apart (Woodbridge & Detrich 1994)), Black Sparrowhawks on the Cape Peninsula built alternative nests in the same patch of trees and nests were, at most, 470 m apart.

Nearest-neighbour distances were smaller and thus density of territories in the study population was greater than recorded in other studies of Black Sparrowhawks. Inter-nest distances range from 2.0–10.5 km in north-east South Africa and 1.9–10.0 km in Zimbabwe (Allan *et al.* in press). Density was also higher than recorded in similarly sized Northern Goshawks (DeStefano et al. 1994, Kostrzewa & Kostrzewa 1990, Penteriani *et al.* 2001, Penteriani 1997) and may be one of the highest recorded in any *Accipiter* of equivalent size. In large patches with multiple territories (Fig. 1), the nests are closest together and their spacing is even, suggesting that these sub-populations may have reached saturation.

Influences on breeding success

Unlike Northern Goshawks, which showed no variation in breeding success with patch size (Woodbridge & Detrich 1994), Black Sparrowhawks breeding in larger patches bred more successfully than those in smaller ones. This may be because birds in larger patches i) are able to position their nests further from the edge of the patch, and are thus more buffered from the effects of cold, windy and wet weather, or ii) are able to avoid interference from geese by having alternative nests. Because of the small sample size, it is impossible to tease these factors apart statistically to determine exactly what benefits birds derive by breeding in the largest patches, but some qualitative lines of evidence that can be followed. In both large and small patches, reproductive success is highest in dry years. However, the greatest increase in breeding success with decreasing rainfall occurs in large patches (Fig. 5). The steady pattern of increasing success with decreasing rainfall experienced in large patches is not mirrored in small patches, suggesting that small-patch breeders may be more uniformly negatively affected by wet weather (regardless of the amount of rain), perhaps reflecting reduced buffering from adverse weather. It would be necessary to determine whether rainfall affects productivity directly or indirectly in order to unravel the mechanisms involved.

The negative exponential relationship between rainfall and breeding success is interesting, as it suggests that some pairs will successfully fledge a chick, no matter what the rainfall in a particular year. The exceptionally long breeding season (lasting up to nine months – Curtis & Koeslag 2004) allows for some very early or very late breeders to avoid the heavy midwinter rain and thus increase their chances of breeding successfully.

Parasitism by Egyptian Geese may be the most significant influence on Black Sparrowhawk breeding success and appears to be an increasing problem for sparrowhawks because the number of geese breeding on the Peninsula is rising rapidly (pers. obs.). Goose numbers in urban areas in the south-western Western Cape were already increasing by the late 1980s, by which time they were suspected to have reduced the numbers of Hamerkops *Scopus umbretta* through nest parasitism (Hockey *et al.* 1989). Aggressive interactions between geese and sparrowhawks do occur, and several failed breeding attempts by sparrowhawks have been attributed to interference by geese (pers. obs., A Koeslag pers. comm.). Although it is not uncommon for Egyptian Geese to parasitize raptor nests (Davies & Allan in press) no other study has recorded this at such high frequencies, nor has any study demonstrated the significant impact that Egyptian Geese can have on the productivity of a raptor population.

Conclusions

Black Sparrowhawks on the Cape Peninsula breed in both large and small forest patches, but large forest patches support a higher density of territories than do small patches. Birds achieve, on average, highest productivity in the largest forest patches, even though there is some evidence that territories may have reached saturation density in such patches. Nests are closer to suburban habitats than to indigenous shrubland, presumably reflecting better hunting opportunities and higher prey densities in the former. Although pairs are more productive in large patches, there is considerable inter-year and inter-pair variability in success, probably linked respectively to weather, with a negative response to cold and rain, and nest parasitism by Egyptian Geese. Birds in large patches may be less affected by these stresses because their nests are more buffered against bad weather and they can (and do) build multiple nests, possibly to lessen the impact of goose parasitism.

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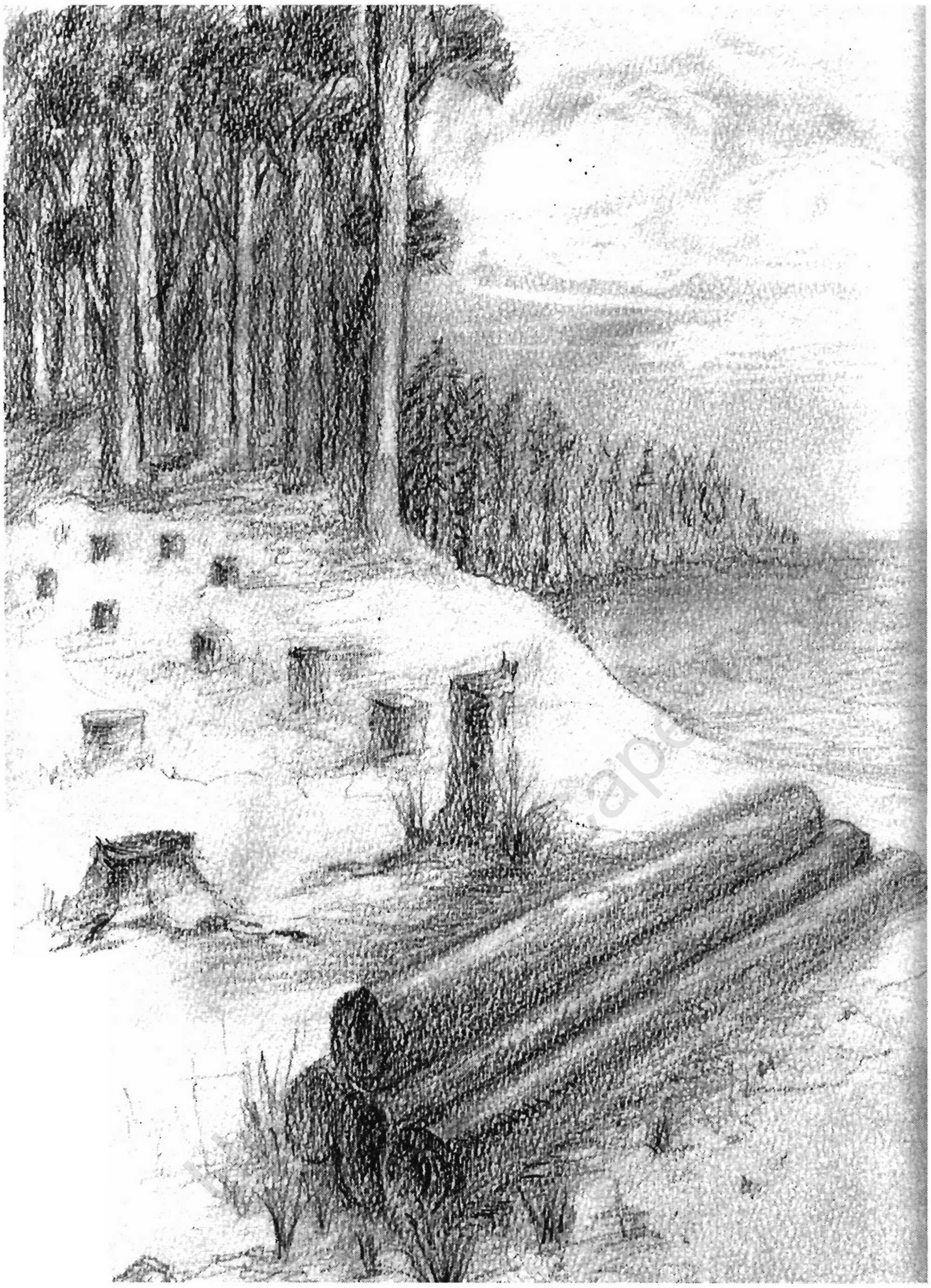
Territory	Nest name & number	Year	# chicks fledged	Nearest neighbour (nearest active nest)	Dist. To nearest neighbour (m)	Dist. To nearest edge (m)	Size (area) of patch (ha)	Distance to fynbos (m)	Distance to suburbia (m)
BC	BC	2003	2	Fern	1195	8	4	1773	45
	BC	2004	0	Shaus	1085	8	4	1773	45
CEC	Cec1	2001	0	Dhel1	1689	94	35	403	308
	Cec1	2004	2	Shaus	1254	94	35	403	308
	Cec2	2002	2	Dhel1	1544	63	35	511	348
	Cec2	2003	2	Dhel1	1671	63	35	511	348
CH	Ch1	2001	2	Lower1	963	65	22	2420	660
	Ch2	2002	1	Lower1	672	74	22	2439	446
	Ch3	2003	2	Lower2	673	65	22	2600	614
	Ch3	2004	2	Lower2	673	65	22	2600	614
DEER	Deer	2003	0	New1(2)	3201	35	4	40	151
	Deer	2004	2	New1(3)	3046	35	4	40	151
DHEL	DHel1	2001	2	Cec1	1544	98	26	124	262
	DHel1	2002	1	Cec2	1685	98	26	124	262
	DHel2	2004	1	Marlene	627	55	26	1676	55
FERN	Fernwood	2002	2	New2	903	58	15	1671	102
	Fernwood2	2004	0	New2	903	58	15	1671	102
HIGHER	Higher	2000	2	nest site not confirmed	-	-	-	-	-
	Higher	2001	1	Nlady	1214	43	190	1137	823
	Higher	2003	2	Arbor	1013	43	190	1137	823
KLK	KLK1	2002	2	Okloof	5023	129	18	774	168
	KLK1	2003	1	Okloof	5023	129	18	774	168
	KLK2	2004	2	Ryter	1553	178	18	574	184
LAKE	Lake	2001	0	Middle1	2971	15	4	94	195
	Lake	2002	0	Zwaans1	2960	15	4	94	195
	Lake	2004	0	Zwaans1	2960	15	4	94	195
LOWER	Lower 1	2000	2	-	-	75	53	3223	436

	Lower 1	2001	0	Ch1	963	75	53	3223	436
	Lower 1	2002	3	Ch2	672	75	53	3223	436
	Lower 2	2002	0	Ch3	673	189	53	3045	378
	Lower 2	2003	0	Ch3	673	189	53	3045	378
	Lower 2	2004	3	Ch3	673	189	53	3045	378
MARLENE	Marlene	2004	1	DHel2	606	30	3	2092	104
MIDDLE	Middle 1	2000	2	-	-	140	18	1700	213
	Middle 1	2001	1	Ch1	1278	140	18	1700	213
	Middle 2	2002	1	Zwaans1	853	30	6	1161	382
	Middle 3	2003	2	Higher	597	44	190	1473	411
	Middle 3	2004	0	Higher	597	44	190	1473	411
	Middle 4	2004	0	Ch3	796	140	18	1700	213
NLADY	NLady1	2001	0	Higher	1186	243	131	961	895
	NLady2	2002	0	Higher	1186	243	131	961	895
	NLady3	2004	1	Arbor	924	243	131	961	895
NEW1	New1(1)	2001	2	Fern	1883	44	27	199	284
	New1(2)	2002	2	New2	1257	24	27	184	286
	New1(2)	2003	2	New2	1257	24	27	184	286
	New1(3)	2004	0	New2	1094	80	27	139	501
NEW2	New2	2002	0	Fern	873	40	12	1089	416
	New2	2003	2	Fern	873	40	12	1089	416
	New2	2004	2	Fern	873	40	12	1089	416
NBORDER	Nborder	2004	2	Nlady2	942	202	131	198	878
OKLOOF	Okloof	2001	2	DHel1	2150	60	8	85	837
	Okloof	2002	1	Dhel1	2150	60	8	85	837
	Okloof	2004	0	Cec1	2505	60	8	85	837
PAG	Pag	2004	0	Pdrive	1430	0	3	1903	111
PDRIVE	Pdrive1	2001	1	DHel1	1685	0	7	0	93
	Pdrive1	2002	0	DHel1	1685	0	7	0	93
	Pdrive2	2004	2	DHel2	1284	32	7	103	229
RMEM	Rmem	2001	2	New1(1)	2314	51	3	194	190

	Rmem	2002	2	New1(2)	2482	51	3	194	190
	Rmem	2003	2	New1(3)	2482	51	3	194	190
	Rmem	2004	3	UCT	1283	51	3	194	190
ARBOR	Arbor	2003	3	Zwaans2	593	58	190	688	791
	Arbor	2004	0	Zwaans2	593	58	190	688	791
UCT	UCT	2004	2	Rmem	1266	22	7	193	184
ZONN	Zonn	2001	0	Cec1	3062	31	1	3143	323
	Zonn	2002	1	Cec1	3062	31	1	3143	323
	Zonn	2004	0	Shaus	1936	31	1	3143	323
ZWAANS	Zwaans1	2002	2	Middle2	898	163	190	386	237
	Zwaans1	2003	2	Arbor	593	163	190	386	237
	Zwaans2	2003	2	Arbor	593	118	190	337	197
	Zwaans2	2004	1	Middle3	1215	118	190	337	197
RPLAATS	Rplaats1	2004	0	KLK	1549	60	9	77	246
SHAUS	Shaus	2004	1	nest site not confirmed					
AVERAGE			**1.23**		**1501**	**77**	**49**	**1101**	**363**
STD. DEV.			**0.96**		**966**	**61**	**65**	**1056**	**246**
MIN			**0**		**593**	**0**	**1**	**0**	**45**
MAX			**3**		**5023**	**243**	**190**	**3223**	**895**



CHAPTER 3

Responses of raptors to habitat fragmentation: from individual responses to population susceptibility

CHAPTER 3

Raptors and habitat fragmentation: using species attributes to predict susceptibility to fragmentation effects

"There is widespread concern over the damage that humans are inflicting upon the environment...There is a need to be able to predict the consequences of such habitat loss for species of conservation concern."

- W. J. Sutherland 1996

Abstract

Habitat fragmentation has different effects on species and communities, depending on a suite of life-history and population traits; some species are more vulnerable to the effects of fragmentation than others. Much research has focused on identifying the traits that can best act as useful and accurate indicators of a species' fragmentation-linked extinction risk. In this study, I compare the responses of two sympatric species (the Black Harrier *Circus maurus* and the Black Sparrowhawk *Accipiter melanoleucus*) to habitat fragmentation. On a broader scale, I use a simple model of susceptibility to fragmentation effects, and a sample of hawks (*Accipiter* spp) and harriers (*Circus* spp) in the family Accipitridae, to predict which attributes predispose species to a negative response to habitat fragmentation. I then compare these predictions with the current global threat status of each species to test whether the model can predict threat status with acceptable accuracy. Black Harriers and Black Sparrowhawks differ substantially in their responses to habitat fragmentation. Most importantly, harriers are highly sensitive to patch size, in terms of their breeding distribution, while sparrowhawks are far more tolerant of fragmentation and are able to use relatively small patches for breeding. This is most likely because harriers use habitat patches for breeding and foraging and have thus responded poorly to opportunities created by the formation of a matrix of 'new habitats'. In contrast, Black Sparrowhawks use patches for breeding only and depend largely on the surrounding matrix for foraging. Despite their ability to make use of various patch sizes for breeding, sparrowhawk productivity decreases with decreasing patch size. This suggests that the relatively low productivity in small patches is nonetheless sufficient to maintain sustainable populations, The susceptibility model was able to make accurate predictions for the majority of threatened species, and identified a handful of species that may warrant some conservation consideration (which are not currently listed in the International Red Data Book). I conclude that even fairly crude biological data can assist in raising early warning flags for species more susceptible to fragmentation.

Introduction

The exponential increase in human populations and subsequent advent of technology has resulted in a rapid and extensive increase in agricultural activity (in the form of improved croplands, pastures and forestry), and the concomitant demise of natural habitats world-wide. A typical product of such loss is the formation of a series of isolated remnants of natural habitat, varying in size, quality and conservation potential, dispersed within an otherwise transformed matrix. Intuitively, these impacts must have deleterious consequences for ecosystems and individual species, as indeed has been demonstrated by a number of studies, covering taxa ranging from insects (Didham 1996, Shahabuddin & Riveros In press) to fish (Fagan *et al.* 2005), primates (Estrada *et al.* 2002, Chiarcello & de Melo 2001) and birds (Diamond *et al.* 1987, Kattan *et al.* 1994, Herket 1994, reviewed by Turner 1996). However, other studies have found weak responses to habitat fragmentation in, for example, plant communities (Kemper *et al.* 1999), small vertebrates (McCoy & Mushinsky 1994) and birds (Schmiegelow *et al.* 1997). Thus, the effects of fragmentation vary dramatically between taxa and species, begging the question, 'what attributes of a particular species render it resistant to, or prone to, the negative impacts of habitat fragmentation?'

Researchers have invoked a series of hypotheses which attempt to identify the most important life-history traits and population attributes that can be used as predictors of a species extinction risk. These include, *inter alia*, body size, rarity, ecological specialisation, matrix use, range size, and turnover rate (Henle *et al.* 2004, Manne & Pimm 2001). Explorations of these ideas have yielded conflicting results (particularly regarding body size as a predictor – Bennett & Owens 2002, Johst & Brandl 1997, Dobson & Yu 1993, Gaston & Blackburn 1993) and at present, there is no standard approach for making predictions about species' extinction risk. It is clear, however, that using a combination of species and population attributes is more useful and informative than using a single variable (Davies *et al.* 2004). For example, a large species with a restricted range is predicted to have a low tolerance of fragmentation and therefore, a high extinction risk. However, if the animal is a super-generalist, in terms of its habitat and dietary requirements, it may adapt relatively well to habitat change. Thus, examining multiple characteristics of the species helps develop a more realistic understanding of the potential threats that it faces.

Among birds, sensitivity to fragmentation has been linked to body size (with contrasting results - Bennett & Owens 2002, Gaston & Blackburn 1995) and habitat specialisation (Bennett & Owens 2002). Overall, habitat generalists are predicted to have more options when faced with habitat loss or change than do habitat specialists (such as inhabitants of forest interiors that both breed and hunt in this habitat). Similarly, species with broad dietary spectra are more likely to be resilient to fragmentation (because they can switch diet) than are dietary specialists constrained to one or two prey types (unless fragmentation increases the availability of this prey type).

The responses of raptors to fragmentation have been the subject of very little focused research, although it is generally accepted that, within the group, species respond differently to habitat loss, according to their ecological requirements (Thiollay 2000, Del Hoyo *et al.* 1994, Meyburg & Balen 1994). Certainly, habitat loss and fragmentation have been associated with many local extinctions and radical population decreases of raptor populations, such as the Madagascan Serpent Eagle *Eutriorchis astur* (Langrand & Meyburg 1984). Even within families, as in the case of the Accipitridae, there are some taxa affected negatively by fragmentation, while others, at least up to a certain degree of fragmentation, may be relatively unaffected or even benefit (e.g. from an increase in edge habitat – Malan & Robinson 2001). Thiollay & Meyburg (1988) studied the effects of fragmentation on 10 forest raptors on Java. All 10 species demonstrated some ability to cope with fragmentation, as they occurred at relatively high densities and had fairly wide distributions and habitat niches (i.e. were not solely dependent on the interiors of forest patches). Thus, they were able – to varying degrees - to make use of the matrix. However, they also concluded that the patch size that a particular species requires will be determined by the size of the species, as well as the extent to which the species uses the patch. In their study on the effects of patch size and territory occupancy in Northern Goshawks *Accipiter gentilis*, Woodbridge & Dietrich (1994) found that despite high levels of timber harvesting and fragmentation in important forest habitats, goshawk breeding densities were high. They also found a positive correlation between occupancy and patch size. Thus, although goshawks appeared tolerant of the level of fragmentation in the study area, they demonstrated a dependence on large patches for breeding, suggesting that there may be a limit to their tolerance.

The problem with making accurate predictions about fragmentation susceptibility in raptors is the difficulty in separating the historical effects of persecution, both direct and indirect, from present-day habitat loss. Some raptor populations have suffered radical decreases due to i) extraordinary levels of shooting (e.g. Hen Harriers in Scotland – Etheridge *et al.* 1997, large eagles in South Africa – Brown 1991) and ii) the deleterious effects of persistent agrochemicals (such as DDT) (Newton 1998). Thus, the present-day status of some raptor populations may reflect a combination of the legacy of historic persecution and the more recent threat of habitat loss. While persecution can be explained *post-hoc*, theoretically it should be possible to *predict* the effects of fragmentation, given a basic knowledge of the species' biology.

In this final chapter, I first compare the responses to, and associated consequences for two species within the family Accipitridae living in fragmented habitats. The Black Harrier *Circus maurus*, is a rare and localised, ground-nesting, dietary generalist, which has been negatively impacted by the effects of fragmentation within its core breeding range. The species now persists in shrubland patches, dispersed in a matrix of primarily agricultural lands, and to a lesser extent, urban sprawl and invasive alien vegetation (Chapter 1). The Black Sparrowhawk *A. melanoleucus*, is a fairly common, tree-nesting, bird-hunting specialist, with a range spanning most of the forested regions of Sub-Saharan Africa. It is dependent on mature forest trees for breeding and adjacent, open areas for foraging. It can tolerate, and even exploit, some degree of forest fragmentation (Malan & Robinson 2001), and has additionally benefited from patches of 'new habitat', formed by the introduction and spread of alien trees (Chapter 2). The level of sensitivity to fragmentation of these two ecologically different raptors, with different spatial, habitat and dietary requirements, are predicted to vary significantly. Thus, there will be different implications for their future conservation.

In the second part of this chapter, I develop a simple model of susceptibility to fragmentation effects, and use a sample of hawks (*Accipiter* spp) and harriers (*Circus* spp) in the family Accipitridae, to predict which attributes predispose species to a negative response to habitat fragmentation. I then compare these predictions with the current global threat status of each species (as developed by the IUCN Species Survival Commission – BirdLife International 2004) to test whether the model can predict threat status with any accuracy. The conservation implications for raptors living in fragmented systems are discussed.

Individual responses to fragmentation: comparisons between a harrier and a hawk

Use of habitat patches for breeding

The most important finding regarding the relative breeding dispersion of the two birds across natural habitat patches was in the selection of large *vs* small patches for breeding (Table 1). Black Harriers avoided patches <100 ha in size, except where levels of patch connectivity were adequate to support a breeding pair – i.e. although harriers occasionally used smaller patches, these were always sufficiently close to large, continuous patches of natural vegetation, thus increasing the total area of natural vegetation available within the birds' estimated foraging range (2800ha). In contrast, Black Sparrowhawks, although also avoiding the smallest patches (<1 ha) in the study area, made use of a wider array of patch sizes and showed no dependence on patch connectivity for breeding – i.e. they can, and do, breed in fairly small, isolated fragments.

Table 1 A comparison of responses of Black Harriers and Black Sparrowhawks to habitat fragmentation.

Black Harriers	**Black Sparrowhawks**
• Breed on the ground within a shrubland (e.g. renosterveld) patch.	• Breed in trees within a forest patch.
• Require a patch of >100ha, or a very closely connected series of smaller patches. In such situations, nests rarely >1 km apart.	• Can persist (and breed) in patches as small as 1 ha. Minimum inter-nest distances of about 500m means that patches <500m are unlikely to support more than one pair.
• Do not appear to favour a particular place in a patch – nest-site selection probably influenced by location of suitable microhabitats.	• Breed close to patch edge.
• No evidence of link between patch size and breeding success.	• Breeding success is reduced in smaller patches.
• Breeding distribution controlled by the availability of food and microhabitats.	• Breeding distribution controlled by territoriality.
• Hunt within the shrubland patch and avoid the matrix.	• Do not hunt in the forest patch, use the adjacent, open matrix

There were, however, performance-linked benefits for sparrowhawks that breed in large patches; these birds have, on average, the highest breeding success. This pattern can probably be attributed to two main factors: 1) large patches provide more buffering around nests from severe winter storms, and 2) large patches provide more opportunity to build alternative nests, thereby reducing the probability of breeding failure due to nests being usurped by Egyptian Geese *Alopochen aegyptiaca*. The fact that sparrowhawks use smaller patches, despite the negative implications for their productivity, suggests that low productivity in small patches may be sufficient to maintain Black Sparrowhawk populations. Alternatively, these populations are maintained by 'source' populations in adjacent, large patches. The former is likely to be the case, as there are other areas where sparrowhawk populations are apparently self-sustaining, despite the fact they breed only in small patches (e.g. Brede River, A. Jenkins, pers. comm.). Black Harrier productivity does not appear to be linked with patch size, at least within the range of patch sizes where harriers were recorded breeding during this study. Thus, fragmentation impacts both species, although these effects are reflected differently: harriers avoid small patches completely, while sparrowhawks use them despite the fact that their productivity decreases with decreasing patch size.

The responses of the two species to edge:patch area ratio differ. Black Sparrowhawks are typical 'edge species' (Malan & Robinson 2001), with an affinity for forest fringes (as they breed close to edges and probably forage mostly from and along edges). They therefore benefit from a certain amount of fragmentation, which creates more edges. Conversely, Black Harriers showed no affinity for the ecotones between patches and transformed land and thus did not benefit from an increased amount of edge habitat.

Black Sparrowhawks were randomly distributed in small, isolated patches, but evenly distributed in large, continuous tracts of forest (Chapter 2). This is probably because territoriality determines nest-spacing in sparrowhawks, irrespective of patch size. Black Harriers showed a similar dispersion, however, this is linked more with resource availability than with territoriality. Where local conditions demand it, i.e. where food availability is high and nesting habitat is localised and scarce, harriers are capable of breeding in loose colonies. However, where these resources are more evenly dispersed in the environment, breeding distribution becomes more dispersed and the birds are distributed according to the availability of patches that provide suitable nest sites.

Use of habitat patches for foraging

The difference in patch-size selection between harriers and sparrowhawks is likely to be rooted in the way in which the birds utilise patches of natural habitat vs the surrounding matrix of transformed habitats. The radio-tracking study (albeit based on small samples) of Black Harriers in Bontebok National Park, a large natural habitat patch surrounded by a matrix of pastures and croplands, demonstrated that harriers hunted almost exclusively within the habitat patch in which they nested and avoided using the adjacent matrix, even though it was readily available within their foraging range from the nest. Sparrowhawks on the other hand, rarely, if ever, forage in the forest patch in which they breed (or in any other forest patch), hunting almost exclusively in the surrounding urban matrix (where their favoured bird prey are abundant)

(Colahan 1997, Colahan & Harrison 1997, Kemp 1993, Rowan 1983) (Table 1).

Being strictly bird-hunters, sparrowhawks could be perceived as being more specialised than harriers, which vary their diet from rodents to reptiles, or birds, according to the availability of prey (Simmons *et al.* 2005, unpubl. data). However, being much larger than harriers, with a higher Reversed Sex Dimorphism Index (Allan *et al.* 1995, Simmons *et al.* 1995), Black Sparrowhawks can (and do) take a far broader spectrum of prey sizes, thereby being fairly generalised in terms of their bird prey-base (Malan & Robinson 1999, unpubl. data). Although harriers take a broader spectrum of prey types, they are constrained, by virtue of their size, to taking relatively small prey.

Species attributes and fragmentation: consequences for species vulnerability

The fact that two, near-sympatric members of the Accipitridae, with very different habitat requirements, show markedly different responses to habitat fragmentation, suggests that a simplistic explanatory model based on e.g. body size (in the absence of biological information) is unlikely to yield robust predictions about response to fragmentation at the species level. Based on body size alone, Black Sparrowhawks (the larger of the two species) are predicted to be more vulnerable to fragmentation than are Black Harriers. In reality, the reverse is true. What is needed is a more inclusive approach, which takes a number of life-history traits and population attributes into account.

To generate a crude 'Fragmentation Susceptibility Index' (FSI), dietary (D) specialisation and habitat (H) specialisation of all *Accipiter* and *Circus* species were each subjectively ranked on a scale of 0 (extreme generalist) to 1 (extreme specialist). The FSI was the product of these two values and thus itself ranged from 0 to 1. Dietary specialisation was ranked according to the relative degree of specialisation, where, for example, a species eating almost exclusively birds (e.g. Rufous-chested Sparrowhawk *A. rufiventris*) was more specialised than a species hunting 'mostly birds, but also some rodents' (e.g. Tiny Hawk *A. superciliosus*), which in turn, was more specialised than a generalist predator of small mammals, lizards and birds (e.g. Shikra *A. badius*) (Appendix 1). Habitat specialisation was ranked on a scale linked to the number of habitats used by each species. This was assumed to be linked to the species' likely response to fragmentation (Henle *et al.* 2000), as distinct from total habitat loss. For example, a species confined to forest interior (e.g. Nicobar Sparrowhawk *A. butleri*) ranks as more specialised than one using both the forest interior and the edge (e.g. Red-thighed Sparrowhawk *A. erythropus*), which itself would be more specialised than one using interior, edge and surrounding open areas (e.g. Slaty-mantled Sparrowhawk *A. luteoschistaceus)* (Appendix 1).

In order to link 'fragmentation susceptibility' (at the level of an individual) to the global vulnerability of the same species, FSIs were plotted against a crude Range Size Index (RSI) for each species. The breeding range of each species was ranked at intervals of 0.1 along a scale from 0.1 (highly range restricted, usually island taxa) to 1.0 (species with very extensive ranges, such as Northern Goshawk). The RSI of each species was calculated as 1-breeding range size: thus, a species with a very small range (such as Nicobar Sparrowhawk or Fiji Goshawk *A. rufitorques*) has a large RSI (Appendix 1). The purpose of these plots was not to assess (or even expect) a statistical relationship between the two indexes, but rather to follow the approach developed by Bond (1995) in an extinction risk model for plants, in which relationships between indices are categorized as a gradient of increasing extinction risk. The model cannot predict the strength of this risk, only its direction. For the purpose of simplicity, the model was divided into three categories (weak, medium and strong response to fragmentation) spaced equidistantly along both axes (Fig. 1).

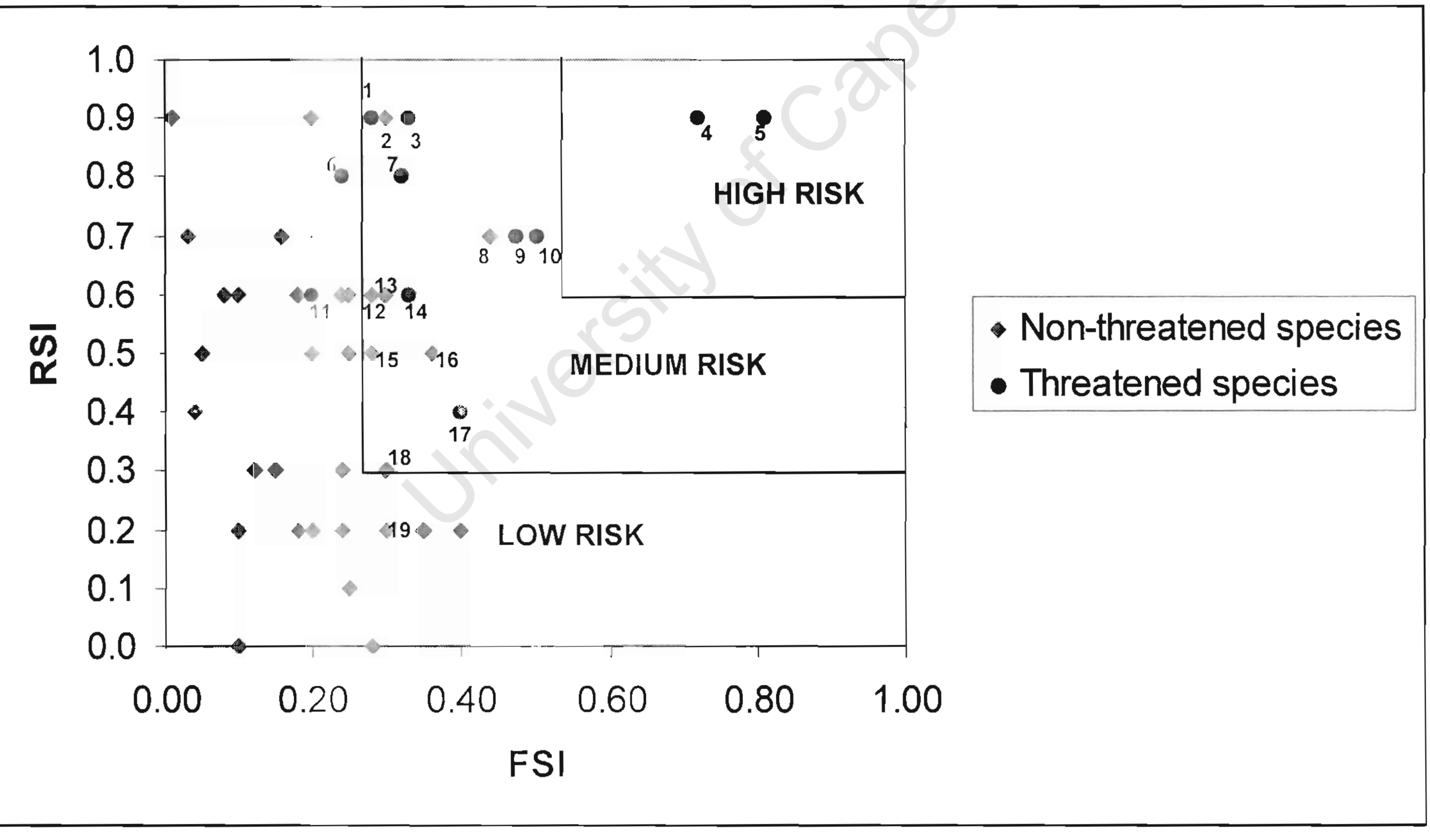


Figure 1 The Fragmentation Susceptibility Model: predicting the level of extinction risk due to fragmentation effects in *Accipiter* and *Circus* species, using

a breeding range size index RSI = 1 – range) plotted against a combined index of habitat specialisation (H) and diet specialisation (D) (H x D = FSI).

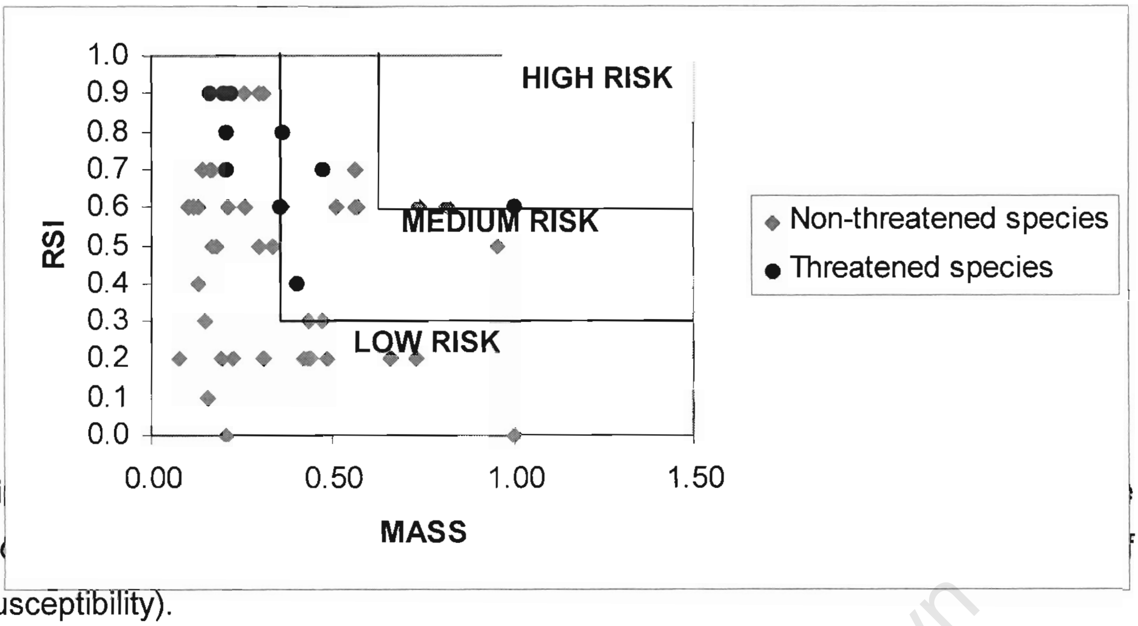
1) Réunion Harrier *C. maillardi,* 2) Pied Goshawk *Accipiter albogularis,* 3) White-bellied Goshawk *A. haplochrous,,* 4) Imitator Sparrowhawk *A. imitator*, 5) Nicobar Sparrowhawk *A. butleri,* 6) Slaty-mantled Sparrowhawk *A. luteoschistaceus,* 7) Gundlach's Hawk *A. gundlachi*, 8) Chestnut-flanked Sparrowhawk *A. castanilius,* 9) Black Harrier *C. maurus*, 10) Madagascar Sparrowhawk *A. madagascariensis,* 11) Madagascar Harrier *C. macrosceles*, 12) Black-mantled Goshawk *A. melanochlamys,* 13) Red-thighed Sparrowhawk *A. erythropus* 14) Henst's Goshawk *A. henstii,* 15) Rufous-chested Sparrowhawk *A. rufiventris*, 16) Tiny Hawk *A. superciliosus,* 17) Pallid Harrier *Circus macrourus*, 18) Cinereous Harrier *C. cinereus*, 19) Black Sparrowhawk *A. melanoleucus.*

Data on range size, habitat and diet were obtained from BirdLife International (2004), Ferguson-Lees & Christie (2001) and Del Hoyo *et al.* (1994). Threat categories and associated causes for decreases were obtained from BirdLife International (2004). Only those species for which there were sufficient data were included in the model.

The model assumes, as a starting point, that habitats are pristine i.e. that all taxa are 'starting from the same position.' It then attempts to predict relative responses of birds should these habitats become fragmented. The model also ignores any other anthropogenic impact on the birds, such as direct persecution and the effects of agrochemicals.

To assess whether the results of the model bore an acceptable relationship to the real world situation, the global conservation status (as determined from criteria developed by the IUCN Species Survival Commission – BirdLife International 2004) of each species was compared with the model's predictions of risk. BirdLife (2004) assigns threat status primarily according to population trends and population numbers. Thus, although range size is also an IUCN threat category indicator, the primary criteria used by BirdLife (2004) in assessing threat are not the same as those used in this model, ergo the IUCN threat categories can be used as a semi-independent standard for assessing the model's robustness.

It has been proposed that fragmentation susceptibility may also be linked to body size (with larger species expected to be more susceptible because of larger spatial requirements – Gaston & Blackburn 1995, although see Bennett & Owens 2002). To test whether this is true for the species examined here, an index of body mass was substituted for the FSI, scaled from 0 (smallest) to 1 (largest), in the susceptibility model (Fig. 2). These figures were calculated using the average mass for a species, as a percentage of the average mass of the largest species, the Northern Goshawk (which has a mass index of 1). Birds used in this analysis ranged in mean body mass from 83 - 1 000 g, but many species exhibit extreme sexual dimorphism – in some species by an order of magnitude, and mean mass is typically a poor reflection of the mass of either males or females. The model was unable to make any predictions about species' vulnerability using mass alone and so the original FSI was used in the model for analyses.



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susceptibility).

In total, 62 species were recognised within the genera *Circus* and *Accipiter* (BirdLife International 2004), but six were left out of the model, due to a lack of sufficient data (thus N = 56 species: Appendix 1). In summary, the model correctly predicted 82% of the threatened species and 84% of non-threatened species (Fig. 1). Forty of the 56 species fell within the 'low risk' category (Fig. 1). These were primarily generalist species (the maximum FSI being 0.3), although two had very small ranges, being confined to islands - Fiji Goshawk and Moluccan Goshawk *A. henicogrammus* (Fig. 1). In theory, a low risk species could also have a very large range and be highly specialized. No species fell into this category, implying that, among these two genera, there are no species that are both habitat and dietary specialists and also have a large range. Fourteen species fell into the medium-risk category and two into the high-risk category (Fig. 1). Nine of these 16 species (medium- and high-risk combined) are island endemics, namely Réunion Harrier *C. maillardi*, Pied Goshawk *A. albogularis*, White-bellied Goshawk *A. haplochrous*, Imitator Sparrowhawk *A. imitator*, Nicobar Sparrowhawk, Gundlach's Hawk *A.*

gundlachi, Madagascar Sparrowhawk *A. madagascariensis*, Black-mantled Goshawk *A. melanochlamys* and Henst's Goshawk *A. henstii* (Fig. 1). The remaining seven species (Chestnut-flanked Sparrowhawk *A. castanilius*, Black Harrier, Red-thighed Sparrowhawk, Red-chested Sparrowhawk, Tiny Hawk, and Pallid *C. macrourus* and Cinereous *C. cinereus* Harriers) are continental species.

Eleven (20%) of the 56 species are included in the International Red Data Book (IRDB - BirdLife International 2004 (Appendix 1). Nine of these appear in either the medium- or high-risk categories, and all are threatened primarily by habitat loss or degradation (including by fragmentation – BirdLife International 2004). Two of the threatened species are predicted by the model to fall into the low-risk category - Slaty-mantled Sparrowhawk and Madagascar Harrier *C. macrosceles* (Fig. 1). Both of these species are island-group endemics, thus have restricted ranges. However, both species are very generalised in terms of their diet and to a lesser extent, their habitat requirements. Thus, it could be predicted that they should be tolerant of a limited amount of fragmentation. However, the island habitats to which they are restricted are under severe threat, mainly due to habitat loss (Ferguson-Lees & Christie 2001), thus both species are classified as *Vulnerable* (BirdLife International 2004).

Seven non-threatened species, as classified by BirdLife International (2004) fell into the medium-risk category, namely Pied Goshawk, Chestnut-flanked Sparrowhawk, Black-mantled Goshawk, Red-thighed Sparrowhawk, Rufous-chested Sparrowhawk, Tiny Hawk and Cinereous Harrier (Fig. 1). All have RSIs ≥ 0.3 and FSIs from 0.28 - 0.44 – i.e. they are fairly, but not extremely, specialised. Although these species are not currently listed as globally threatened in the IRDB, they might be important research/conservation focal points in future, particularly those with very restricted ranges, such as Pied Goshawk. Some species, such as the Rufous-chested Sparrowhawk, although predicted by the model as potentially threatened, have adapted to the spread of alien trees and, as a result, have expanded their ranges. Therefore, despite a fairly restricted range and a highly specialised bird diet, the species has managed to exploit man-altered environments and is unlikely to be threatened by habitat loss in many parts of its range.

In terms of the two main target species of this study, both Black Sparrowhawks and Black Harriers have fairly high FSIs (0.30 and 0.40 respectively – Fig. 1), but the Black Harrier, a globally *Vulnerable* species, is ranked as being at considerably higher risk due to its much smaller range and greater sensitivity to habitat quality.

General discussion

Although a larger bird and possibly a more specialised species in terms of its diet, the Black Sparrowhawk is far more tolerant of fragmentation than is the Black Harrier. The reason for this lies in the different ways in which the two species use patches: Black Sparrowhawks use, and in fact, depend on, the surrounding matrix, comprising a variety of open habitats, while harriers depend almost exclusively on natural habitats. Thus, increasing fragmentation and an expanding matrix have negative consequences for harriers, while sparrowhawks can tolerate and exploit such habitat loss up to a point. What this threshold is has not been established. Therefore conservation-management strategies for Black Sparrowhawks may simply involve maintaining adequately sized patches of mature trees, within a productive (in terms of prey), open matrix, although larger patches will ensure greater productivity and possibly, more viable and sustainable populations. Conversely, maintaining sufficient habitat for Black Harriers is more complicated, and rests on the maintenance of large, continuous, or well-connected tracts of high-quality natural habitat.

Even apparently similar species may respond differently, due to subtle differences in their ecology. For example, despite considerable overlap in their use of resources, Ferruginous *Buteo regalis* and Swainson's Hawks *B. swainsonii* differ in their responses to habitat change. This can be attributed to differences in the two species' ecology and more specifically, their prey utilisation (Schmutz 1987). A similar principle applies to members of the genus *Circus*, where despite similar nesting requirements, body size and methods of hunting, some species have exploited altered habitats (e.g. Montagu's Harrier– Arroyo *et al.* 2002, Cinereous Harrier – Figueroa & Corales1999), while others, such as Black and Pallid Harriers, are seemingly less adaptable or unable to do so (Chapter 1, Serebryakov 1997).

Within *Accipiter*, it appears that species which use the habitat matrix require smaller patches of forest trees (e.g. Henst's Goshawk), while those that avoid the matrix and hunt in forest interiors are unlikely to persist in small, isolated stands of trees (e.g. Nicobar Sparrowhawk). The Black Sparrowhawk's northern counterpart, the Northern Goshawk, although also a large and fairly specialised species, appears to be equally successful in exploiting a certain amount of fragmentation (Bijlsma & Sulkava 1997, Woodbridge and Dietrich 1994) and thus has been little affected by changes to its habitat. In contrast, Gundlach's Hawk, the only globally *Endangered* species of *Accipiter*, is threatened because of a combination of small range and specialised dietary requirements. Having a small range, however, does not automatically qualify a species as potentially threatened – the island-endemic Fiji Goshawk, for example, is a habitat and dietary generalist (Appendix 1), and is thus able to tolerate some degree of fragmentation (Ferguson-Lees & Christie 2001).

Intuitively one would expect larger-bodied species, assumed to have the greatest spatial requirements, to be most prone to extinction as a result of habitat loss. However, this is not always the case (Johst & Brandl 1997, Fig. 2). The two target species of this study are also a case in point. Black Sparrowhawks are considerably larger than Black Harriers, yet fragmentation has to proceed very much further before the former are negatively impacted. Among the species used in the model, body mass ranged from *ca* 80 -1000 g, a relatively small range compared with the overall range in raptor body mass, which is ca 40 - 9000 g. Within the former size range, body mass was not nearly as effective a predictor of extinction risk as were species' ecological attributes. If the same model was to include all raptors, the extinction risk of those species at either extreme of the size spectrum may be predicted correctly, but within subsets of the body size range, the model's resolution would continue to be poor.

In addition to using a simple model such as this for identifying conservation priority species, the current extent of habitat destruction within the species' range also needs to be taken into account. This model is useful in predicting responses to a certain level of fragmentation, but cannot be used to predict the effects of complete habitat loss, nor does it account for direct and indirect persecution. This is likely to explain why the threat status of two globally threatened species (Slaty-mantled Sparrowhawk and Madagascar Harrier) could not be predicted by the model: extensive habitat losses within their already limited ranges has severely impacted these populations.

Conclusions

This study suggests that even fairly crude biological data, such as species range and degree of habitat and dietary specialisation, can assist in raising warning flags about a species' expected susceptibility to fragmentation – and thus, their extinction risk. However, simple extrapolations of risk, based for example on body size, are very unlikely to generate even vaguely accurate predictions about species–level threats arising from fragmentation (Fig. 2).

Species dependent on remnant patches for all aspects of their existence may be those most prone to local extinction, whereas those dependent on the patch for only a limited suite of their requirements may be able to persist, or even thrive, in much smaller patches. This study also reinforces the notion that if scientists are to become more accurate in predicting the relative responses of species as patch sizes decrease, it is of fundamental importance to understand precisely why a particular species needs the patch. We should not underestimate the importance of 'basic' biological data, which can be used in simple models such as this one, and applied to conservation planning. That even such basic data do not exist for

10% of accipiters (most of which are in the RDB- Appendix 1) is, in itself, a cause for concern.

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Species common name	Species Latin name	1 - range	Habitat specialisation (H)	Diet specialisation (D)	Body mass (M)	HD	HDM	Threat status (IRDB)	Risk category according to model's predictions
Northern Goshawk	*Accipiter gentilis*	0.0	0.5	0.2	1.00	0.10	0.10	LC	LOW
Eurasian Sparrowhawk	*Accipiter nisus*	0.0	0.4	0.7	0.21	0.28	0.06	LC	LOW
Shikra	*Accipiter badius*	0.1	0.5	0.5	0.16	0.25	0.04	LC	LOW
Bicolored Hawk	*Accipiter bicolor*	0.2	0.2	0.5	0.31	0.10	0.03	LC	LOW
Little Sparrowhawk	*Accipiter minullus*	0.2	0.3	0.6	0.08	0.18	0.01	LC	LOW
Cooper's Hawk	*Accipiter cooperii*	0.2	0.5	0.4	0.43	0.20	0.09	LC	LOW
Montagu's Harrier	*Circus pygargus*	0.2	0.5	0.4	0.31	0.20	0.06	LC	LOW
Ovambo Sparrowhawk	*Accipiter ovampensis*	0.2	0.4	0.6	0.20	0.24	0.05	LC	LOW
Northern Harrier	*Circus cyaneus*	0.2	0.5	0.6	0.44	0.30	0.13	LC	LOW
Black Sparrowhawk	*Accipiter melanoleucus*	0.2	0.5	0.7	0.73	0.35	0.26	LC	LOW
African Goshawk	*Accipiter tachiro*	0.2	0.7	0.5	0.23	0.35	0.08	LC	LOW
African Marsh Harrier	*Circus ranivorus*	0.2	0.8	0.5	0.49	0.40	0.19	LC	LOW
Western Marsh Harrier	*Circus aeruginosus*	0.3	0.6	0.2	0.66	0.12	0.08	LC	LOW
Long-winged Harrier	*Circus buffoni*	0.3	0.5	0.3	0.47	0.15	0.07	LC	LOW
Sharp-shinned Hawk	*Accipiter striatus*	0.3	0.4	0.6	0.15	0.24	0.04	LC	LOW
Cinereus Harrier	*Circus cinereus*	0.3	0.5	0.6	0.43	0.30	0.13	LC	LOW
Eastern Marsh Harrier	*Circus spilonotus*	0.3	0.6	0.2	0.66	0.12	0.08	LC	LOW
Japanese Sparrowhawk	*Accipiter gularis*	0.4	0.1	0.4	0.13	0.04	0.01	LC	LOW
Pallid Harrier	*Circus macrourus*	0.4	0.8	0.5	0.40	0.40	0.16	NT	MEDIUM
Brown Goshawk (Australian Goshawk)	*Accipiter fasciatus*	0.5	0.5	0.1	0.30	0.05	0.02	LC	LOW
Collared Sparrowhawk	*Accipiter cirrocephalus*	0.5	0.4	0.5	0.18	0.20	0.04	LC	LOW
Crested Goshawk	*Accipiter trivirgatus*	0.5	0.5	0.5	0.34	0.25	0.08	LC	LOW
Rufous-chested Sparrowhawk	*Accipiter rufiventris*	0.5	0.4	0.7	0.17	0.28	0.05	LC	LOW
Tiny Hawk	*Accipiter superciliosus*	0.5	0.6	0.6	0.96	0.36	0.35	LC	MEDIUM
Frances's Sparrowhawk	*Accipiter francesii*	0.6	0.4	0.2	0.13	0.08	0.01	LC	LOW
Sulawesi Goshawk	*Accipiter griseiceps*	0.6	0.5	0.2	0.51	0.10	0.05	LC	LOW
Australian Marsh Harrier	*Circus approximans*	0.6	0.6	0.3	0.74	0.18	0.13	LC	LOW
Meyer's Goshawk	*Accipiter meyerianus*	0.6	0.5	0.4	0.82	0.20	0.16	LC	LOW
Spotted Harrier	*Circus assimilis*	0.6	0.5	0.4	0.56	0.20	0.11	LC	LOW
Madagascar Harrier	*Circus macrosceles*	0.6	0.5	0.4	0.36	0.20	0.05	VU	
Levant Sparrowhawk	*Accipiter brevipes*	0.6	0.4	0.6	0.22	0.24	0.05	LC	LOW
White-breasted Hawk	*Accipiter chionogaster*	0.6	0.4	0.6	0.15	0.24	0.04	LC	LOW
Plain-breasted Hawk	*Accipiter ventralis*	0.6	0.4	0.6	0.15	0.24	0.04	LC	LOW
Grey-headed Goshawk	*Accipiter poliocephalus*	0.6	0.5	0.5	0.11	0.25	0.03	LC	LOW

Besra	*Accipiter virgatus*	0.6	0.5	0.5	0.12	0.25	0.03	LC	LOW
Pied Harrier	*Circus melanoleucus*	0.6	0.5	0.5	0.36	0.25	0.09	LC	LOW
Black-mantled Goshawk	*Accipiter melanochlamys*	0.6	0.6	0.5	0.26	0.28	0.08	LC	MEDIUM
Red-thighed Sparrowhawk	*Accipiter erythropus*	0.6	0.6	0.5	0.12	0.30	0.04	LC	MEDIUM
Henst's Goshawk	*Accipiter henstii*	0.6	0.5	0.6	1.00	0.33	0.30	NT	MEDIUM
Chinese Goshawk	*Accipiter soloensis*	0.7	0.3	0.1	0.17	0.03	0.01	LC	LOW
Spot-tailed Goshawk	*Accipiter trinotatus*	0.7	0.8	0.2	0.14	0.16	0.02	LC	LOW
Grey Goshawk	*Accipiter novaehollandiae*	0.7	0.7	0.3	0.56	0.21	0.12	LC	LOW
Chestnut-flanked Sparrowhawk	*Accipiter castanilius*	0.7	0.8	0.6	0.16	0.44	0.08	LC	MEDIUM
Madagascar Sparrowhawk	*Accipiter madagascariensis*	0.7	0.8	0.59	0.21	0.47	0.10	NT	MEDIUM
Black Harrier	*Circus maurus*	0.7	0.8	0.6	0.47	0.50	0.23	VU	MEDIUM
Slaty-mantled Goshawk	*Accipiter luteoschistaceus*	0.8	0.6	0.4	0.21	0.24	0.05	VU	LOW
Gundlach's Hawk	*Accipiter gundlachi*	0.8	0.4	0.8	0.36	0.32	0.12	EN	MEDIUM
Fiji Goshawk	*Accipiter rufitorques*	0.9	0.1	0.1	0.26	0.01	0.00	LC	LOW
Rufous-necked Sparrowhawk	*Accipiter erythrauchen*	0.9	0.5	0.4	0.30	0.20	0.06	LC	LOW
Moluccan Goshawk	*Accipiter henicogrammus*	0.9	0.5	0.4	0.30	0.20	0.06	LC	LOW
Reunion Harrier	*Circus maillardi*	0.9	0.7	0.4	0.36	0.28	0.05	EN	LOW
Pied Goshawk	*Accipiter albogularis*	0.9	0.5	0.6	0.31	0.30	0.09	LC	MEDIUM
Rufous-thighed Hawk	*Accipiter erythronemius*	0.9	0.5	0.6	0.16	0.30	0.05	LC	LOW
White-bellied Goshawk	*Accipiter haplochrous*	0.9	0.8	0.4	0.22	0.33	0.07	NT	MEDIUM
Imitator Sparrowhawk	*Accipiter imitator*	0.9	0.9	0.8	0.20	0.72	0.14	VU	HIGH
Nicobar Sparrowhawk	*Accipiter butleri*	0.9	0.9	0.9	0.16	0.81	0.13	VU	HIGH
(New Britain Sparrowhawk	*Accipiter brachyurus*	DATA DEFICIENT						VU	
Collared Hawk	*Accipiter collaris*	DATA DEFICIENT						NT	
Small Sparrowhawk	*Accipiter nanus*	DATA DEFICIENT						NT	
Grey-bellied Goshawk	*Accipiter poliogaster*	DATA DEFICIENT						LC	
New Britain Sparrowhawk	*Accipiter princeps*	DATA DEFICIENT						NT	
Vinous-breasted Sparrowhawk	*Accipiter rhodogaster*	DATA DEFICIENT						LC	

** shaded areas denote threatened species