the spatial ecology off the Guina (Oncifelis guigna) in Southern Chile

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The Spatial Ecology of the Güiña (*Oncifelis guigna*) in Southern Chile

by

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2004

This thesis is submitted in candidature for the degree of

Doctor of Philosophy

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Declaration

The material contained in this thesis has not previously been submitted for a degree at the University of Durham or any other university. The field research presented within this thesis was conducted with the help of Raleigh International volunteers, expeditions 1997H, 1998A, 1998H, 1999A, 1999I, 2000A, 2000I and 2001A. All data collation was conducted by the author apart from expeditions 1997H and 1998A, which were overseen by Dr L. Durbin and Dr I. Wyllie, respectively. All analyses were conducted by the author.

Cats no less liquid than their
shadows
Offer no angles to the wind
They slip, diminished, neat through
loopholes
Less than themselves; will not be
pinned

A.S.J.Tessimond

This thesis is dedicated to anyone who has ever attempted to track a cat in its element.

The Spatial Ecology of the Güiña (Oncifelis guigna) in Southern Chile.

PhD thesis submitted by Rachel A. Freer 2004

Abstract

This thesis describes the diet, activity, home range and habitat utilisation of güiña (*Oncifelis guigna*) within two populations located inside regions of minimal anthropogenic disturbance in southern Chile. Fieldwork was comprised of several components: güiña captured in live traps were fitted with radio collars and monitored on foot using standard radiotelemetry techniques; landcover maps were created for each study area from satellite data, aerial photography and ground truthing, and the relative abundance and diversity of potential small mammal prey were assessed by means of grid-based live-trapping studies and tree-mounted hair-traps.

The behavioural data obtained from the radiotelemetry study were analysed using RANGES V to assess the area requirements of the güiña and to determine how the home ranges and movements of individuals were distributed with respect to those of conspecifics. This data was also investigated with reference to the landcover maps generated for each site to identify habitat categories that were preferentially utilised or avoided by güiña. The diet of this species was determined via faecal analysis. The composition of the güiña diet within each site was then related to small mammal relative abundances determined in the field.

Small mammals, particularly rodents represented the major component of the güiña diet, and no evidence of prey selection was determined. Trapping surveys indicated both sites had abundant prey resources in the form of relatively dense rodent populations. Radiocollared güiña were largely arrhythmic in their activity pattern and neighbouring individuals within both populations showed a high degree of spatial overlap, both within and between sexes. Core use areas also overlapped extensively, and no evidence was found to indicate that güiña actively avoid conspecifics. These cats exhibited a consistent preference for relatively dense, thicket-forest habitat over less complexly structured vegetation, including stands of *Nothofagus* forest, the habitat category previously assumed to be key for this species.

The results of this study are discussed within the context of conservation management for the continued survival of this endangered felid.

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Chapter 1

Introduction and General Background

1.1 Introduction

As conservation agencies and land managers struggle to stem the current 'extinction crisis' they are often faced with having to decide where limited resources might best be employed for maximum benefit. To this end, many criteria have been applied to the determination of whether particular species or taxonomic groups are pivotal in terms of conservation status. Priority is typically given to those that are considered vulnerable to extinction and/or likely to become extinct in the absence of human intervention; vulnerability being indicated by biological traits such as low genetic variability, few and/or small or declining populations, specialised niche requirements, narrow geographical range, or a history of exploitation or persecution by humans (Terborgh, 1974; Wilson, 1987; McKinney, 1997; Purvis *et al.*, 2000). Conservation efforts may also focus on indicator species (those that reflect environmental quality and critical damage), keystone species, (those that play a pivotal role in ecosystem stability) (Paine, 1995; Power and Mills, 1995; Power *et al.,* 1996), umbrella species (species with demanding habitat requirements that, if protected, indirectly afford protection to other taxa), and flagship species (popular, often charismatic species that attract much favourable public attention) (Heywood, 1995; Meffe and Carroll, 1997; Simberloff, 1998).

Good-quality life history information is fundamental to the development of conservation management guidelines for focal species. Base-line data that describe the distribution, social organisation, habitat associations or resource requirements of species for example facilitate prioritisation among taxa and sites, as well as the prediction of population responses to future ecological or management scenarios. Within the fields of conservation biology and wildlife management, successful conservation strategies require that species-environment relationships are understood within the context of patterns and processes of change that occur at the landscape scale, such as habitat loss and fragmentation (Haslett, 1990; Maehr and Cox, 1995; Knick and Dyer, 1997; Myers, 1997). Recent investigative studies in landscape ecology (Forman, 1995; Hanson *et al.,* 1995) and community ecology (Hanski and Gilpin, 1997) are united in their emphasis on 'spatial ecology' (see Tilman and Kareiva, 1997), the central premise of this concept being the manner in which landscape configuration influences the population and community dynamics of species.

Habitat loss, alteration, and fragmentation represent the most serious and widespread threats to biological diversity (Groombridge, 1992; Bibby, 1995; Ehrlich, 1995; Thomas and Morris, 1995). Fragmentation of native habitats can reduce once continuous coverages to the point where mere remnants of original habitat remain within a modified matrix (Miller and Cale, 2000). As distances between these patches increase, the probability of extinction for populations dependent on that habitat also increase. Simultaneously, the probability of recolonisation by individuals from surviving populations diminishes (Verboom *et al.,* 1991). Over time the degradation, fragmentation and substitution of original habitat can result in the loss of populations, and ultimately species (Katten *et al.,* 1994; Koopowitz *et al.,* 1994; Short and Turner, 1994). Conservation strategies must therefore consider not only the amount of suitable habitat that must be retained, but also the spatial configurations of habitat across landscapes of concern (Cutler, 1991; Pulliam *et al.,* 1992).

One of the keys to predicting animal distribution lies in the ability to develop spatially referenced estimates of key environmental resources on a landscape-wide basis. This requires that environmental models be integrated, for example within a Geographical Information System (GIS), to generate the necessary spatial data. The growing accessibility of remotely sensed data and GIS software has encouraged the extensive application of such an approach to a wide variety of management problems, including the design of species-specific conservation strategies from a landscape perspective (for example, Haslett, 1990; Doak and Mills, 1994; Maehr and Cox, 1995; Pearson *et al.,* 1999).

A number of empirical models, for example probabilistic functions and qualitative rules, are increasingly being applied within a spatially explicit context towards the prediction of species' occurrence and/or survival, or towards establishing conservation priorities (Margules and Austin, 1994). Such models are commonly based on the association of species presence-absence data with quantitative patterns of landscapes; their outcomes interpreted in terms of habitat suitability (Buckland and Elston, 1993; Boyce and McDonald, 1999). Predictive geographical modelling may further be applied to the assessment of future environmental alteration and the potential impact on species' distributions (for example, climate change; Kienast *et al.,* 1996; 1998). The value of empirical models has been particularly emphasised for the investigation of conservation problems where species are highly vulnerable to habitat alteration or have large spatial requirements.

That the order Carnivora is the focus of intense attention in conservation biology and receives a disproportionately large share of available resources reflects the importance society attaches to a group that represents less that 1% of known vertebrate species. Many of the biological traits indicative of extinction vulnerability apply to carnivores (Myers, 1994; Noss and Csuti, 1994; Terborgh *et al.,* 1999). Their position at the top of the food chain, relatively low reproductive rates and often specific habitat requirements mean that these species require large areas over which to forage and are often vulnerable to ecosystem alteration and loss. The preservation of habitat for carnivores therefore frequently requires integrative ecosystem management at broad spatial scales (e.g., Wikramanayake *et al.,* 1998; Merrill *et al.,* 1999; Mladenoff *et al.,* 1999; Carroll *et al.,* 2001). Consequently, many other species within the same ecosystems also potentially benefit from such management regimes (Noss *et al.,* 1996).

Whereas considerable research and conservation effort has been directed towards the large, widely recognised carnivores, smaller, more cryptic species have received comparatively little attention. The güiña, *Oncifelis guigna* is one such species, and one that potentially meets all the criteria for priority attention listed previously. It is a small felid native to Chilean and Argentinean Patagonia and has the smallest geographic range of any of the New World felids. The güiña appears to have a very specific association for a shrinking habitat resource and it is believed this cat has been extirpated from many sites within its former range (Nowell and Jackson, 1996). In the past it has been hunted as a predator of poultry and this practice may continue still in agricultural regions. Despite this there is much local interest in this rarely observed animal, and the potential for flagship status is high.

1.2 The güiña, *Oncifelis guigna* (Molina, 1782)

The güiña (pronounced 'hwee-nya') is a small and little-known felid from southern Chile and Argentina. First described by Juan Iguacio Molina a Chilean librarian, this species remained relatively unknown to science until the German naturalist Philippi noted its presence in the Valdivian Region of Chile and published the first description of this species (Philippi, 1873). Outside of its geographic range the güiña was until recently known only from museum specimens, the majority of which were collected during the 1920s and 1930s. Until this study (and that of Sanderson *et al.* (2002) on Isla Grande de Chiloé) began, no study of this species had been conducted, and the limited information relating to the güiña was largely anecdotal.

The origin of the güiña's alternative name 'kodkod' remains obscure and possibly originates from one of the Mapuche Indian dialects, with reference to the pampas cat *O. colocolo* which is also native to Chile and Argentina. It has been suggested that 'kodkod' might be a Spanish corruption of the name 'colocolo' (F. Jaksic *in litt.* 1993).

1.2.1 Physical description

The güiña is the smallest felid species in the western hemisphere. Weighing approximately 2.2 kg, it stands approximately 22 cm at the shoulders and has an overall body length of between 50 and 68 cm, including a tail length of 19-25 cm (Greer, 1965). The tail is very bushy, more so than that of a domestic cat, and the feet are comparatively large. The base coat colour ranges from grey brown to buff, to reddish brown, and is heavily patterned with small black spots on the back and flanks. The undersides are lighter and also spotted (see Plate 1). The tail is ringed with several narrow black bands, and many individuals have prominent dark bands across the throat and dark markings on the face and head. The backs of the ears are black with pale central spots.

The incidence of melanism among güiña is high (Osgood, 1943; Greer, 1965). According to Miller and Rottmann (1976) the frequency of melanism increases with latitude and is particularly common on Isla Grande de Chiloé and the Guaitecas islands. In sunlight the spots and banding on the tail of melanistic cats are often visible (see Plate 2).

1.2.2. Taxonomy

The güiña is very similar in appearance to the Geoffroy's cat (*O. geoffroyi*), to which it is closely related. In appearance the Geoffroy's cat has a comparatively larger face and a less bushy tail than the güiña (P. Quillen *in litt.* 1993), and at between 2.2 and 7.8 kg (Redford and Eisenberg, 1992; Lucherini *et al.*, 2000) Geoffroy's cat is also moderately larger. The suggestion has been made that the güiña may merely represent a sub-species of the more numerous and widespread Geoffroy's cat (Nowell and Jackson, 1996), and an early report by Osgood (1943) remarked on the similarity of a güiña collected from the Valparaiso area, central Chile, to the "salt desert" race of Geoffroy's cat from the Andes of north-western Argentina. Osgood speculated that further specimens might arise to link the two cats, although this has not occurred. In Chile, Geoffroy's cats are known to occur only in the Nothofagus beech forests of the far south, where they bear little resemblance to the neighbouring Valdivian güiña (Cabrera, 1961).

The species status of both cats has more recently been confirmed via genetic analyses (Masuda *et al.*, 1996; O'Brien *et al.*, 1996; Johnson and O'Brien, 1997; Johnson *et al.*, 1999). Both species belong to the ocelot lineage, of which they represent the most recent divergence (O'Brien *et al.*, 1996; Johnson and O'Brien, 1997; Johnson *et al.*, 1999). Phylogenetic reconstruction based on two-dimensional electrophoretic data and isozyme markers (O'Brien *et al.*, 1996) and on comparison of base-pair divergence rates for 16S rRNA and NADH-5 mtDNA (Johnson and O'Brien, 1997) estimate the timing of divergence between the two species as approximately 3 MYA and no more than 5.1 MYA respectively.

Two subspecies of güiña have been proposed (Cabrera, 1957): *O. g. guigna* and *O. g. tigrillo*. *O. g. guigna* is purported to be the smaller and more brightly coloured of the two and is believed to be associated with the temperate rainforests of southern Chile and Argentina. *O. g. tigrillo* in contrast, is allied more closely with the coastal scrubland areas of central Chile and has a paler coat colour than *O. g. guigna* (Osgood, 1943).

A recent study conducted by Johnson *et al.* (1999) found low levels of intraspecific variation among güiña populations compared to other neotropical small cats, although this result could be an artefact of sample size ($n = 6$). All six samples were obtained from within the presumed *O. g. guigna* range, indeed DNA material from alleged *O. g. tigrillo* populations has yet to become available, hence there is no information regarding the potential genetic substructure of the güiña at the subspecies level.

1.2.3 Ecology and behaviour

Very little is known of the ecology and life history of the güiña, and much of that which has been published to date relies heavily upon speculation and folklore. Weigel (1975) suggested that individuals may live for up to 11 years. Quillen (*in litt* 1993) estimated a gestation period of 72 to 78 days and a litter size of one to three kittens. Housse (1953) suggested a litter size of three or four. Philippi (1873) proposed that a high degree of sociality might exist among this species, citing as evidence reported raids on hen houses by groups of up to 20 individuals, although no other claims of co-ordinated behaviour among güiña have been made.

Although the güiña is considered an agile climber there is some controversy over the degree to which it may be considered arboreal. Housse (1953) described cats hunting, resting, and rearing their young in trees, and Cereceda (1996) added that they cut sticks with their teeth to construct arboreal lairs, within which he claimed they gave birth. Others, Greer (1965), Guggisberg (1975), and Sanderson *et al.* (2002) among them, suggest that the species is primarily terrestrial, and uses trees only occasionally for shelter during inactive periods, or to climb as an escape tactic when pursued. Individuals radio-tracked by Sanderson *et al.* (2002) in northwestern Isla Grande de Chiloé rested at night in thick piles of ground-level vegetation including the almost impenetrable bamboo-like quila (*Chusquea quila*). During the day these cats were most likely to utilise dense vegetation along ravines and streams for cover, or rest under gorse bushes (*Ulex europa*) and logged forest brush piles. Housse (1953) also noted that güiña hid within dense quila thickets to rest.

The güiña is frequently described as a primarily nocturnal hunter (Cabrera and Yeppes, 1960; Greer, 1965; Guggisberg, 1975; Miller and Rottmann, 1976). Green (1991) however noted that among captive individuals most activity occurs during the day. Sanderson *et al.* (2002) found radio-tracked individuals on Isla Grande de Chiloé displayed no consistent activity patterns other than a slight tendency towards crepuscular behaviour, and were as likely to be active during the day as at night.

Once believed to be wholly allopatric (Hemmer 1978), Geoffroy's cat has been recorded present at a number of localities that are in close proximity to the güiña's historic range (Redford and Eisenberg 1992), and the two species were recently confirmed to be occurring in sympatry within the Los Alerces National Park, Chubut, southern Argentina (Lucherini *et al.*, 2001; 2002). This locality is close to the easternmost limits of the güiña's current range.

1.2.4 Diet

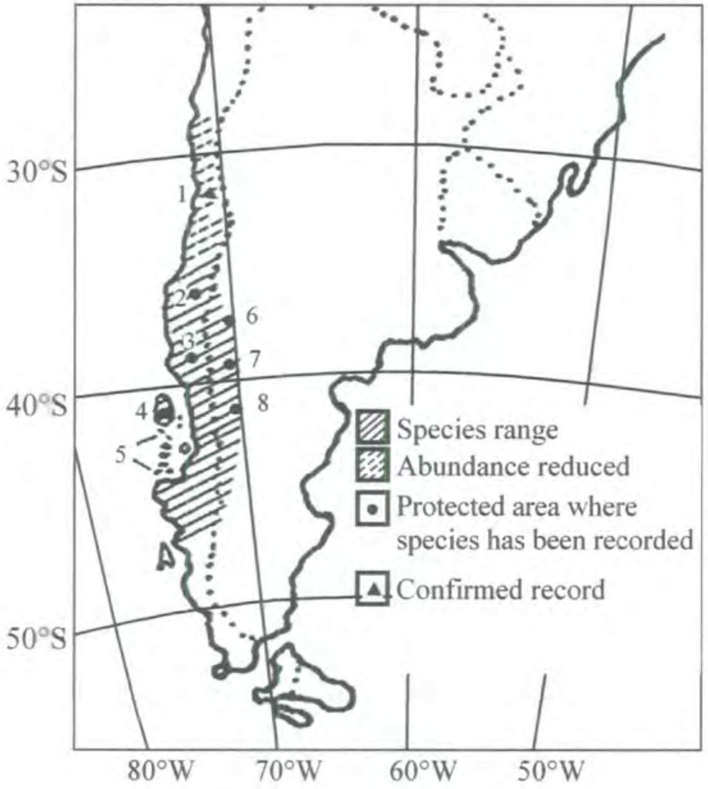
Güiña, like all members of the family Felidae, are obligate carnivores. Given the strong positive correlation between the size of carnivores and their prey (Rosenzweig, 1966), particularly amongst the felids (Leyhausen, 1965), the diminutive stature of the güiña predisposes it towards the predation of small prey items. Small body size facilitates arboreal behaviour however, and although an essentially arboreal lifestyle is questioned, none dispute the species' well-developed tree climbing abilities. The güiña is considered an occasional hunter of birds that roost and nest in trees (Cereceda, 1996).

No detailed study of the güiña diet has previously been attempted. Existing records include limited details based largely on ad hoc observations, and on reports of poultry depredation. Dove remains were recorded in the stomach of one individual (Housse, 1953), whilst two rats (*Rattus* sp.) were found in one specimen from the Malleco province, Chile, and a rat and an unidentified bird in a second (Greer, 1965). Sanderson *et al* (2002) described güiña on Isla Grande de Chiloé as agile, stalking predators capable of taking prey as large as domestic geese (*Anser domesticus*). Observations of Isla Grande güiña and analyses of their scats identified the undigested remains of unidentified small mammals, austral thrush (*Turdus falklandii*), Southern lapwing (*Vanellus chilensis*), chucao tapaculo (*Scelorchilus rubecula*), huet-huet (*Pteroptochos tarnii*), domestic chicken (*Gallus domesticus*), geese, and Chiloé lizard (*Liolaenus pictus chiloeensis*) (Sanderson *et al.*, 2002). In addition to taking poultry, güiña have also been reported to attack domestic goats (Cabrera and Yeppes, 1960). Considering the small size of this felid this behaviour seems unlikely. No further evidence has been proposed hence this report is here assumed to be anecdotal in origin.

1.2.5 Distribution and habitat associations

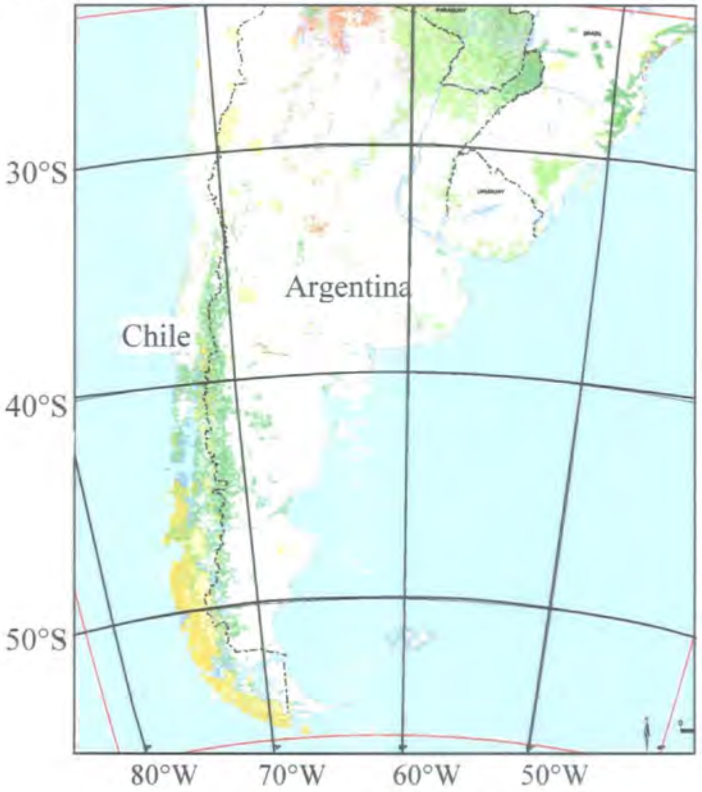
At just 160, 000 km^2, the geographic range of the güiña is the smallest of any New World felid (Nowell and Jackson, 1996). This species occurs only within Chile and Argentina, in a narrow geographic range that extends from approximately 70° to 75° W and from 30° to 48° S (Figure 1.2.1). Written records of the güiña exist from the Santiago province (33° 00′ S) south to the islands of Chiloé and Guaitecas (sites 4 and 5 in Figure 1.2.1). Murúa (1996) found güiña spoor on three transects to the north of Coyhaique, but not at the latitude of Coyhaique itself (45° 30′ S), or within the Torres del Paine National Park (51° 00′ S). In western Argentina the güiña has been recorded present in a limited number of sites, specifically the Rio Negro and Neuquen provinces (63° 00′ W, 41° 00′ S and 68° 00′ W, 39° 00′ S respectively), the Lanín, Nahuel Huapi and Los Alerces national Parks (Figure 1.2.1) and the Andean lake areas of Chubut and Santa Cruz (Cabrera, 1957; 1961; Melquist, 1984; Redford and Eisenberg, 1992; Lucherini *et al.*, 2001; 2002).

Figure 1.2.1 Distribution of the güiña (from Nowell and Jackson, 1996).



1. Valparaiso
2. Conguillío (National park)
3. Puyehue (National park)
4. Isla Grande de Chiloé (National park)
5. Las Guaitecas (Managed nature reserve)
6. Lanín (National park)
7. Nahuel Huapi (National park)
8. Los Alerces (National park, Argentina)

Figure 1.2.2 Temperate forest and protected areas in southern South America (landcover map from the World Conservation Monitoring Centre)



- ☐ Non-forest landcover
- ▨ Water bodies
- 🟩 Evergreen temperate forest
- ▨ Deciduous broadleaf forest
- 🟥 Sclerophyllous dry forest
- 🟩 Sparse trees/parkland
- ▨ Protected areas: IUCN categories I-IV

The restricted distribution of the güiña implies a narrow environmental niche, and this animal is widely considered to be strongly associated with the temperate mixed rainforests of Chile and Argentina, particularly the Valdivian forests of the south (Miller and Rottmann, 1976; Melquist, 1984; Nowell and Jackson, 1996). Most records of güiña presence (nine out of ten in Redford and Eisenberg (1992)) coincide with the original distribution of temperate Araucarian, Valdivian and Magellanic evergreen forest (Udvardy, 1975; Nowell and Jackson, 1996; Figure 1.2.2). The Andean and coastal forests of this region are characterised by the presence of southern beech (*Nothofagus* spp.), and have quila in the understory (IUCN, 1992). In Argentina the species has also been recorded within the Valdivian-like montane forest (Dimitri, 1972; Herrera *in litt* 1992).

A government-backed policy during the 1800s of burning forest to create pasture resulted in the deforestation of large areas of the Chilean landscape, particularly in the northern parts of the güiña's distribution range (Armesto *et al.,* 1994). Despite widespread deforestation and considerable degradation of native vegetation cover however, güiña have been recorded utilising areas of sclerophyllous scrub (Udvardy, 1975) and non-native pine and eucalyptus plantations that have replaced native forests (C. Weber *in litt.* 1993). Sanderson *et al.* (2002) noted that güiña on Isla Grande de Chiloé utilised modified landscapes. With the exception of one female, the territories of all radio-tracked güiña on Isla Grande encompassed areas of agricultural land, occupied buildings, and other highly modified landscape. These habitats differ noticeably in both species assemblage and vegetation structure to the presumed Valdivian stronghold of this species. Despite, the narrow habitat selectivity implied by the güiña's restricted distribution range, this species therefore appears able to utilise a variety of alternate habitats, including areas of secondary forest and semi-open country, shrub and the perimeters of settled and cultivated areas (Greer, 1965; Melquist, 1984; Green 1991; Sanderson *et al.,* 2002).

1.2.6 Population status and principal threats

Little is known of the present status of the güiña though it is believed extensive habitat modification has resulted in local extirpations in the northern region of the species' historic range (see Figure 1.2.1). Once considered 'fairly common' (Osgood 1943; Cabrera and Yepes, 1960), even locally abundant (Greer, 1965), the güiña is now regarded as 'endangered' in Chile and 'vulnerable' in Argentina (Glade 1988; IUCN, 1996; Díaz and Ojeda 2000). The Wild Cat Status Survey (IUCN/SSC Cat Specialist Group, 1990) categorised the güiña as one of the two most vulnerable felid species in the Americas, although its exact status remains 'indeterminate' due to the small and fragmented nature of many populations, and the paucity of baseline data (Nowell and Jackson 1996). The güiña has CITES Appendix II status and is fully protected under Chilean and Argentinean legislation.

The güiña is considered particularly vulnerable to habitat loss due to the restricted nature of its geographical distribution (Nowell and Jackson, 1996). Population fragmentation and localised decline in the northern half of its range have been attributed to logging and deforestation by burning for agricultural development (Nowell and Jackson, 1996). Further south, logging of the Valdivian forest is increasing for export to Japan (Ancient Forest International, 1990).

Despite its role as a predator of rodents, the güiña still retains a poor reputation in many agricultural areas. Much folklore surrounds the cat; a common belief on Isla Grande is that güiña are vampires that drain the blood of their prey (Cereceda, 1996; Sanderson, pers. comm.). Philippi (1873) recorded that farmers killed multiple güiña in a single day following predatory raids on chicken coops, and complaints of poultry depredation continue today (Melquist 1984). Güiña therefore still face persecution as a pest species, even a local variant of its name, the 'hüiña' means 'thief'. J. Rottmann (*in litt.* 1993) suggested that fox hunting with dogs and traps (both legal and illegal) remains a potential threat despite protective legislation, citing hunt data indicating that between one and five percent of fox hunt kills are small cats.

Up until the 1970s the trade in cat skins was concerned primarily with the large, spotted species. As concern for the status of remaining populations grew however, interest turned towards smaller cats from Asia (for example, jungle cat *Felis chaus*, and oncilla *Leopardus tigrinus*) and South America (Geoffroy's cat and ocelot *F. pardalis*). The diminutive size of the güiña allowed it to escape the full attention of the fur industry and it seems probable the cat was never intensively trapped, although no official data exists on the trade of güiña pelts or of live animals (McMahan, 1986). By comparison, international trade in Geoffroy's cat during the 1970s and 1980s was at times second only to that of the bobcat (*Lynx rufus*). The official number of Geoffroy's cat pelts exported from South American countries in 1979-1980 was 157,789, plus an additional 102,000 (unofficial estimate) as finished garments (McMahan, 1986). The restrictions on the trade of endangered species as recommended by CITES were first introduced in 1975, and Chile was among the original signatories to the agreement. Argentina became a signatory to the CITES convention in 1981, ensuring the güiña benefited full legal protection throughout its entire range. Illegal trade of güiña pelts appears uncommon at present. Melquist (1984) reported only once seeing a garment of what appeared to be güiña pelts in a local market. It does remain possible however that in the past güiña skins were traded internationally as the similar and closely related Geoffroy's cat.

1.2.6 Conservation and management

The güiña is believed to have been extirpated from many sites within its former range (Nowell and Jackson, 1996). As rate of extinction is strongly influenced by the size, diversity and quality of areas of available habitat (MacArthur and Wilson, 1967, Willis, 1974; Dueser and Brown, 1980) there is concern for the survival of remaining güiña populations in the face of continuing habitat alteration. If the species' continued presence is to be assured there is first an urgent need to understand the ecological requirements and behaviour of this species. There is also clearly a need for well-publicised studies that differentiate fact from folklore.

Basic behavioural and life history information are fundamental to the development of land-use plans and forest management guidelines. Although frequently quoted as a Valdivian forest specialist, no attempts have been made to assess the habitat utilisation of güiña, and ad hoc observations sometimes appear contradictory. This study aims to provide the first ecological data for this felid from populations inhabiting landscapes of minimal anthropomorphic modification. Two study populations in southern Chile were chosen for this purpose: Parque Nacional Laguna San Rafael and Parque Nacional Queulat.

1.3. The Study Region

1.3.1 Location and general description

Chile extends from approximately 17° 30' to 56° 00' latitude South within the southern cone of South America. The country is 4,300 km in length, but has an average width of just 160 km. As a result of such a wide latitudinal range Chile encompasses a broad range of climates, including desert, steppe, Mediterranean, humid warm temperate, maritime humid, cold steppe, tundra and polar (CONAF, 1997). The country has a total surface area of 757,000 km^2, of which 338,000 km^2 are classified as forested areas (INFOR, 1996).

Much of southern Chile underwent dramatic geological upheaval throughout the Quaternary period. The sharp topographic relief created by the uplift of the Andean mountains to the east, and frequent volcanic and seismic activity to the south of the country contributed to extensive glaciation processes and variable sea levels that persisted until as recently as 10,000 years ago (Porter, 1981; Mercer, 1983; Villagrán, 1990a; 1990b). This geological upheaval, in conjunction with close proximity to open ocean resulted in the biogeographic isolation of a 2,200 km latitudinal strip of temperate rainforest between the western slope of the Andes and the Pacific Ocean. The strong westerly winds along the Pacific coast during the winter and summer months and the cool northward-flowing oceanic Humboldt Current contribute to the high humidity that sustains this forest, which extends from approximately 36° to 52° latitude South (Figure 1.2.2). This region encompasses two evergreen forest bioregions: Valdivian and Magellanic temperate rainforest, collectively termed the North Patagonian rainforest.

In the southern reaches of the North Patagonian rainforest the Andean mountains rise above 3,000 m, and the tree line descends to approximately 1,000 m. Temperatures are moderate throughout most of the region (Huesser, 1974; Pearson and Pearson, 1982; Pearson, 1983); maximum annual average temperatures vary between 21 °C and 13 °C in the northern and southern extremes of the ecoregion respectively, minimum annual average temperatures range from 7 °C to 4 °C (Conama 1999). Annual precipitation varies from 1,000 mm in the north to more than 6,000 mm per year in the more southern latitudes (Huesser, 1974; Huber 1979; Pearson and Pearson, 1982; Pearson, 1983; Pérez *et al.* 1998). Snow cover persists only at the higher elevations, however towards the southern extremes the Patagonian influence becomes stronger; precipitation levels are lower, and the winter temperatures lower.

Chile encompasses more than half the temperate rainforests of the southern hemisphere, or one-quarter of the global total (Kellogg, 1993, Wilcox, 1996). Separated by c. 1500-2000 km from climatically similar closed-canopy forests by the Andes to the east, the Atacama Desert to the north, Antarctica to the south and the Pacific Ocean to the west, the North Patagonian rainforest represents a true biogeographic island (Arroyo *et al.*, 1996). This bioregion was recently included among the most globally threatened ecoregions in the Global 200 initiative launched by WWF and the World Bank (Olson *et al.*, 2000).

1.3.2 Regional community assemblages

The North Patagonian rainforest is dominated by evergreen broadleaf and coniferous taxa. The lowlands and mid-elevation regions support a dense forest of *Nothofagus nitida*, *N. dombeyi*, *N. betuloides*, *Weinmannia trichosperma*, *Podocarpus nubigena*, *Drimys winteri* and *Laureliopsis philippiana*. Vines, shrubs, woody epiphytes and epiphytic ferns are common in the understory and *Chusquea* spp. occur in forest gaps and along forest edges (Veblen *et al.*, 1983; Arroyo *et al.* 1996). On poorly draining sites bog-communities including *Tepualia stipularis* and *Pilgerodendron uviferum* form extensive inundated forests (Martínez 1981; Veblen and Schlegel 1982). Above 400 m conifer species, particularly *Saxegothaea conspicua* and *P. nubigena* become more prevalent. At altitudes approaching the treeline (c. 900-1200 m) these species are succeeded by deciduous forest and high Andean vegetation (Pearson, 1987; Reise and Venegas, 1987).

The Patagonian rainforests have evolved in isolation since the break up of Gondwanaland approximately 135 million years ago, giving rise to a high level of endemism amongst the resident flora and fauna. 34% of resident angiosperm genera (28 of 82 genera) and one family (*Aextoxicaceae*) are endemic to the southern temperate region of Chile and Argentina. At least one-third of the woody plants are of Gondwanic origin, their closest living relatives now occurring in Australia, New Zealand, New Caledonia and Tasmania. 36% of reptiles, 30% of birds, 50% of fresh water fish, 76% of amphibians and 33% of mammals are also unique to southern Chile and Argentina (Armesto *et al.*, 1996). Patterson (1993) noted 36 species and 12 genera of endemic mammals inhabit the *Nothofagus* dominated forests, including seven of the nine small mammal genera present: *Dromiciops, Rhyncholestes, Irenomys, Geoxius, Abrothrix, Aconaemys* and *Pearsonomys*. Such a high level of endemism within a community is comparable only to ancient or insular biota, indicating the periods of climatic upheaval and geographic isolation have exerted a strong influence on evolutionary processes within this region (Villagrán and Hinojosa, 1997).

1.3.2.1 Mammals of the North Patagonian rainforest

Discounting alien species, 38 mammal species are known to inhabit the North Patagonian rainforest region, less than 50% of the number recorded from temperate forests on the Pacific coast of North America (Meserve and Jaksic, 1991). The reduced species diversity throughout the Patagonian rainforest is in part due to the absence of the order Insectivora and the rodent families Sciuridae and Arvicolidae. These forests also lack specialised arboreal and frugivorous mammals such as squirrels and monkeys, despite approximately 60% of the woody plant species and genera bearing fleshy fruits and/or edible seeds (Armesto *et al.*, 1987; Armesto and Rozzi, 1989; Aizen and Ezcurra, 1998).

In contrast to the overall trend of relative species paucity, small mammal studies in the southern temperate rainforests indicate that their diversity and abundance often equals or exceeds those within many forests elsewhere, including the tropics (Meserve *et al.*, 1982; 1988; 1991a; 1991b; Pearson and Pearson, 1982; Pearson, 1983; Patterson *et al.*, 1989). The Rodentia are numerous and represent 50% of the mammal species native to the forests of southern Chile. The family Cricetidae is the most diverse, numbering 14 species. Widespread and abundant small mammal species in the Valdivian region include *Akodon olivaceus, Abrothrix longipilis, Oligoryzomys longicaudatus, Geoxus valdivianus, Irenomys tarsalis, Chelemys macronyx, Auliscomys micropus,* and the marsupial *Dromiciops gliroides*.

The Carnivora are represented in southern Chile and Argentina by eleven species in three families: the Canidae, Felidae and Mustelidae. The culpeo fox (*Pseudalopex culpaeus*) and the South American grey fox (*Pseudalopex griseus*) occur occasionally within the temperate forests, although both are more strongly associated with open habitats, steppe, pampas and matorral (Medel and Jaksic, 1989; Ginsberg and Macdonald, 1990). The family Felidae is represented by the puma (*Felis concolor*), Geoffroy's cat, pampas cat and the güiña. Whereas the güiña is believed to be strongly associated with the Valdivian temperate rainforest, and the pampas cat with grass and shrub habitats (Cabrera, 1961; Grimwood, 1969; Cabrera and Willink, 1980), Geoffroy's cat and the puma both occur across a wide variety of habitats (Koford, 1976; Melquist, 1984; Broad, 1987; Redford and Eisenberg, 1992).

Patagonian mustelids include the southern river otter (*Lutra provocax*), marine otter (*L. felina*), little grisón (*Galactis* cuja), Patagonian weasel (*Lyncodon patagonicus*), and the American mink (*Mustela vison*). The American mink is an introduced species that has invaded many South American forests. Its presence in southern Chile was hastened by escapes from fur farms, and in particular the illegal release of animals from a failed farm close to Coyhaique (Murúa, 1996). It is an efficient predator both in terrestrial and aquatic environments and is currently exerting an unknown impact on forest vertebrate populations within southern South America.

1.3.2.2 Birds of the North Patagonian rainforest

Although several endemic bird species live within the forests, many accounts emphasise the scarcity of birds and a low avian diversity (Vuilleumier, 1967; 1972; Rabinovich and Rapoport, 1975). There are also large-scale variances in abundance of avian species throughout the year as a result of migratory movement. Approximately two thirds of resident bird species emigrate totally or partially during winter when temperatures drop and flora and fruit abundance decrease (Smith-Ramírez and Armesto, 1994). Some species and groups such as the family Rhinocryptidae are resident yearlong due to their poor flying abilities (these birds 'flutter' rather than fly) (Rozzi *et al.*, 1996a). Some species migrate locally, the Green-backed firecrown hummingbird (*Sephanoides galeritus*) for example moves into larger forested regions where temperatures are less extreme (Sabag, 1993; Smith-Ramírez, 1993).

Of the more than 60 resident bird species of the North Patagonian Rainforest, 31 are passiforms, the most diverse order. Rozzi *et al.* (1996b) identified the most commonly censused birds as: *Sephanoides galeritus, Elaenia albiceps, Aphrastura spinicauda, Phrygilus patagonicus, Scelorchilus rubecula* and *T. falcklandii*. These represented more than 80% of those individuals censused.

1.3.3 Anthropomorphic influences

The climate and steep topography of Patagonia, in conjunction with the strong resistance of indigenous peoples to the settlement of European immigrants ensured the retention of most of the region's native forest cover until the 1800's, when the rate of settlement escalated. Rapid and extensive deforestation for the creation of pasture for grazing ensued, as did the widespread establishment of monospecific crops for timber harvest, specifically *Pinus radiata* (Armesto *et al.*, 1994; Lara *et al.*, 1996). Large areas of forest were cleared using fires, however clearing fires frequently became forest fires that burned out of control and often lasted for days, months, and in some cases for more than a year. Forest clearance for agricultural activities were initially confined to the more northern part of the güiña's distribution range, but from the 1850s onwards began to encroach on native habitats throughout southern Chile as the number of settlers increased (Armesto *et al.*, 1994).

Historically those areas colonised relatively early in the settlement process such as those surrounding the towns of Coyhaique and Puerto Aisén were encroached upon more severely than relatively isolated sites. The Chilean Central Valley and the precordilleran Andes region between approximately 35° S and 41° S were affected most dramatically (Lara *et al.*, 1996), resulting in a reduction and fragmentation of forest habitat and much local site impoverishment (Veblen and Ashton, 1978). As Chile and Argentina have become increasingly integrated into the global economy, the conversion of native primary growth forest has accelerated rapidly. In 1997 the rate of forest loss was estimated at 120,000 ha per year, with 40-90,000 ha of this area representing conversion to non-native tree plantations. Chile now has the greatest area devoted to pine plantations in the world and the nation is the third largest exporter of woodchips (Rozzi *et al.*, 1996).

1.4 The study sites

The primary aim of this study was to assess the behaviour and ecology of güiña in the absence of human-mediated habitat disturbance. Fieldwork was therefore conducted within two largely pristine study sites: Parque Nacional Laguna San Rafael (PNLSR) and Parque Nacional Queulat (PNQ). These sites are located within the North Patagonian rainforest, within the broad transition zone between Valdivian and Magellanic forests. Recent evidence of güiña presence (spoor) was identified at both sites prior to the commencement of this study.

Parque Nacional Laguna San Rafael is a remote, wilderness area situated near the Taitao Peninsula and Golfo de Penas, west of the San Valentín ice field (part of the North Patagonian Icecap). The park extends from 73° 51′ to 73° 53′ W and from 46° 38′ to 46° 40′ 30″ S. Parque Nacional Queulat is centred on the Queulat valley, 72° 24′ to 72° 25′ W and from 44° 34′ to 44° 35′ S (see Figures 1.4.1 and 1.4.2). Both areas are affected by sub-Antarctic influences; the climate (Maritime Cold Temperate; Köppen, 1948) is temperate and humid, the mean annual rainfall in the region is 3,700 mm and monthly temperatures range from a mean of 6.7°C in winter to 11.3°C in summer.

Parque Nacional Laguna San Rafael extends over approximately 1.7 million hectares. Despite its international renown as natural beauty spot the area has been little studied, largely due to its remoteness and the roughness of terrain. The PNLSR study area is situated next to the San Rafael glacier at the heart of the park. The area is a successional zone, having been recently glaciated, and incorporates temperate, *Nothofagus* dominated forest, páramo (high-altitude grasslands), scrubland, thicket, saltmarsh (sedge and reed communities), beach communities and rocky outcrop habitats (Pisano, 2002).

The decision was made to include fieldwork from a second site (PNQ) in order to determine whether patterns of güiña spatial distribution identified within PNLSR were due to site-specific factors, such as the relative geographic isolation of this site or the presence of a permanently occupied building, or whether populations elsewhere displayed similar social organisation. The second site was selected on the basis of habitat and topographical similarity with PNLSR as far as was possible. The two parks however contain unique faunal and floral assemblages including different carnivore guilds that potentially compete with the güiña for resources. For example, the puma, culpeo fox, Patagonian weasel and American mink all occur within the PNQ study site. In contrast, PNLSR has few sympatric carnivore species other than occasional visits by puma in the winter months. Many raptor and strigid species are present however and these also rely on rodent and avian prey (Jaksic *et al.*, 1981, Rau *et al.*, 1992), hence are potential competitors with güiña. During the course of this study, several mink were sighted and captured on the opposite (western) side of the Laguna San Rafael. Given this species' dispersal capabilities it can be presumed only a matter of time before this obstacle is surmounted and the mink becomes a resident within the PNLSR study area also.

Figure 1.4.1 Location of the PNLSR and PNQ study sites (from http://www.usgs.gov)

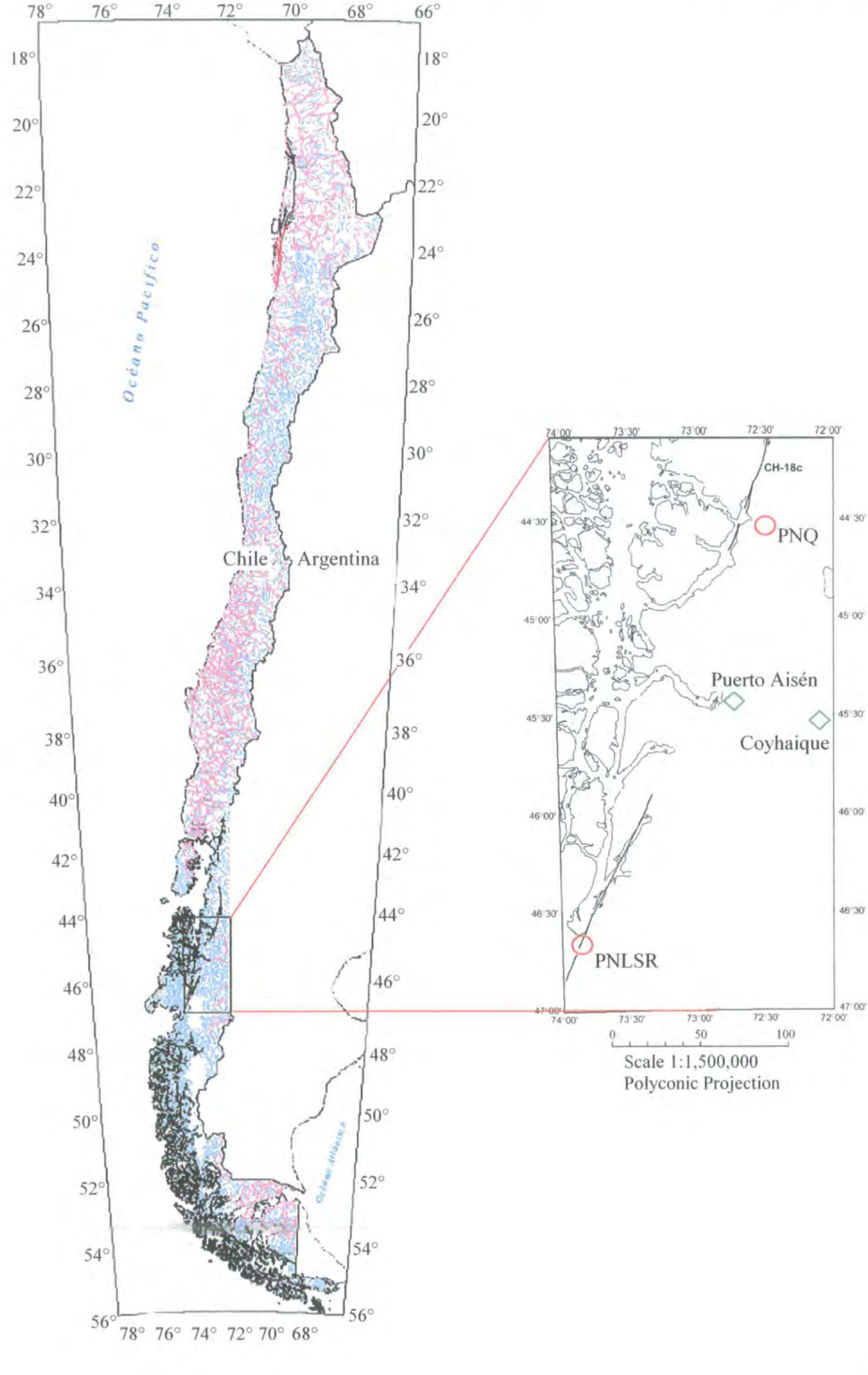
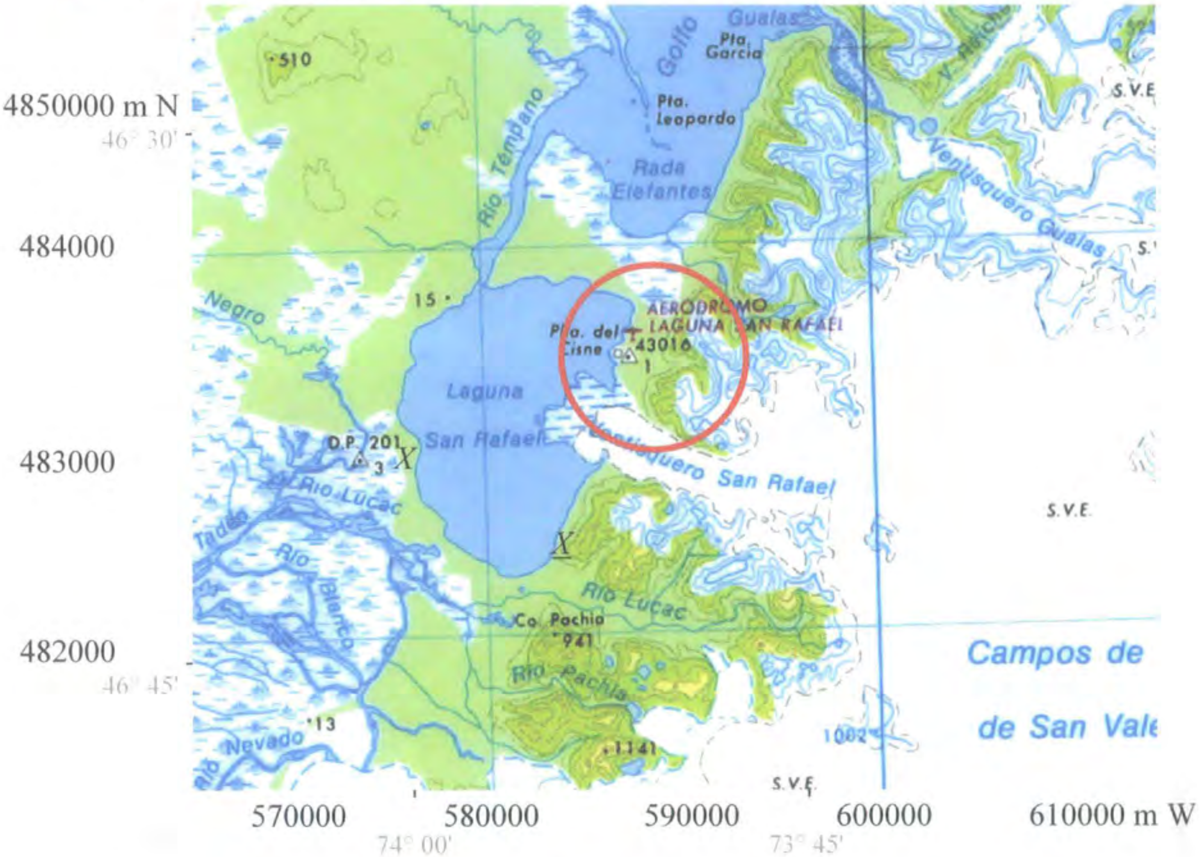
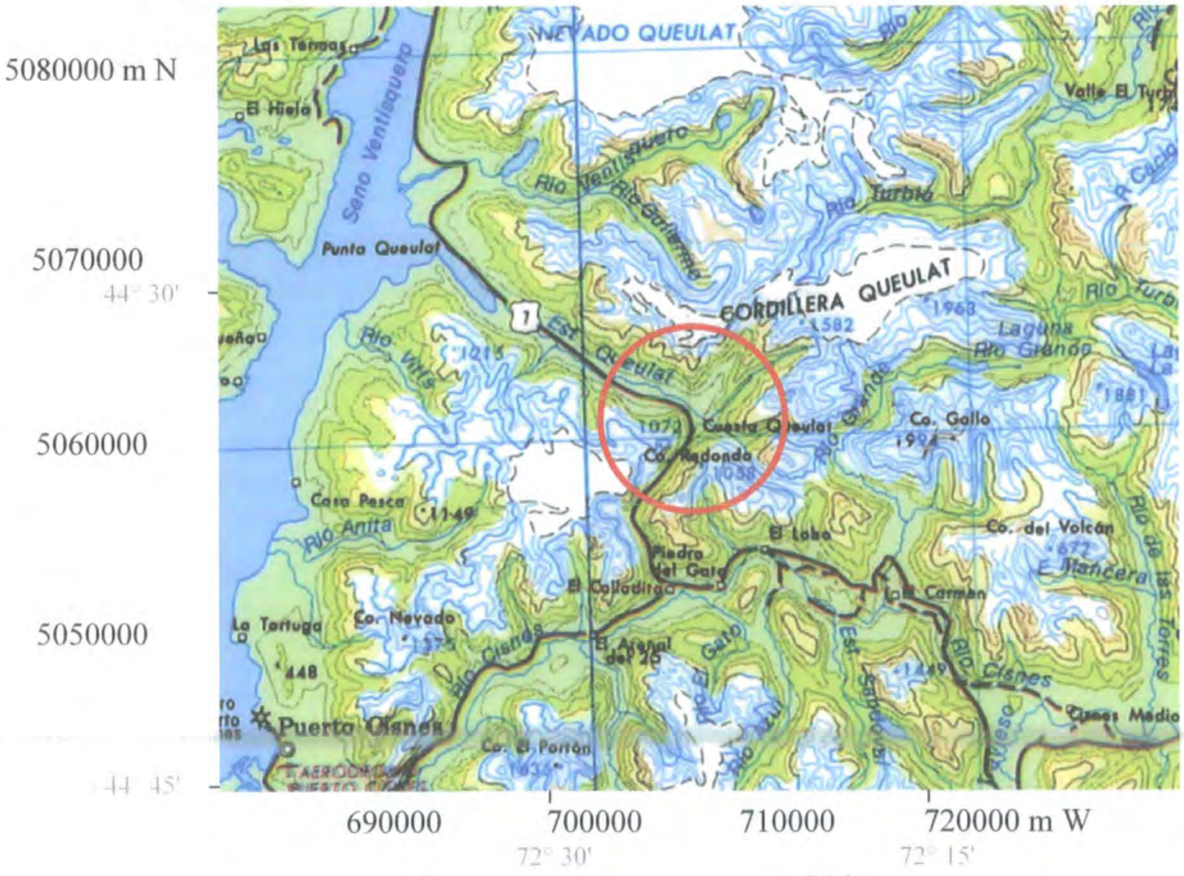


Figure 1.4.2 Detail of the PNLSR and PNQ study sites

Parque Nacional Laguna San Rafael (from Instituto Geográfico Militar map 4600-7115)
X = **PNLSR recce sites**



Parque Nacional Queulat (from Instituto Geográfico Militar map 4600-7100)



Nothofagus nitida is the characteristic tree species of coastal and riparian forest up to an altitude of 200-250 m, and predominates within the park where it is found in association with *Nothofagus betuloides, Laureliopsis philippiana* and *Drimys winteri.* Scrubland within the site is characterised by relatively open areas of low (< 1 m) shrubby vegetation including *Gaultheria phillyreifolia, Escallonia alpina, Empetrum rubrum* and *Acaena megallanica.* Thicket species (*Berberis buxifolia, Berberis chilensis, Fuschia magellanica* and *Desfontainia spinosa*) form a belt between the forest and the coastal communities to a height of 1.5 m, interspersed with small trees, most notably *Embothrium coccineum.* The beach communities are varied and include psammophyllus species such as *Arenaria serpans* and *Senecio candidans*, salt-tolerant species, including *Colobanthus quitensis* and *Puccinellia glaucescens* and upper level beach communities dominated by *Leptinella scariosa*, *Cardamine glacialis* and *Ranunculus apiifolius* amongst others. Collectively these communities are termed ‘coastal scrub’. The study site is bordered along its western edge by Laguna San Rafael. Much of the site is at or near sea level, though further inland and in the southeast of the site it rises steeply in parts.

Two park rangers, employed by CONAF (the National Forestry Commission within Chile) are stationed within PNLSR throughout the year. Their house and associated buildings are the sole permanent constructions within the park.

Parque National Queulat is a remote area located to the north of Coyhaique. The study area incorporates an extensive area of old growth forest and is centred on a three-sided valley through which the Río Queulat runs approximately east to west. The valley floor is close to sea level, whereas the steep valley sides rise to between 1000 and 2000 m. Not only was this area unaffected by clearance fires, but its rugged terrain has also made it marginal for agro-forestry. Three habitat types predominate this site: forest, thicket-forest and waterlogged thicket or ‘swamp’. Stands of ‘pure’ forest are largely composed of *Nothofagus nitida and N. betuloides* and have little understory other than moss and hymenophyllaceous fern ground cover. Where the soil is thin or landslides have occurred grassy open patches have replaced areas of forested slope. Mixed thicket-forest is more diverse and includes *N. nitida, N. betuloides, D. winteri, Laurelia semperirens, Podocarpus nubigen* and *Weinmaninia trichosperma. Chusquea quila, Gunnera chilensis* and *B. chilense* form a thick understory. An area of standing water and swamp covers part of the Queulat valley interior, the vegetation community here is characterised by the hydrophyllic species *P. nubigena, Luma apiculata, Pilgerodendron uviferum* and *B. chilense.* Elsewhere, stands of thicket resemble those in PNLSR and include *F. magellanica, B. buxifolia, B. chilensis,* and *D. spinosa.*

1.5 Scope and aims of study

Effective conservation of extant güiña populations requires a more detailed understanding of those factors that govern the species' spatial organisation and influence it spatial requirements. Information that describes the movements and ecology of güiña is particularly important given the species' vulnerable status and the threat of accelerated habitat modification and loss. It was the intention of this study to provide much needed data on the naturalistic behaviour and ecology of the güiña to support current management and conservation strategies throughout its current range. Previous studies although valuable in terms of providing preliminary descriptions of habitat and diet did not taken resource availability into account. Furthermore, earlier studies have mainly been conducted in agricultural or otherwise human-modified habitat.

Two güiña populations were studied within this species' Valdivian stronghold during the spring, summer and autumn months between October 1997 and April 2001. Specific objectives of this study were to: (1) examine the composition of the güiña diet in relation to relative prey abundance and selection; (2) describe the spatial extent and arrangement of güiña home ranges, the activity patterns of focal individuals and the spatial and temporal interactions among conspecifics; (3) investigate whether güiña activity is associated with any specific habitat, specifically *Nothofagus* forest, or whether this species is able to utilise and inhabit a variety of habitat categories, and (4) to evaluate the potential threats to the long-term survival of this species and provide guidelines for the management of existing güiña populations and of suitable habitat within this species' current range.

Chapter 2

Field Methods and Map Construction

2.1 Methods

2.1.1 Creation of a land cover (habitat) map

Ten discrete categories of land cover were identified and characterised during field surveys conducted within the PNLSR and PNQ study sites: forest, thicket-forest, thicket, scrub-thicket, scrub, open grassland, saltmarsh, rock, open water and snow (see Appendix 1 and Plate 3 for descriptions of each classification). Areas representative of each category were plotted onto georeferenced field maps of each study area, created using Global Positioning System (GPS; Garmin 45) ground survey data. Each site had a network of access trails, each with numbered marker posts at 50 m intervals, the co-ordinates of which were also plotted onto the field maps. All maps generated as part of this study are based on the Universal Transverse Mercator (UTM) co-ordinate system. This is a metric configuration that, unlike co-ordinate grids based on longitude and latitude, provides a continuous Cartesian co-ordinate system that allows easy calculation of distances between points.

In the absence of accurate published maps, planometric aerial photographs of each study area were commissioned from which photomontages were constructed within PhotoShop 5.0 (Adobe Systems Incorporated, California) (Plates 4 and 5). In addition, a raster-based map of both the study areas and of the wider region was developed from satellite imagery purchased from the United States Geological Survey (two LANDSAT 7 Enhanced Thematic Mapper scenes, pixel size 30 × 30 m). When merged using the Idrisi geographic information system and digital image processing software package (Idrisi version 32.11, Clark Labs, Massachusetts, USA) these images described a total area of approximately 61,400 km^2 (map dimensions 185 × 332 km). Six spectral bands were processed via a maximum-likelihood supervised classification process within Idrisi, whereby land cover was categorised according to surface reflectance values into one of the ten classes identified in the field. The resulting classifications were verified through reference to the aerial photomontages and ground truth data.

The Idrisi software encountered some difficulty in classifying land cover accurately in areas of steep terrain owing to shaded slopes having different surface reflectance values. Splitting the forest category into two subcategories: 'forest' and 'forest slope' circumvented this problem. The two forest categories were then repooled for subsequent analyses.

2.1.2 Capture and handling of güiña

Güiña were trapped using heavy gauge galvanised wire mesh live-traps (Tomahawk Live trap Company, Wisconsin, USA). Trapping occurred over a variable number of days each field season (Table 2.1.1). Nine traps were deployed in total, seven single door traps (model 209.5) of dimensions 105 × 50 × 37.5 cm and two double door traps (model 206) of dimensions 81 × 23 × 23 cm. Trap sites were situated within all major habitat categories, typically 25 m or more from access trails and at intervals of at least 250 m. The traps were set using the most sensitive trigger settings and baited using a variety of fresh meat, fish, proprietary cat food and tinned fish; the bait being replaced every second day. Active traps were sheltered using local vegetation and brush and were checked twice daily, at first light and early evening.

Table 2.1.1 Duration of live-trapping surveys

Study site	Field season	Number of trap days*
PNLSR	Spring 1997	369
	Summer/autumn 1998	468
	Spring 1998	180
	Summer/autumn 1999	36
PNQ	Spring 1999	306
	Summer/autumn 2000	234
	Spring 2000	243
	Summer/autumn 2001	207

*Number of days traps were activated × number of traps.

Brief trapping studies were also conducted for güiña at two additional sites, one on the eastern shore of Laguna San Rafael (575280, 4830880 UTM), the second to the south of the San Rafael glacier (584130, 4826045 UTM, see Figure 1.4.2). These recce surveys were each of one-week duration, and were conducted in conjunction with ad hoc surveys for güiña spoor in an attempt to detect new populations within the park.

Captured güiña were initially immobilised using a plywood squeeze panel to restrict the cat's movements inside the cage and reduce trauma. When the animal was pressing against the cage it was anaesthetised with an intramuscular dose of Ketaset (ketamine hydrochloride (100 mg/ml), Parke, Davis & Co., Detroit, Mich.) and the muscle relaxant Rompum (xylazine hydrochloride (20 mg/ml), Bayer). Dosages were calculated with the assistance of a veterinarian and were based on visual assessments of bodyweight. Actual dosages administered were 14.5 ± 1.1 mg/kg ketamine hydrochloride and 8.6 ± 0.9 mg/kg xylazine hydrochloride. Most cats were ataxic within 5 minutes and remained so for at least 20 minutes.

Whilst anaesthetised the cats were sexed, weighed and measured. To aid subsequent identification each was labelled with a subcutaneous PIT tag and a uniquely coloured ear tag. A small tissue sample was taken from one ear and preserved in $DMSO_4$ for DNA analysis in the UK. Individuals were classified as juvenile, subadult or adult on the basis of size, weight, dentition, and reproductive condition. Independent animals that had not yet reached the age of full sexual maturity were classed as subadults. Fourteen güiña were fitted with radio collars purchased from Telonics, Arizona, USA (configuration 1A). These collars incorporated radio transmitters and whip-antennae within a butyl construction. The transmitter package (weight 22g, operational frequency range 173-174 MHz) had an operational battery life of 4.3 months and a potential line of sight range of 4 km, although within the forest a 500-750 m range was more typical.

Following handling, animals were returned to the traps in which they were caught and given water. These traps were covered with vegetation to minimise disturbance during recovery. Güiña were released at the site of capture only when alert and co-ordinated, usually some 2-3 hours later.

2.1.3 Determination of movements via radio-telemetry

Radio-collared güiña were monitored on foot using radio receivers (model TR-4, Telonics, Arizona, USA) and hand-held 3-element Yagi antennae. Individual animals were located via triangulation from three or more bearings taken at fixed trail marker posts using a hand-held compass pointed in the direction of the strongest transmitter signal (Mech, 1983). Signal bounce was minimised by obtaining bearings from elevated locations whenever possible, and location errors were minimised by using only azimuths that differed by 60°-120° and by using the trail systems to get close to the focal animals (White and Garrott 1990). A distance of between 100 and 500 m was maintained between the observer and the focal animal whenever practical to avoid influencing the animal's movement.

Radiolocations were taken systematically at 30-minute intervals whenever this was possible, then plotted as UTM co-ordinates onto field maps. Effort was made to record all bearings relating to a single radiolocation within a ten-minute interval to reduce error due to the movement of focal animals during triangulation. The time and daylight variables (day, dawn, dusk, night) were recorded for each radiolocation. Habitat categories were not assigned to an individual's location in the field but were allocated later during data analysis. Consecutive location fixes less than 30 minutes apart were removed from the data set prior to analysis to reduce autocorrelation between sequential data.

The radio transmitters were fitted with reset activity sensors (S6B). Movements of collared animals therefore caused the signal pulse rate to change from the 'inactive' base rate of 50 pulses per minute (ppm), to a faster rate of 75 ppm. Periods of activity could hence be distinguished from inactive behaviour by noting pulse frequency and fluctuations in signal strength during radio contact (Garshelis *et al.*, 1982; Ferguson *et al.*, 1988). Complete 24 hour coverage of focal cats was attempted whenever possible, using small groups of observers. The timing of the tracking shift changeovers and intervals between fixes were pre-determined and therefore not influenced by the behaviour of the animals. Most radio contact focused upon a single individual at a time, though simultaneous monitoring of two or more güiña was attempted whenever terrain and accessibility allowed. Each animal was tracked intermittently until the collar failed or was removed, or the animal migrated out of the area.

Radiotelemetry surveillance of güiña was conducted during 175 days over four 10-week field seasons in PNLSR (October to December 1997, January to March 1998, October to December 1998, January to March 1999), and over a total of 202 days during five 10-week periods in PNQ (October to December 1999, January to March 2000, May to July 2000, October to December 2000, January to March 2001). Where possible, continuous radio contact was maintained with individual güiña for periods of 24-72 hours. When this was not possible, effort was made to sample each period of the day equally.

During the winter 2000 season (May to July) it was not possible to radio-track continuously due to difficulties achieving access to the site. Location fixes were therefore recorded on a largely opportunistic basis during daylight hours.

2.1.4 Estimation of bearing error

Bearing errors, where error is defined as the difference between the true bearing and that estimated using a receiver, may be caused by numerous factors including terrain, equipment and observer error. The accuracy of directional bearings consists of both bias and precision (White and Garrott, 1990, see also review in Salz, 1994). Imprecision typically occurs when the location of the observer or geographical features in the habitat cause signal to be reflected and/or absorbed prior to it reaching the radio-receiver. Alternatively, the signals may be precise yet biased, frequently as a result of the observer's compass or pointer being aligned incorrectly (White and Garrott, 1990). Errors associated with the radio-receivers and the triangulation methodology were therefore examined using the program LOAS (version 2.03, Ecological Software Solutions) to calculate bearing error and error ellipses for a random subset of 40 bearing sets from the radiotelemetry dataset.

The maximum likelihood estimator of signal location was used in preference to simpler estimators such as the arithmetic mean, as these methods are frequently highly sensitive to outlying bearings (Lenth, 1981). The maximum likelihood estimator is based upon an iterative algorithm that, in a manner similar to linear regression identifies the minimum angular error between the observed set of bearings and the signal's estimated location. This process identifies the most likely location of a signal source, and permits the description of the variability of the estimated location, in the form of an error ellipse.

The fieldwork component of this study was conducted across nine 10-week field seasons. The first four seasons took place within PNLSR; the remaining five were undertaken within PNQ (Table 2.1.2).

Table 2.1.2 Timing and duration of radiotelemetry fieldwork

Study Site	Season	Months
PNLSR	Spring 1997	October-December
	Summer/autumn 1998	January-March
	Spring 1998	October-December
	Summer/autumn 1999	January-March
PNQ	Spring 1999	October-December
	Summer/autumn 2000	January-April
	Winter 2000	May-July
	Spring 2000	October-December
	Summer/autumn 2001	January-April

Statistical analyses were conducted using the SPSS software package (version 11, SPSS Inc., Chicago). All variables were tested for normality and equality of variances before statistical analyses. Variables that did not meet these assumptions and which could not be normalised through standard techniques were analysed with appropriate non-parametric tests following Siegel (1956). Mean values are quoted throughout as means ± standard error values. Unless otherwise stated, a significance level of $P < 0.05$ was accepted for all statistical analyses.

For species with both Latin and common (English) names, both names are provided on the first mention, thereafter only the common name is given.

2.2 Results

2.2.1 Creation of a land cover (habitat) map

The maximum-likelihood supervised classification of the LANDSAT 7 satellite data created the raster-based map displayed in Figure 2.2.1. The proportion of this area represented by each of the ten land cover categories is detailed in Table 2.2.1 below.

Table 2.2.1 Land cover coverages (km^2) and category representation within the total reference area described by Figure 2.1.1

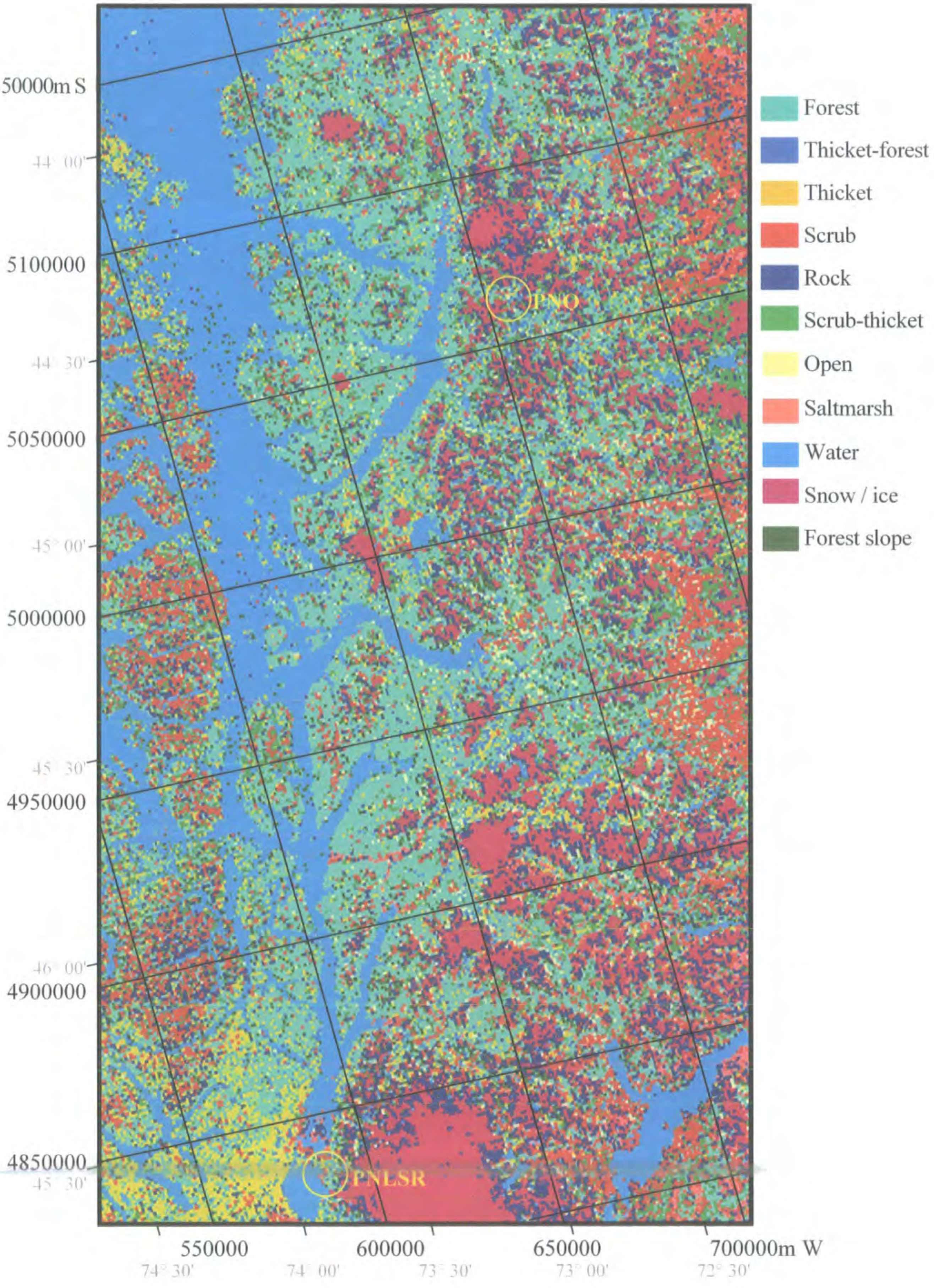
Habitat category	Area (km^2)	Percentage of entire site
Forest	17730	28.87
Thicket-forest	1800	2.93
Thicket	4230	6.89
Scrub-thicket	5310	8.65
Scrub	5400	8.79
Open	1080	1.76
Saltmarsh	1125	1.83
Rock	6700	10.91
Water	11520	18.76
Snow	6525	10.62
Total	61420	100.00

2.2.2 Study animals

Nine traps set over 117 days in PNLSR resulted in 43 captures of 10 individual güiña (Table 2.2.2). In PNQ, the same nine traps set over 110 days captured 13 güiña a total of 27 times. There was no evidence to indicate that capture and radio-monitoring disrupted subsequent activity and movement patterns; radiocollared animals regularly travelled through the area in which they were trapped, and both animals QAM1 and QSF11 were recaptured within three days and at the same trap site as their initial capture.

Trapping efforts at two additional locations on the western and southern edges of the Laguna San Rafael resulted in the capture of only one güiña. This adult male was caught on the western shoreline, approximately 1.2 km from the PNLSR population, but separated by the open water of the San Rafael Laguna and by the North Patagonian ice sheet, of which the San Rafael glacier represents the easternmost extension (see Figure 1.4.2). There is no route connecting the PNLSR güiña population with either of these two sites that does not require the negotiation of expanses of open water or ice. No güiña spoor were found in either recce site.

Figure 2.2.1 Land cover composition of area described by the merged Enhanced Thematic Mapper (LANDSAT 7) images (USGS path 232, rows 91 and 92, UTM projection). Locations of study sites are indicated. Total area represented is 614200 km^2; pixel size is 30 × 30 m.



The morphometric measurements of captured animals, as recorded at the time of their initial capture, are detailed in Table 2.2.2. Age classes were assigned in the field on the basis of body size and tooth wear. Sexual dimorphism in body weight was apparent among adult güiña ($t_{14} = 5.346$, $P < 0.001$). Adult females weighed between 1.3 and 1.5 kg ($n = 9$) whereas males were larger and weighed between 1.4 and 1.9 kg ($n = 6$). All subadult güiña weighed between 1.1 and 1.5 kg, two juveniles both weighed 0.9 kg each.

The biometrics recorded for animal SJM4, captured with its mother (SAF7) on 28/2/98 suggested that this animal had reached approximately 76% of adult length, but only 51% of the average weight of an adult male. Based on size and dentition this animal's age was estimated as approximately four months, giving a likely birth period of late October (spring). SJM4 was subsequently recaptured on two occasions; when re-measured on 25/10/98 his body weight had increased to 1.4 kg and total length to 59.0 cm. When this animal was re-trapped for collar removal on 12/3/99 his body weight had increased to 1.7 kg and total length to 62.5 cm. In October 1999 local park rangers observed SJM4 fighting and defeating other male güiña, indicating he had probably reached or was approaching adult status.

2.2.3 Determination of movements via radio-telemetry

Fourteen güiña were radiotracked during this study. Additional güiña known to be present within the study areas were not radiotracked due to the finite availability of radio-collars. 3818 radiolocation fixes were obtained from six güiña in PNLSR, and 2026 from eight güiña in PNQ. Each animal was monitored across a period of between three days and over a year (Table 2.2.2), although no radiotelemetry work occurred during late autumn and winter months (May through to early September) except during winter 2000. Two male güiña (QAM2 and QAM5) dispersed out of the PNQ study area within three and six days of capture respectively, and did not return during the remainder of the study. These animals were hence presumed to be transient animals. Animal QAF10 died during the study, apparently from natural causes, and her collar was retrieved. All other güiña were recaptured towards the end of their transmitter's expected battery life, or when the telemetry study ended in the relevant study area, when their radio-collars were removed.

Analyses of telemetry accuracy indicated a mean bearing error of 5.15° ± 0.46° ($n = 127$ bearings) and a mean error ellipse size of 1.30 ± 0.19 ha ($n = 40$ bearing groups), a degree of error that was considered acceptable (White and Garrott, 1990). Further analyses of the radiotelemetry data are detailed in Chapters 4, 5 and 6.

Table 2.2.2. Morphometric measurements from captured güiña and periods of radio-monitoring.

Study site	ID	Age	Coat colour	Weight (kg)	Total length (cm)	Tail length (cm)	Period of radio-monitoring[2]		Number of radiolocations
							Start	End	
PNLSR	SSM1[1]	Subadult male	spotted	1.4	62.5	21.2	19/10/97	15/12/97	511
PNLSR	SSM2[1]	Subadult male	spotted	1.5	64.3	23.2	11/11/97	13/3/98	434
PNLSR	SAM3[1]	Adult male	black	1.9	64.0	21.3	29/11/97	27/2/99	497
PNLSR	SJM4[1]	Juvenile male	black	0.9	48.0	17.2	7/3/98	25/2/99	476
PNLSR	SAM5	Adult male	black	1.9	59.0	19.5			
PNLSR	SAM6	Adult male	spotted	1.9	66.5	23.0			
PNLSR	SAF7[1]	Adult female	spotted	1.5	59.8	21.1	24/1/98	1/3/99	779
PNLSR	SAF8[1]	Adult female	spotted	1.4	59.8	21.0	7/3/98	1/3/99	1121
PNLSR	SAF9	Adult female	spotted	1.3	60.0	20.3			
PNLSR	SJF10	Juvenile female	black	0.9	51.5	17.0			
E. PNLSR		Adult male	black	1.8	66.0	22.5			
PNQ	QAM1[1]	Adult male	black	1.8	62.0	22.5	7/11/99	6/12/00	521
PNQ	QAM2[1]	Adult male	spotted	1.4	61.0	20.5	14/11/99	16/11/99	52
PNQ	QSM3[1]	Subadult male	black	1.4	42.0	No tail	3/3/00	24/3/00	151
PNQ	QSM4[1]	Subadult male	black	1.5	62.5	23.0	8/11/00	9/12/00	128
PNQ	QAM5[1]	Adult male	spotted	1.7	62.0	21.5	14/2/01	20/2/01	54
PNQ	QAM6	Adult male	black	1.8	65.0	21.5			
PNQ	QAM7	Adult male	black	1.8	62.0	20.0			
PNQ	QSM8	Subadult male	black	1.3	59.0	19.0			
PNQ	QAM9	Adult male	black	1.7	61.0	20.5			
PNQ	QAF10[1]	Adult female	black	1.5	60.5	20.0	7/11/99	12/12/99	174
PNQ	QSF11[1]	Subadult female	black	1.1	58.0	21.0	12/2/00	8/3/00	129
PNQ	QAF12[1]	Adult female	black	1.4	57.5	19.0	12/2/00	1/4/01	817
PNQ	QAF13	Adult female	black	1.4	61.0	21.0			

[1] Radio-collared individuals

[2] These dates do not indicate continual or regular radio contact, rather the first and last date on which radio contact was made.

Chapter 3

Prey Availability and the Güiña Diet

3.1 Introduction

3.1.1 The felid diet

From the perspective of diet and feeding the Felidae are among the most highly specialised families within the Carnivora. Wild felids consume mostly vertebrate, predominately mammalian prey, and the dietary spectra of individual species typically include significantly fewer taxonomic groups than, for example, those of the Canidae or the Viverridae (Kruuk, 1986). Relatively little intra-specific variation in diet breadth occurs across geographic ranges (Kruuk, 1986), suggesting that the Felidae in general are either very selective of habitats or have highly specialised hunting methods, or both.

Dietary breadth is frequently influenced by prey availability, which in turn can be allied to habitat structure (Brodmann *et al.,* 1997; Taber *et al.,* 1997; Drennan and Beier, 2003). Both Canadian lynx (*Lynx canadensis*) and Iberian lynx (*L. pardinus*) for instance inhabit relatively open habitats and feed almost exclusively upon a single prey species, the snowshoe hare (*Lepus americanus*) and European rabbit (*Oryctolagus cuniculus*) respectively, which they hunt by 'cursorial pursuit'. Forest-dwelling cats, in contrast, appear relatively catholic in their diet and more reliant upon 'ambush' tactics by which to capture their prey (Muckenhirm and Eisenberg, 1973; Bothma and Richie, 1986; Emmons, 1987; 1988; Konecny, 1989; Grassman, 1998a; 1998b). Leopards within the Täi National Park of the African Ivory Coast for example are opportunistic hunters, and take all available prey species within a size limit determined by their own body size (Hoppe-Dominik, 1984).

Ecological data for many of the smaller felids is limited due to their secretive nature and because the general focus of field research has been towards the larger species. Prior to the commencement of this study the only literature describing the güiña diet was anecdotal, provided minimal detail, and was occasionally of questionable accuracy. Since then Sanderson *et al.* (2002) have, through opportunistic observation on Isla Grande de Chiloé recorded the presence of rodents and several native bird species in the güiña diet, including austral thrush, Southern lapwing, chucao tapaculo and huet-huet, in addition to domestic poultry and small lizards.

3.1.2 Determination of dietary components from prey remains

Investigation of the dietary composition of carnivores, particularly of the more elusive species such as the forest-dwelling felids, is frequently undertaken via analyses of scat contents. Dietary items are identified from indigestible prey remains retrieved from scats and compared to reference samples of known origin (for example see Day, 1966). Relative contributions to the diet made by each prey category can then be expressed in terms of prey occurrence or transformed to represent proportional contribution to biomass ingested. This approach has been used in numerous studies including those of ocelot (Emmons, 1987; 1988), Iriomote cat (*Felis iriomotensis*) (Sakaguchi and Ono, 1994), jaguar (*Panthera onca*) (Rabinowitz and Nottingham, 1986), leopard, and golden cat (*Profelis aurata*) (Hart *et al.*, 1996), and for the close relative of the güiña, Geoffroy's cat within pampas grassland regions of Chile (Johnson and Franklin, 1991) and Argentina (Manfredi *et al., in prep.*).

3.1.3 Chapter Aims

The purpose of this chapter is to provide the first quantitative description of the güiña diet, and attempt to relate this to availability indices calculated for potential small mammal prey. Specifically, the aim was to determine whether güiña are generalist predators, and hence consume prey items in accordance to their relative availability, or alternatively, whether güiña preferentially select particular prey categories from among those available.

Dietary composition is here assessed via analyses of scat samples, then contrasted with small mammal abundance indices derived from i) live-trapping studies and ii) an alternative field protocol designed to sample the arboreal distribution of potential prey. Field data are further examined to determine whether indices of small mammal occurrence differed between the two study sites, or between the major habitat categories.

3.2 Methods

3.2.1 Estimation of small mammal field abundances

The relative abundances of small mammal species were evaluated within each study area via grid-based live-trapping studies. Small mammals were captured at ground level within each of the principal habitat types using Sherman live traps (23 cm × 9 cm × 7.5 cm, model LFA, H.B. Sherman Traps, Florida) baited with wheat and peanut butter. Pairs of traps placed 1 m apart were deployed at 20 m intervals within grid configurations, the dimensions of which were determined in part by habitat fragment size. Within PNLSR, live trap grids inside thicket-forest and thicket habitat comprised 12 trap pairs arranged in three rows of four pairs (0.24 ha). Because it was suspected that organic waste inside the park rangers' garden might support relatively dense small mammal populations and hence could potentially affect güiña foraging decisions, the garden and surrounding area was also sampled. This was achieved using a larger grid of 40 trap pairs arranged in five rows of eight (1.12 ha). All other grids were 0.48 ha in area (20 trap pairs in four rows of five). A minimum of 350 m was maintained between grids and only habitat stands large enough to contain an entire grid plus a buffer zone of 20 m width were selected. To minimise trapping bias between species one trap in each pair was placed under or adjacent to some structural component of the microhabitat (for example, beside logs or under stumps), the second was placed within 1 m, but in the open (Gurnell and Langbein, 1983).

Each grid was checked at dawn and operated for a minimum of three consecutive nights (Olsen, 1975; Steele *et al.*, 1984), corresponding to a maximum of 264 and a minimum of 72 trap nights per grid. Closed, empty traps were recorded as 'unavailable' for that trap night and subtracted from the total trap effort. Captured animals were identified to species level following Muñoz-Pedreros (2000). Standard morphological measurements were recorded with a Vernier calliper, and body weights were determined to the nearest gram using a 100 g Pesola balance. Hair samples were taken from the dorsal, lateral and ventral regions to add to an existing reference collection and to verify species identification where required. Each individual was marked with a unique fur-clip of the dorsal pelage to permit the recognition of recaptured animals, before being released at the site of capture.

Health and safety issues concerning the endemic and rodent-borne hantavirus and the availability of protective biohazard apparatus restricted the frequency and duration of rodent-related fieldwork. It was therefore not possible to conduct live-trapping surveys across all seasons. A single such survey was conducted in PNLSR during September (spring) 1999. Trapping surveys took place in the PNQ site during July (winter) and September/ October (spring) 2000. The same trapping grid locations were used on both occasions.

Several small mammal studies have been conducted within southern Patagonian forests in habitats similar to those found inside PNLSR and PNQ (for example Murúa and González, 1982; Pearson, 1983; Meserve *et al.*, 1991a; 1991b). These studies examined only terrestrial populations however, and did not consider arboreal species. Because güiña can climb it was felt necessary to consider also the three-dimensional nature of their habitat, i.e. prey potentially available in the trees. An alternative sampling protocol with minimal hantavirus risk was therefore devised after Rau *et al.* (1995) to supplement the live-trapping data. Hair-sampling tubes were utilised within PNQ in conjunction with the trapping grids to survey the occurrence of arboreal prey. These were constructed from 55 mm diameter PVC tubes cut to 14 cm lengths. A strip of parcel tape (50mm wide, Sellotape® Company), sticky side exposed was attached to the inside of each tube and a bait bag (peanut butter wrapped in muslin) wired to the facing side. The hair traps were attached to vegetation at 20 m intervals along line transects within or adjacent to the live trapping grids inside stands of forest, forest-thicket and thicket, taped side upmost. Each transect comprised 20 hair traps, two attached to each of ten trees at heights of 1 m and 2 m above ground level. The hair tubes were left in position for a four week period during June and July (winter) and October (spring) 2000. The bait and sticky tape were replaced at fortnightly intervals to ensure both remained effective. Hair samples were identified in the laboratory from cuticular morphology (see Appendices 2 and 3). An attempt to census small mammal species at ground level using hair tubes was abandoned due to water logging and removal of bait by ground living birds.

Bird lists were compiled for each site, however although güiña are known to consume avian prey, this study did not attempt to assess the actual and relative abundance of bird species within the study areas or within the güiña diet. This was primarily due to time constraints in the field, and a lack of suitable reference keys for the identification of avian prey remains. Bird remains extracted from faecal samples were also invariably too degraded to permit identification even to family level, though this was attempted whenever possible.

3.2.2 Determination of prey components in the güiña diet

Güiña scats were collected whenever and wherever they were encountered, rather than by systematic survey. Güiña are not known to bury their faeces. During this study scats were located either singly on prominent positions on tree roots or forest paths, or clumped in defecation spots. No evidence was found of midden sites situated in the crooks of trees, as is common for Geoffroy's cat (Johnson and Franklin, 1991). Each scat was labelled according to date of collection, location and relative age. Scat samples were air-dried to constant mass inside a fume cupboard before inspection. Misclassification of scats from the sympatric culpeo fox (*Dusicyon culpaeus*) and American mink (*Mustela vison*) was considered unlikely due to their distinctive size, shape and odour. Güiña scats were typically 6-10 cm in length and approximately 1.5-2 cm in diameter. They lacked any twisting at the ends and had no distinguishing smell (Plate 6).

Small mammal trapping studies were combined with a review of the relevant literature to identify those species potentially present within each of the two study areas. From these a dichotomous key based on cuticular hair characteristics was devised to facilitate the identification of mammalian remains from scat samples (Appendix 3; Table 3.2.1). This key was validated using museum specimens. High-resolution photographs of scale pattern imprints taken from the guard hairs of representative specimens were made using a Normarski light microscope at ×40 magnification to illustrate inter-specific variation among the most likely species present at the site (Plates 7a-7h).

Table 3.2.1 Guard hair morphological characteristics used in the identification of small mammal species from the forests of the Valdivian and Magellanic bioregions.

		Akodon longipilis	*Akodon olivaceus*	*Auliscomys micropus*	*Geoxus valdivianus*	*Irenomys tarsalis*	*Oryzomys longicaudatus*	*Phyllotis darwini*	*Dromiciops gliroides*
Distal section	Secondary section	Crenated	Crenated	Toothed mosaic	Crenated	Mosaic	Mosaic	Mosaic	Fine mosaic
	Primary section	Toothed mosaic	Mosaic (v. slightly toothed)	Mosaic	Crenated	Mosaic (slightly toothed)	Mosaic	Mosaic	Fine mosaic
Proximal section	Distal	Fused	Fused	Unequal, fused poly-mosaic	Broad rounded lanceolate	Uneven lanceolate	V-shaped & elongate	Coronal *en vaina*	Rhomboid, uneven lanceolate, some fused
	Middle	Fused lanceolate, rounded towards proximal end	Lanceolate, fused towards proximal end	Lanceolate	Uneven lanceolate	Lanceolate, fused towards proximal end	Lanceolate, fused towards proximal end	Coronal *en vaina*	Lanceolate, some fused
	Proximal	Fused lanceolate, *en vaina* towards proximal end	Fused lanceolate, *en vaina* towards proximal end	Coronal *en vaina*	Coronal *en vaina*	*En vaina* Uneven diamond petal shaped	Coronal *en vaina*	Coronal *en vaina*	Lanceolate, *en vaina* towards proximal end

Of those species known to be present in each study area, the endemic pudu (*Pudu pudu*) (Artiodactyla) and sympatric carnivores including the culpeo fox, lesser grison and the American mink were considered too large to be preyed upon by güiña. Any occurrences of these species in the diet were therefore attributed to their ingestion as carrion. The majority of species included as potential prey had body masses of less than 150 g; the bird species most commonly observed in the field (*S. rubecula*, *Aphrastura spinicauda* and *Sephanoides galertus*) and all small mammals captured during this study weighed less than 70 g (Morgado *et al.,* 1987; Redford and Eisenberg, 1992; Sieving *et al.,* 2000).

Following Ackerman *et al.* (1984) it was considered possible that individual scats would contain ingested remains of more than one prey animal because of the considerably smaller size of potential prey relative to that of güiña. A sub-sampling technique was therefore applied to ensure all species present in scats were represented, whereby five samples of approximately 1.0 cm^3 were extracted from random locations within each scat. These samples were rinsed in warm water to remove excess debris from the prey remains, and air-dried before detailed inspection. Feather barb structures from largely intact feather samples were compared directly with a photographic reference guide for South American bird species (courtesy of S. Corales and J. Rau). Where mammalian guard hairs were retrieved, impressions of cuticular scale patterns were made on films of clear varnish before microscopic observation at × 40 magnification and comparison with the identification key and high-resolution photographs. Imprints of several hairs were made from each sub-sample to allow for poor impressions. Other food items were examined macro- and microscopically and assigned to the most specific taxa possible. Large, intact beetles were assumed to have entered scats subsequent to their deposition and were hence excluded from all analyses.

3.2.3 Quantification of the güiña diet

Dietary composition was expressed as *frequency of occurrence* - the percentage of scats in which a particular item was found, and as *percentage occurrence* - the number of times a prey item was found, expressed as a percentage of all items recorded (Lockie, 1959). The terms 'prey item' and 'prey category' here refer to the categorisation of prey to the lowest taxonomic resolution possible. This was undertaken to species level whenever this was feasible, but in the case of birds or insects for example, all occurrences were pooled within a single, inclusive category for each class.

Frequency of occurrence provides a simple indication of how common an item is in the diet, but percentage occurrence accounts also for the presence of multiple prey items in individual scats. Ackerman *et al.* (1984) considered percentage occurrence to provide a better indication of the relative frequency with which each item is consumed, however this method can over-represent minor items and under-represent major ones (Lockie, 1959; Wise, *et al.*, 1981; Corbett, 1989; Medina, 1997). Both indices were therefore utilised to describe dietary composition in order to take the limitations imposed by each single method into consideration, and to make these results comparable with other descriptions of carnivore diet (Reynolds and Aebischer, 1991).

Estimates of relative contribution to the diet derived solely from occurrence frequency may be distorted when prey sizes are highly variable (Floyd *et al.*, 1978; Ackerman *et al.*, 1984). In the absence of conversion factors specific to güiña or similarly sized felids I did not correct for differential ingestion and digestion of prey items or prey size, but instead assumed the proportion of prey remains in scats provided a fair representation of the items ingested. This was considered valid due to the narrow size spectrum of prey species present (live weights of small mammals captured in the field were all between 14 and 67g).

No attempt was made to analyse scat content according to habitat type because each home range encompassed several habitat patches, hence site of scat deposition was unlikely to reflect the patch choice of the individual whilst foraging. Variation in predation within prey classes between sites and seasons was investigated using log-likelihood ratio tests on percentage occurrence data. Constant digestibility of prey categories was assumed across each year.

To corroborate the above, dietary overlap between seasons and study sites was investigated using Schoener's (1968) proportion of similarity index (PS), calculated at the level of taxonomic resolution of prey categories:

$$PS = 1 - 0.5\left(\sum_{i=1}^{n} \left| p_{ij} - p_{ik} \right|\right) \qquad \text{Equation 3.2.1}$$

where n is the total number of resource states, p_{ij} is the proportion of the *i*th prey utilised in season or site *j*, and p_{ik} is its proportion in the diet in season or site *k*. This index weights matched data more heavily than mismatches and is the most appropriate for use when it is suspected sampling techniques may miss many species (Krebs, 1989).

Colwell and Futuyama's (1971) standardised form of Levins' index (Levins, 1968) was applied to the diet composition data to examine overall and seasonal food-niche breadth:

$$B_i = \frac{1}{h-1}\left(\frac{1}{\sum p^2_i} - 1\right) \qquad \text{Equation 3.2.2}$$

where B_i is Levin's standardised index for food item i; p_i is the relative frequency of food item i in the diet of predator p, and h is the maximum possible niche breadth (i.e., the number of general prey taxa available). Food-niche breadths were measured at the level of taxonomic resolution of prey categories. Seasonal and site differences were evaluated using a multi-way contingency table to compare the association of diet categories and seasons or sites.

Levin's standardised index provides an indication of niche breadth by describing the contribution of prey categories to the güiña diet in terms of the uniformity of category occurrence. Whereas Levins' index produces values ranging from 1 to n (for n equally used resource categories), the standardised index is confined to between 0 and 1. Higher values indicate a more generalised diet, and reach a value of one when all available categories are exploited equally (Krebs, 1989). The standardised index is considered preferable because it permits comparison between diets of different prey category numbers (Krebs, 1989).

3.2.4 Relative utilisation of available prey

The incidence of small mammals in the güiña diet was compared to estimated field abundances using Spearman rank correlation (Zar, 1984). The similarity between the diversity of species detected by the two sampling techniques: hair tubes and live traps was then contrasted, both separately and in combination against species representation in the güiña diet using Sorensen's coefficient of similarity (S) (Brower *et al.*, 1990):

$$S = \frac{2a}{2a+b+c} \qquad \text{Equation 3.2.3}$$

where: a is the number of species in both sample A and sample B (i.e. joint occurrences); b = number of species in sample B but not in sample A, and c = number of species in sample A but not in sample B. Field data obtained from PNLSR were not included because no hair tube data were recorded within this site.

Following Rau *et al.* (1995) a jack-knifing procedure was used to further examine the concordance between the güiña diet–live-trap coefficient and the güiña diet–hair tube coefficient (Sokal and Rholf, 1981; Krebs, 1989). Pseudo-values were calculated by recomputing each coefficient following the sequential removal of each species in turn from the data set of one sampling procedure and then the other. The pseudo-values generated for each sampling technique were contrasted using a two-sided t-test.

3.3 Results

3.3.1 Small mammal occurrence and density estimates

3.3.1.1 Live-trap estimates

Four species of small mammals were captured, 49 individuals were trapped a total of 71 times within the PNLSR study site during 660 trap-nights in spring (October) 1999 (7.4% trap success) (Table 3.3.1). The two trapping periods conducted at the PNQ study site resulted in 199 captures of 111 individuals during 400 trap nights in winter (July) 2000, and 100 captures of 61 individuals in 328 trap nights the following spring (27.8% and 18.6% trap success respectively). The majority of traps were unfilled each day, hence captures could be considered independent of one another (i.e. 'trap competition' was considered to be negligible).

Within the PNQ site similar numbers of small mammals were trapped per hectare during winter and spring ($t_2 = 0.126$, $P = 0.911$). The greatest population densities were recorded within thicket-forest habitat during both spring-time trapping studies (Table 3.3.1). There was no significant difference however among small mammal population densities in each of the forest, thicket-forest and thicket habitat categories across the three trapping periods (one-way generalised linear model (GLM): $F_{6,8} = 1.797$; $P = 0.245$).

Two species, *Akodon olivaceus* and *Oryzomys longicaudatus* accounted for the majority of captures during each trapping study. There was no effect of habitat category on capture frequency for either of these species (*A. olivaceus*: $F_{2,6} = 0.693$; $P = 0.536$; *O. longicaudatus*: $F_{2,6} = 0.237$; $P = 0.796$ (one-way ANOVAs; Table 3.3.2). *Irenomys tarsalis* and *Phyllotis darwini* were also captured using the live traps; each however was captured during a single survey only. Five *P. darwini* were trapped on the forest habitat trap grid in PNLSR during spring 1999, and three *I. tarsalis* individuals were captured during the winter survey in forest and thicket-forest habitat within PNQ.

Table 3.3.1 Relative trap success and species density estimates from rodent live trapping surveys. Study periods were spring (September) 1999 in PNLSR and winter (July) and spring (September/October) 2000 in PNQ. Trap effort was adjusted for closed traps.

Site	Habitat Type	Grid area (ha)	Trap effort	Number of captures[a]	Trap Success[b]	Captures per 100 trap nights ha^{-1} (number of captures)[c]				
						A.o.	*I.t.*	*O.l.*	*P.d.*	Total
PNLSR	Forest	0.48	126	12	9.52	11.57 (7)	0.00 (0)	0.0 (0)	8.26 (5)	19.83
Spring	Thicket-forest	0.24	72	9	12.50	40.51 (7)	0.00 (0)	11.57 (2)	0.00 (0)	52.08
October 1999	Thicket	0.24	72	4	5.55	11.57 (2)	0.00 (0)	11.57 (2)	0.00 (0)	23.13
	Scrub-thicket	0.48	126	8	6.35	9.92 (6)	0.00 (0)	3.31 (2)	0.00 (0)	13.23
	Garden and surrounding area	1.12	264	16	6.06	4.40 (13)	0.00 (0)	1.01 (3)	0.00 (0)	5.41
PNQ	Forest	0.48	146	45	30.82	39.95 (28)	1.43 (1)	22.83 (16)	0.00 (0)	64.21
Winter	Thicket-forest	0.48	151	34	22.52	36.39 (27)	2.70 (2)	6.74 (5)	0.00 (0)	45.83
June 2000	Thicket	0.48	103	32	31.07	54.62 (27)	0.00 (0)	10.11 (5)	0.00 (0)	64.73
PNQ	Forest	0.48	120	22	18.33	31.25 (18)	0.00 (0)	6.94 (4)	0.00 (0)	38.19
Spring	Thicket-forest	0.48	118	48	40.68	61.80 (35)	0.00 (0)	22.95 (13)	0.00 (0)	84.75
October 2000	Thicket	0.48	90	19	21.11	34.72 (15)	0.00 (0)	9.26 (4)	0.00 (0)	43.98

[a] excluding recaptures
[b] = captures/100 trap nights, excluding recaptures.
[c] Species are: *Akodon olivaceus, Irenomys tarsalis, Oryzomys longicaudatus* and *Phyllotis darwini.*

Table 3.3.2 One-way ANOVAs of *Akodon olivaceus* and *Oryzomys longicaudatus* capture frequencies within forest, forest-thicket and thicket habitats.

Source	*d.f.*	Sum of squares	Mean square	*F*	*P*
A. olivaceus					
Habitat category	2	711.888	355.944	0.693	0.536
Error	6	3079.654	513.276		
Total	8	3791.541			
O. longicaudatus					
Habitat category	2	64.489	32.245	0.237	0.796
Error	6	815.320	135.887		
Total	8	879.809			

3.3.1.2 Hair tube trap results

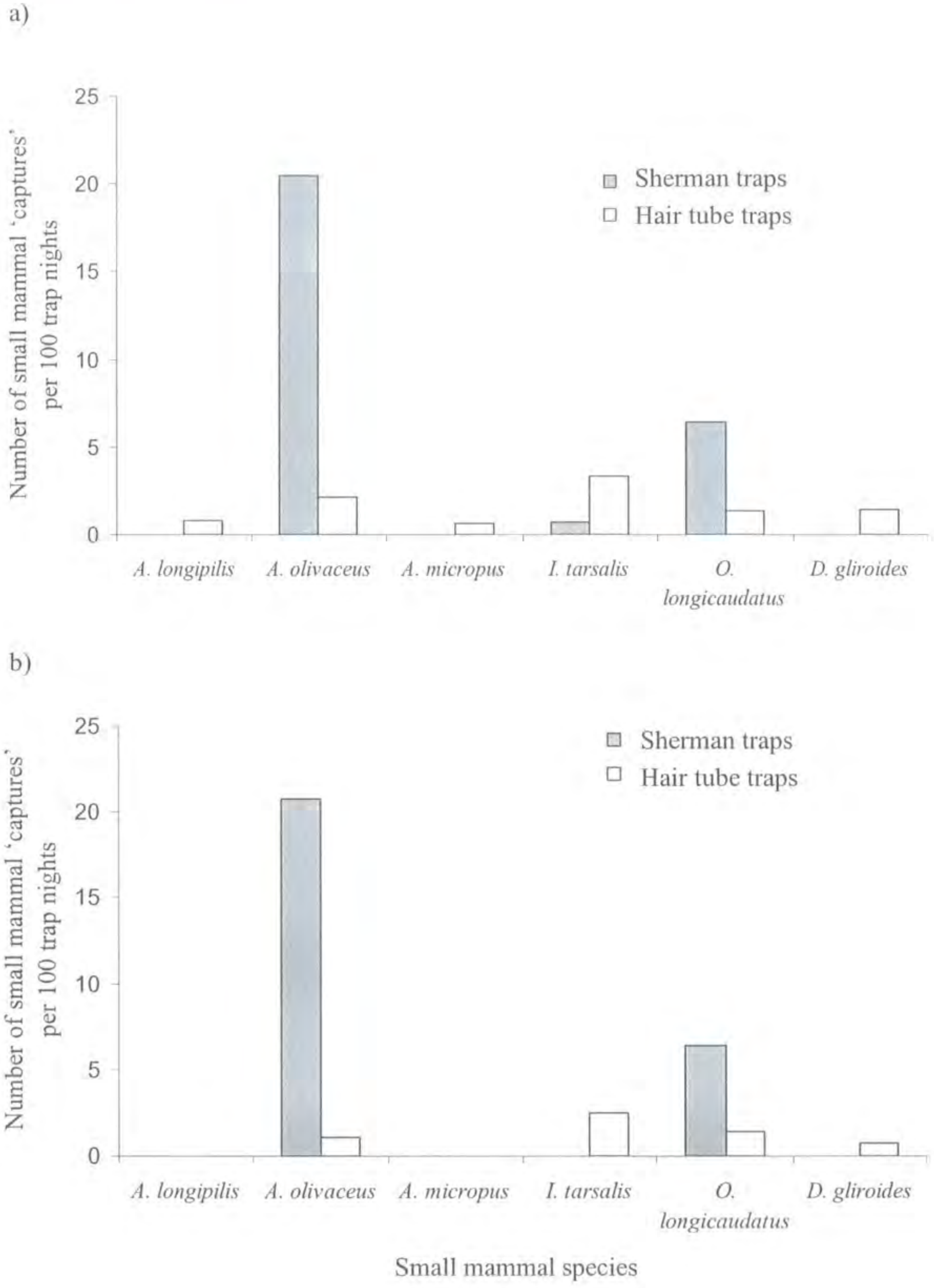
Table 3.3.3 summarises the results from the two hair tube trap surveys conducted within the PNQ site during 2000. Visits by multiple individuals of the same species to the same hair trap could not be distinguished. Absolute frequencies are therefore minimum estimates.

Table 3.3.3 Small mammal species (rodents and marsupials) registered by hair-sampling tubes in PNQ. Values are number of hair samples collected per 100 hair-sampling tubes per night. Absolute frequencies of species recorded are provided in parentheses.

Species	Winter (June/July) 2000		Spring (October) 2000	
RODENTIA				
Akodon longipilis	0.80	[9]	0.00	[0]
Akodon olivaceus	2.14	[24]	1.07	[12]
Auliscomys micropus	0.63	[7]	0.00	[0]
Irenomys tarsalis	3.30	[37]	2.50	[28]
Oryzomys longicaudatus	1.34	[15]	1.43	[16]
MARSUPIALIA				
Dromiciops gliroides	1.43	[16]	0.71	[8]
Subtotal	9.64		5.71	
Captures		[108]		[64]
Effort	1120		1120	

Figure 3.3.1 presents the relative success rates of the trap grid and hair tube sampling procedures within the PNQ study site. No concordance in the distribution of species ‘captures’ was detected between the two methodologies within or across seasons (Pearson correlation coefficients, all $r \leq 0.26$, $P > 0.05$). The trap grids captured only three species, predominantly *A. olivaceus* and *O. longicaudatus*, whereas the hair tubes registered a greater diversity of small mammals, up to a maximum of six species.

Figure 3.3.1 Percentage of Sherman live-traps and hair tube traps that registered the presence of small mammal species in PNQ during a) winter 2000 (June-July), and b) spring 2000 (October).



3.3.2 The güiña diet in PNLSR and PNQ

Table 3.3.4 describes the composition of the güiña diet within PNLSR and PNQ based on the analysis of 135 and 35 scats respectively. Scats collected from PNQ contained significantly more prey categories per scat than those from PNLSR (median [25th–75th percentile] PNLSR: 1 [1-2]; PNQ: 2 [1-2]; $U = 1616$, $P = 0.001$, Mann-Whitney U-test). Mammalian remains occurred in all scats. Rodents and the marsupial *D. gliroides* in particular dominated the diet and comprised 72.5% of all prey identified in PNLSR, and 67.7% in PNQ. The relative frequencies of small mammal prey items in the güiña diet differed between the study areas, although *A. olivaceus* was the most commonly consumed species at both sites. Avian prey were also consumed frequently and represented approximately 20% of all prey items identified in each study area. Occasionally it was possible to confidently identify avian remains to species level. Where bird remains could be identified to species, these were all either *Scelorchilus rubecula* or *Aphrastura spinicauda*.

Only two instances of carrion in the diet could be confirmed, both from within the PNLSR study area. One occurrence of pudu hair was recorded, and one of sheep (*Ovis aries*) wool, suggesting güiña on occasion stole mutton from the guardeparques' meat store. Carrion, invertebrates and vegetation occurred relatively infrequently in the diet, suggesting these were of low importance to the güiña.

Small mammal species characterised as terrestrial (Pearson, 1983) represented 61.11% of small mammal prey items identified from scats collected in PNLSR, and 71.05% of those from PNQ. Arboreal species represented 26.19% and 7.89% respectively. Güiña preyed predominantly upon nocturnal species; these comprised 88.89% of small mammal prey in PNLSR, and 68.42% in PNQ.

Dietary composition was similar across the two sites (Schoener's PS = 0.79; G = 8.22, $d.f. = 5$, $P > 0.05$). All but two trophic categories (carrion and vegetation) occurred in scat samples collected at both sites and there was close similarity between the standardised niche breadths of each güiña population (Table 3.3.4).

Table 3.3.4 Overall composition of the güiña diet in PNLSR (1997 to 1999) and PNQ (1999 to 2001), as determined by faecal analyses. To the right of each small mammal species is denoted its spatial activity (T = terrestrial, A = arboreal, F = fossorial), and its temporal activity (N = nocturnal, D = diurnal) using activity classifications from Pearson (1983). Numbers of scats are provided in parentheses.

	PNLSR [135]			PNQ [35]		
Prey item	Prey item occurrence	Frequency of occurrence	Percentage occurrence	Prey item occurrence	Frequency of occurrence	Percentage occurrence
Akodon longipilis (T; D, N)	9	6.67	3.50	8	22.86	12.90
Akodon olivaceus (T; N)	40	29.63	20.00	12	33.29	19.35
Auliscomys micropus (T; N)	17	12.59	8.50	5	13.29	8.06
Geoxus valdivianus (F; D-N)	5	3.70	2.50	4	11.43	6.45
Irenomys tarsalis (A; N)	23	17.04	11.50	1	2.86	1.61
Oryzomys longicaudatus (T, A; N)	11	8.15	5.50	4	11.43	6.45
Phyllotis darwini (T; N)	11	8.15	5.50	2	5.71	3.23
Dromiciops gliroides (A; N)	10	7.41	5.00	2	5.71	3.23
Unidentified small mammal	19	13.07	9.50	4	11.43	6.45
Carrion	2	1.48	1.00	0	0.00	0.00
AVES	41	30.37	20.50	12	33.29	19.35
INSECTA	4	2.96	2.00	8	22.86	12.90
Vegetation	8	5.93	3.00	0	0.00	0.00
Total prey items	200	148.15	100.00	62	177.14	100.00
G-value (*d.f.*)	8.215 (5)					
P	0.145					
Standardised niche breadth[a]	0.604	0.544				

[a] Discounting unidentified prey.

3.3.3 The güiña diet - seasonal comparisons

Dietary composition by season is indicated in Tables 3.3.5 and 3.3.6 and Figure 3.3.2. Güiña fed predominantly on small mammalian prey items across all seasons (percentage occurrence $\bar{x} \pm SE = 71.25 \pm 5.97\%$, range 42.85-100%), however avian prey also occurred frequently in the diet (20.42 ± 3.56%, range 0-28.57%). Invertebrates, carrion and vegetation were consumed less frequently (invertebrates 9.75 ± 3.75%; carrion 0.51 ± 0.51%; vegetation 2.75 ± 1.64%).

The spring/summer 2000, autumn 2000 and spring/summer 2001 field seasons were excluded from further analysis because of small sample sizes (Hanson & Graybill, 1956), but are included in Tables 3.3.4 and 3.3.5 and Figure 3.3.2 for comparative purposes. The composition of the güiña diet did not vary significantly across the remaining field seasons ($G = 7.89$, *d.f.* = 8, $P > 0.05$). Dietary overlap as indicated by Schoener's proportion of similarity (PS) was relatively high between seasons (range 0.68 - 0.84) and there was close similarity between the standardised niche breadths of each (range 0.42 - 0.54), indicating prey diversity remained relatively constant across those seasons.

Table 3.3.5 Composition of the güiña diet as determined from the analysis of scats collected within the PNLSR study site. Prey species occurrence is displayed as frequency of occurrence (percentage of total scats in which a prey item was found), and percentage occurrence (number of times a specific item was found as a percentage of all items recorded). Sample sizes are given in parentheses by season of collection.

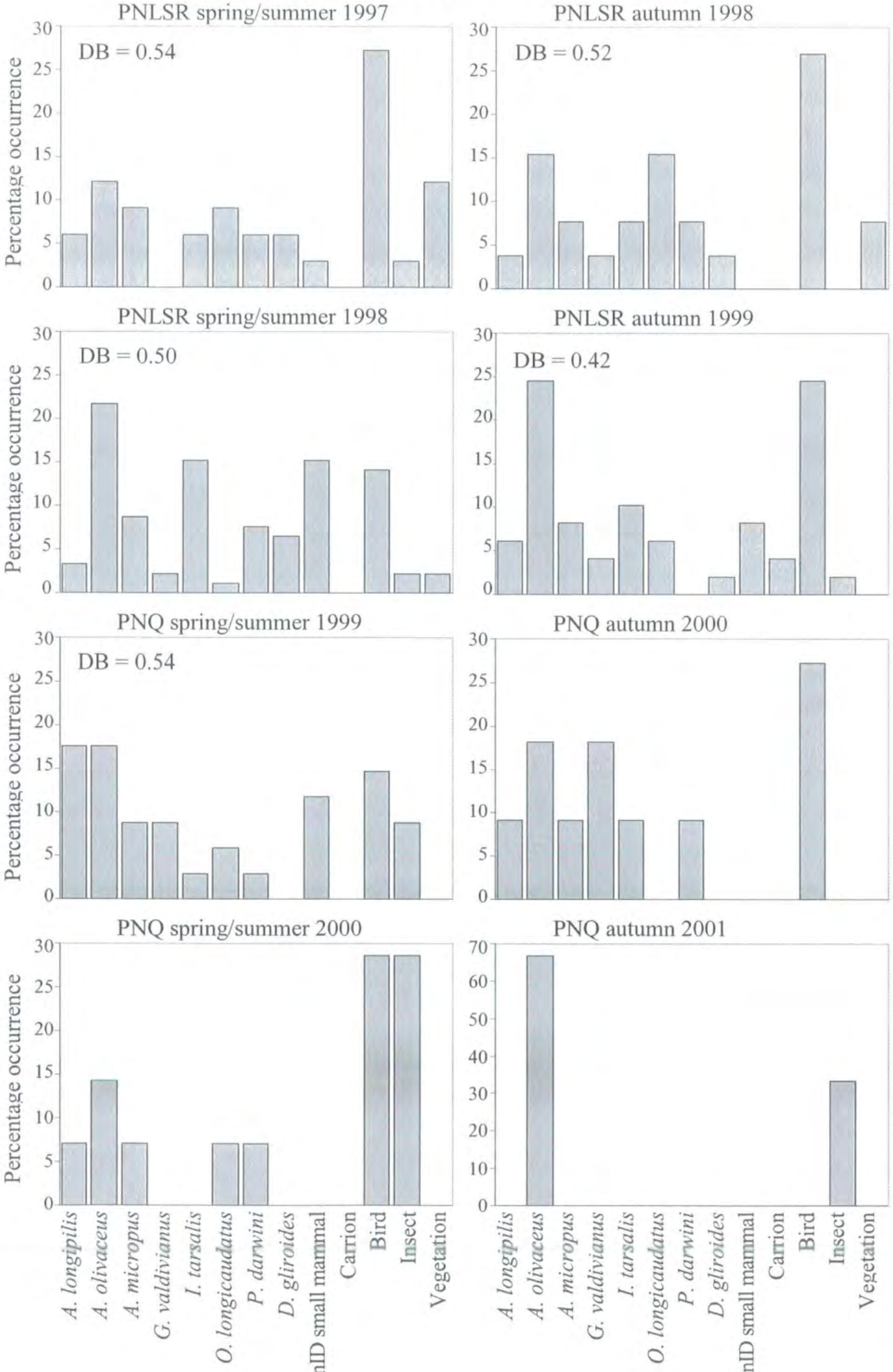
Prey Item	Spring/summer (Oct – Nov) 1997 [15]		Autumn (Jan – March) 1998 [15]		Spring/summer (Oct – Nov) 1998 [69]		Autumn (Jan – March) 1999 [36]	
	Frequency of occurrence	Percentage occurrence	Frequency of occurrence	Percentage occurrence	Frequency of occurrence	Percentage occurrence	Frequency of occurrence	Percentage occurrence
Akodon longipilis	13.33	6.06	6.67	3.85	3.35	3.26	8.34	6.12
Akodon olivaceus	26.67	12.12	26.67	15.38	28.99	21.74	33.33	23.49
Auliscomys micropus	20.00	9.09	13.33	7.69	11.59	8.70	11.11	8.16
Geoxus valdivianus	0.00	0.00	6.67	3.85	2.90	2.17	5.56	3.08
Irenomys tarsalis	13.33	6.06	13.33	7.69	20.29	15.22	13.89	10.20
Oryzomys longicaudatus	20.00	9.09	26.67	15.38	1.45	1.09	8.33	6.12
Phyllotis darwini	13.33	6.06	13.33	7.69	10.14	7.61	0.00	0.00
Dromiciops gliroides	13.33	6.06	6.67	3.85	8.70	6.52	2.78	2.04
Unidentified small mammal	6.67	3.03	0.00	0.00	20.29	15.22	11.11	8.16
Carrion	0.00	0.00	0.00	0.00	0.00	0.00	5.56	3.08
AVES	60.00	27.27	46.67	26.92	18.84	13.13	33.33	23.49
INSECTA	6.67	3.03	0.00	0.00	2.90	2.17	2.78	2.04
Vegetation	26.67	12.12	13.33	7.69	2.90	2.17	0.00	0.00
Total	220.00	100.00	173.34	100.00	133.34	100.00	136.12	100.00

Table 3.3.6 Composition of the güiña diet as determined from the analysis of scats collected within the PNQ study site. Prey species occurrence is displayed as frequency of occurrence (percentage of total scats in which a prey item was found), and percentage occurrence (number of times a specific item was found as a percentage of all items recorded). Sample sizes are given in parentheses by season of collection.

Prey Item	Spring/summer (Oct – Nov) 1999 (19)		Autumn* (Jan – March) 2000 (8)		Spring/summer* (Oct – Nov) 2000 (6)		Autumn* (Jan – March) 2001 (2)	
	Frequency of occurrence	Percentage occurrence	Frequency of occurrence	Percentage occurrence	Frequency of occurrence	Percentage occurrence	Frequency of occurrence	Percentage occurrence
Akodon longipilis	31.58	17.65	12.50	9.09	16.67	7.14	0.00	0.00
Akodon olivaceus	31.58	17.65	25.00	18.18	33.33	13.29	100.00	66.67
Auliscomys micropus	15.79	8.82	12.50	9.09	16.67	7.14	0.00	0.00
Geoxus valdivianus	15.79	8.82	12.50	9.09	0.00	0.00	0.00	0.00
Irenomys tarsalis	5.26	2.94	0.00	0.00	0.00	0.00	0.00	0.00
Oryzomys longicaudatus	10.53	5.88	12.50	9.09	16.67	7.14	0.00	0.00
Phyllotis darwini	5.26	2.94	0.00	0.00	16.67	7.14	0.00	0.00
Dromiciops gliroides	0.00	0.00	25.00	18.18	0.00	0.00	0.00	0.00
Unidentified small mammal	21.05	11.76	0.00	0.00	0.00	0.00	0.00	0.00
Carrion	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
AVES	26.32	13.71	37.50	27.27	66.67	28.57	0.00	0.00
INSECTA	15.79	8.82	0.00	0.00	66.67	28.57	50.00	33.33
Vegetation	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Total	178.95	100.00	137.50	100.00	233.35	100.00	150.00	100.00

*Seasons not included within analyses due to small sample sizes.

Figure 3.3.2 Seasonal variation in the diet of güiña within the PNLSR and PNQ study areas (PNLSR: spring 1997 - autumn 1999; PNQ spring 1999 - autumn 2001). DB is diet breadth; sample sizes are as for Tables 3.3.5 and 3.3.6.



3.3.4 Comparison with availability

Table 3.3.7 contrasts the relative availability of small mammal prey in the field against the incidence of these species in the güiña diet. Field abundances were calculated using data collected simultaneously within PNQ using the two sampling methodologies, live-trap grids and hair trap transects. Only spring data are presented as no winter dietary data were recorded. Because no significant difference in diet composition was detected between sites all dietary data were pooled. No significant correlation was detected between prey availability and representation within the diet ($r_s = 0.495$; $P > 0.05$). The principal discrepancies were due to *A. micropus* and *A. longipilis* (ranked 3rd and 4th in the diet respectively, but absent in the traps) and *O. longicaudatus,* which was the second most frequently encountered small mammal in the field, but ranked only 5th in the güiña diet.

Table 3.3.7 Standardised percent frequencies of small mammals assessed in the field against their representation in the güiña diet. Rankings are denoted in parentheses.

Species	Field		Diet	
A. olivaceus	66.38	(1)	31.71	(1)
O. longicaudatus	23.84	(2)	9.15	(5)
I. tarsalis	7.61	(3)	13.63	(2)
D. gliroides	2.16	(4)	7.32	(7)
A. micropus	0.00	(6.5)	13.41	(3)
A. longipilis	0.00	(6.5)	10.37	(4)
P. darwini	0.00	(6.5)	7.93	(6)
G. valdivianus	0.00	(6.5)	5.49	(8)

The coefficient of similarity (S) between the species detected by the hair tube and live trapping survey procedures within PNQ was 66.7%. The similarity between the small mammal population composition estimated using the hair tube sample technique and that estimated from the güiña diet was 83.3% and that between the live trap data and the güiña diet was 54.5%, i.e. the species lists generated by the hair tube sampling and the dietary analysis showed the greatest concordance. Pseudo-values generated for the güiña diet–hair tube trap coefficient (0.757 ± 0.020) were greater than those calculated for the güiña diet–live trap coefficient (0.491 ± 0.031; $t_{21} = 7.22$, $P < 0.001$).

3.4 Discussion

3.4.1 Dietary composition

Small mammals, in particular cricetine rodents dominated the güiña diet within both study areas and occurred in all 170 scats examined. Rodents and other small mammal species form the major part of the diet of numerous other small felids including European wildcat (*Felis silvestris*; Hewson, 1983), jungle cat (*F. chaus*; Schaller, 1967), leopard cat (*Prionailurus bengalensis*; Inoue, 1972; Rabinowitz, 1990; Grassman, 1998a; 2003), Geoffroy's cat (Johnson and Franklin, 1991; Novaro *et al.*, 2000), serval (*Leptailurus serval*; Geertsema, 1976; 1985; Smithers, 1978), African wildcat (*F. silvestris libyca*; Palmer and Fairall, 1988) and the black-footed cat (*Felis nigripes*; Sliwa, 1994). Hewson (1983) for example found European wildcats in Scotland to preferentially feed on rodents regardless of the availability of rabbits, which offer greater energetic returns.

The composition of the güiña diet was similar across both study areas. *A. olivaceus* was the most frequently occurring prey species though *I. tarsalis* and *A. micropus*, and the marsupial *D. australis* were also regularly taken. Together these represented approximately 67% of small mammal items consumed. Other species were preyed upon less extensively, possibly due to infrequent encounter rates or behavioural patterns that reduced their relative vulnerability to predation. Tail autotomy has been observed in *P. darwini* for example (Jaksić and Simonetti, 1987), which might afford this animal some defence against capture.

Avian remains occurred in several scats. Although many could not be identified to species level it was notable the majority of those that could were from the flightless *S. rubecula*. Güiña on Isla Grande de Chiloé also frequently took avian prey (Sanderson *et al.*, 2002), and, with the exception of the austral thrush these were species that predominantly forage on the ground (Southern lapwing, chucao tapaculo and huet-huet). Observations made on Isla Grande indicate that güiña will occasionally predate considerably larger prey, including domestic hens and geese (Sanderson *et al.*, 2002). Comparatively sized potential prey such as Ashy-headed Geese (*Chloephaga poliocephala*), Kelp Geese (*Chloephaga hybrida*), and buff-necked ibis (*Theristicus caudatus*) were present within the PNLSR study site, yet no evidence was found to suggest that these were predated by güiña. Adult cats trapped during this study were approximately 30% smaller, on average, than those on Isla Grande however, therefore these comparatively large bird species may have been effectively unavailable to PNLSR güiña due to their more diminutive stature.

Invertebrates and vegetation comprised a minor component of the güiña diet and possibly represented incidental ingestion or contents of the digestive systems of prey. Plant matter retrieved from scats consisted of barbed seeds and single blades of grass, which may have been ingested inadvertently whilst grooming, or whilst consuming prey. Vegetation is not a necessary component of the felid diet, as it appears to be for canids (Lloyd, 1980), and rarely represents more than a very minor constituent of the overall diet (Triggs *et al.*, 1984). No evidence of fish predation was detected from scat analysis, despite one occasion when animal SAM3 was observed over a ten-minute period attempting to catch fish in tidal pools.

Only two probable cases of scavenging were noted. No data were available to describe the approximate densities of pudu populations in the vicinity of the study sites, however sightings were uncommon within each. It is considered unlikely therefore that pudu carcasses represent a food source that is regularly available to güiña. Fresh mutton was a relative luxury for the guardeparque hence it is probable that opportunities to steal fresh meat from the meat store were also infrequent. The occurrence of large mammal remains in the güiña diet suggests these cats feed opportunistically on carrion. No scats were collected during the late winter months, but as small mammal populations typically decline to low densities during this period (R. Figueroa pers com.), scavenging may be expected to become an increasingly important mode of feeding at this time.

No significant dietary trends were observed across seasons, suggesting relative abundances and vulnerability of prey did not vary greatly during this period. The absence of dietary data for the winter months, when pronounced climate variation is expected to strongly influence food availability, prevented comparison across the entire year.

3.4.2 Relative estimates of small mammal abundance

A total of six small mammal species were detected using the hair-sampling transects, in contrast the live traps captured only four species. The two sampling techniques caught slightly different groups; *P. darwini* was recorded on the trap grids but not using hair tube traps, these in turn detected *A. longipilis*, *A. micropus* and *D. gliroides* which were not captured on any trap grid. *I. tarsalis* and *D. gliroides* both have predominantly arboreal lifestyles, which is reflected in the trap data. The remaining small mammals are considered either terrestrial or fossorial in their habits (Pearson, 1983), however several reputedly 'terrestrial' species were also detected at heights of up to 2 m in trees.

In this study, live trap capture frequencies were not found to vary between habitats. This is in agreement with Pearson and Pearson (1982) who noted a lack of correlation between the number of small mammals recorded within Argentinean temperate rainforests and habitat structural complexity. Patterson *et al.* (1989) suggested that differences in small mammal abundance occurred with elevation, and found capture rates varied two-fold between 425 and 1135m altitude. At higher elevations species number and diversity were lower, possibly reflecting altered levels of food resources and cover due to increasing severity of environmental conditions such as temperature extremes, snow cover persistence and progressively reduced vegetation structure (Pizzimetiti and De Salle, 1980). As both the PNLSR and PNQ study areas occur at elevations below 100 metres above sea level, the influence of altitude was considered to be comparable at each site.

Greater trap success was recorded on the PNQ trap grids during early winter than the following spring. Small mammal capture rates at these latitudes typically peak in late autumn/early winter (R. Figueroa pers. comm.; Meserve, 1981; Murúa *et al.*, 1986) as juveniles born the previous spring become mobile and join the trappable population, but prior to increased mortality levels during the cold weather of later months. Increased capture rates do not necessarily reflect an increase in absolute abundance however, as small mammals increase their foraging rates and therefore activity and associated vulnerability in response to food scarcity. The trapping success rate of red-tailed squirrels (*Sciurus granatensis*) on Barro Colorado Island for example, was significantly greater during seasons of "dietary stress" than when food was abundant (Glanz *et al.*, 1982), and house mice (*Mus domesticus*) became less cautious when staple food sources became depleted (Ylönen *et al.*, 2002).

Small mammal abundances estimated in the field did not correspond with the relative incidence of species in the diet. Although this result implies güiña did not consume prey items in accordance to their relative availability, the utility and accuracy of the small mammal sampling procedures employed must be called into question, as evidenced by their failure to detect *A. longipilis*, *A. micropus* and *P. darwini* during spring 2000 when all three species occurred in the güiña diet. Brunner *et al.* (1975) and Rau *et al.* (1995) have previously commented upon the value of carnivore dietary studies in the context of small mammal studies. These authors, in similarity to this study, identified more small mammal species through investigation of grey fox and red fox (*Vulpes vulpes*) scat components respectively, than they accomplished through trapping studies and the use of hair sampling tubes.

Low trappability of some species may be responsible, in part, for the poor agreement between the live trap sampling procedure and the güiña diet. *G. valdivianus*, *I. tarsalis*, *A. micropus* and *D. gliroides*, for example, all display partial avoidance of live traps (Patterson *et al.,* 1989), whereas species such as *A. olivaceus* readily enter many trap designs. Any single trap type will almost inevitably be biased toward or against a subset of species within a community, and different survey methodologies can yield widely variable abundance estimates for the same species (e.g. Malcolm, 1990; 1991).

Hair tube traps represent a complementary methodology to live-trap surveys. They provide some of the same information, including species richness and relative abundance data, but at a greatly reduced effort and cost. The use of hair tubes facilitates simultaneous sampling of small mammal populations over several areas or over a short time period, and can reduce the risk of exposure of researchers to hantavirus because handling of animals is not required (Mills *et al.*, 1995). This approach only indicates species presence however; hence the quantitative assessment of relative abundances can be problematic. In this study hair tube traps did not operate efficiently at ground level. Some modification to the trap design would be required to prevent bait removal by non-target animals and the accumulation of excess water. Nevertheless, when these two sampling methodologies are assessed in conjunction they can potentially provide qualitative distribution data for the small mammal species present.

3.4.3 Potential sources of bias

A. olivaceous and *O. longicaudatus* are known to undergo pronounced seasonal and annual fluctuations in population density (Murúra and González, 1986). However the number, timing and duration of small mammal trap surveys were severely restricted by the precautionary measures necessary to avoid hantavirus transmission. It is acknowledged, therefore that the trap results presented here may represent only "snapshots" of temporally cyclical small mammal populations.

The degree to which scat contents represent actual dietary composition can be influenced by numerous factors. For example, the proportion of meat in the diet obtained from large carcasses may be underestimated because this contains comparatively little fur or bone in contrast to small mammal prey, hence is readily digested. In contrast indigestible prey components are typically over-represented in analyses of scat contents (Bearder, 1977; Floyd *et al.,* 1978; Putman, 1984).

In this study the assumption was made that hair detected in a scat represented the remains of only one animal of that species. In support of this assumption the remains of multiple small mammal species (indicating more than one prey item) were detected in only 17% of scats analysed. Some underestimation of the dietary contribution of the more common prey items is expected however.

Finally, the results presented here must be interpreted with due consideration given to the limitations of the small sample sizes obtained. It is possible that real differences exist, for example between the small mammal densities present within each of the three predominant habitat categories, but that these were not detected due to the low power of the analyses employed (Type 2 error).

Summary

Live traps placed at ground level detected fewer small mammal species than hair tube traps. Faecal analysis identified the presence of all of the same species registered by the two survey procedures, plus an additional two species. To reduce bias when evaluating the available prey in a forest environment it is therefore recommended that more than one sampling technique be used, and that consideration is made also of the effective 'sampling' behaviour of local predators.

Small mammals, specifically rodents were the staple prey of güiña, though birds represented an important secondary food. No significant seasonal differences in diet were found. Prey diversity was high in both study populations and it is suggested güiña will prey upon any readily captured vertebrate.

Chapter 4

Spatial Organisation of the Güiña

4.1 Introduction

4.1.1 Spatial organisation

The manner by which animals distribute themselves in relation to their environment and to conspecifics provides insight into many ecosystem and population processes including competition, territoriality and dispersal (Haslett, 1990; Minta, 1992; Wennegren *et al.,* 1995; Gehrt and Fritzell, 1998). A basic understanding of the mechanisms that influence the spatial organisation of vagile species is therefore fundamental to hypotheses relating to resource use and social behaviour, and can ultimately be used to guide management strategies. Such an approach has been applied constructively to the management of several wildlife and game populations (Haslett, 1990; Maehr and Cox, 1995) and to the ecologically sensitive control of pest species (Knick and Dyer, 1997) and predators (Knowlton, 1972; Till and Knowlton, 1983; Goodrich and Buskirk, 1995; Alterio *et al.*, 1998; Edwards *et al.*, 2001).

The space an animal uses during a specified time period is most conveniently described in terms of home range area, defined by Burt (1943) as that area 'normally traversed by an animal or group of animals during activities associated with feeding, resting, reproduction, and shelter-seeking'. The depiction of a home range can therefore facilitate the description of an animal's movements and habitat utilisation, and also identify the neighbouring conspecifics it might possibly encounter (White and Garrott, 1990; Kenward, 1992). This concept is distinct from that of 'territory' which can be defined as that part of a home range defended through aggressive behaviour (Burt, 1943), or by 'identifying acts' (Brown and Orians, 1970) such as scent-marking (Ralls, 1971; Gorman and Trowbridge, 1989; Smith *et al.*, 1989) or vocalisations (Ryan, 1988; Wells and Taigen, 1989).

4.1.2 Temporal spacing and interactions between animals

An individual's home range might overlap partially or completely with those of conspecific animals. Within a shared area conspecifics may respond to each other randomly, in a purely spatial, or purely temporal manner, or by a combination of these mechanisms. Range area overlap generates the potential for interference competition for food and other resources. Hence, in the absence of spatial avoidance or overt aggression many solitary carnivores minimise the simultaneous use of shared areas and frequency of encounter through structured temporal responses mediated by vocal, visual and olfactory communication (Seidensticker *et al.*, 1973; Bailey, 1974; Macdonald, 1985; Mace and Minta, 1992; Waller, 1997; Gehrt and Fritzell, 1998).

Macdonald *et al.* (1980) termed the comparison of animal movements independent of time as 'static interactions', and proposed the investigation of 'dynamic interactions', which involve consideration of the simultaneous movements between neighbouring animals. The identification of dynamic interaction is often difficult when species are secretive, and is frequently only possible through the simultaneous tracking of multiple animals occupying contiguous ranges (Doncaster, 1990; Minta, 1992). Nevertheless, the collection of concurrent data has provided insight into the structured temporal and spatial organisation of several elusive carnivores including the grizzly bear (*Ursus arctos*; Mace and Waller, 1997), bobcat (Chamberlain and Leopold, 2001; Nielson and Woolf, 2001), coyote (*Canis latrans*; Chamberlain *et al.* 2000) and culpeo fox (Salvatori *et al.* 1999a).

4.1.3 Spatial organisation of the Felidae

The spatial organisation of wild felids is normally characterised as solitary and territorial (Gittleman and Harvey, 1982; Sandell, 1989). With the exception of lions (Schaller, 1972; Bertram, 1975; Packer and Pusey, 1982) and male cheetahs (Graham, 1966; Caro and Collins, 1986; 1987a; 1987b), characteristic social units are single adults and small family groups consisting of an adult female and dependant young. Despite a largely solitary existence, individuals nevertheless interact within a complex social system maintained through scent-marking, vocal communication and occasional encounters.

With the notable exception of lions and male cheetahs, wild felids typically space themselves within a land tenure system whereby the ranges of conspecifics are maintained with little intersexual overlap (Sunquist, 1981; Geertsema, 1985; Emmons, 1988). These systems of tenureship are often very stable and are maintained without the need for frequent direct social interaction (Kitchener, 1991). There is much variability among spacing mechanisms however, from nearly exclusive and actively defended home ranges, to flexible spacing systems based on mutual tolerance or temporal avoidance (for example bobcat: Bailey, 1974; Koehler and Hornocker, 1989; ocelot: Emmons, 1988; Ludlow and Sunquist, 1987; Konecny, 1989; jaguar: Rabinowitz and Nottingham, 1986; Crawshaw and Quigley, 1991; and see reviews in Leyhausen, 1965; Liberg and Sandell, 1988). These patterns may furthermore be influenced by relatedness, particularly among female kin. Data from long-term population studies of Iberian lynx (Aldama and Delibes, 1991; Ferreras *et al.*, 1997), tigers (Smith *et al.*, 1987), puma (Lindzey *et al.*, 1994), and leopards (Bailey, 1993) indicate that female felids are often philopatric, and female neighbours are frequently related. For example, clusters of neighbouring tigresses in Chitwan Reserve, Nepal were as closely related as lionesses belonging to a single pride (Smith, 1993).

Home range size typically increases as a function of increasing body size and metabolic requirements, or decreasing food availability (McNab, 1963; Harestad and Bunnell, 1979; Gittleman and Harvey, 1982; Grant *et al.*, 1992). Large species maintain large home ranges and carnivorous species utilise more extensive areas than similarly-sized herbivores (Swihart *et al.*, 1988). Much of the intra-specific variability among felid social systems has been attributed to differences in prey distribution and abundance, and trends of diminishing foraging area size as a function of increasing food abundance are often apparent. In temperate regions for example, where prey abundance is high and relatively stable, tigers utilise home ranges as small as 16 km^2 and attain densities of more than three adults per 100 km^2. In comparison the taiga of Eastern Asia has a lower carrying capacity for prey and supports tiger densities of less than 0.2 per 100 km^2 (Sunquist, 1981).

When prey densities are high and/or patchily distributed it can become more economically efficient for felids to share limited areas rather than reduce home range size, providing aggressive encounters can be avoided (Schaller, 1972; Seidensticker *et al.*, 1973; Bailey, 1974; Brand *et al.*, 1976; Goodhall, 1977; Corbett, 1979; Liberg, 1980). Jaguars inhabiting the forests of Belize for example forage mostly for small, relatively abundant and uniformly distributed prey of restricted mobility (Rabinowitz and Nottingham, 1986). Because this prey base is easily defended (Greenwood and Swingland, 1983) social tolerance is low. In western Brazil jaguars typically take larger, more highly mobile prey species of often-inconsistent distribution. Marking behaviours and territorial defence are of lesser importance for these predators and temporal separation of conspecifics is instead achieved by simple avoidance within overlapping ranges (Crawshaw and Quigley, 1991). Similar spatial organisation has been documented among adult male pumas (Seidensticker *et al.*, 1973), tigers (Schaller, 1967, Sunquist, 1981) and jaguars (Rabinowitz and Nottingham, 1986).

At a local scale, ecological and biological processes inevitably influence spatial patterning, undermining any simple generalisation regarding home range structure and dynamics. In addition to prey availability, home range size and distribution is influenced by habitat composition (Macdonald, 1983), intraspecific population densities (Knowles, 1985; Litvaitis *et al.*, 1986) and the consequences of competition, predation, age and sex (Wolda, 1983; Crawshaw and Quigley, 1991; Bailey, 1993). Range boundaries can alter with season or reproductive status, and can include transitional locations between frequently utilised areas.

Intersexual differences in resource requirements and therefore spatial distribution are common amongst felids, as they are among other solitary carnivores. With the exception of lions and cheetahs, the home ranges of male felids are typically larger than those of females, and several female ranges may be included within a single male range (Gittleman and Harvey, 1982; Sandell, 1989). Female reproductive success is primarily dependent on the distribution of food and denning resources, and hence is closely tied to an ability to exploit these resources. In contrast, male reproductive success is coupled with an ability to find and mate with females. Consequently, male spatial dynamics, during the mating season at least, are highly sensitive to the spatial distribution of females (Macdonald, 1983; Rowell, 1988; Clutton-Brock, 1989; Sandell, 1989).

4.1.4 Home range delineation

Numerous statistical and non-statistical approaches to range delineation have been applied to behavioural data. Different estimation techniques are useful for different purposes, and none are entirely free from bias (Macdonald *et al.*, 1980; Voigt and Tinline, 1980; Kenward, 1987; Worton, 1987; Harris *et al.*, 1990; White and Garrott, 1990). The selection of a range estimator remains largely at the discretion of the researcher and is often chosen either on the basis of providing the most biologically meaningful results for the population of interest, or for ease of comparison with previous studies (Kenward 1987). Different software programs do not necessarily produce identical outputs, or even comparable accuracy (Lawson and Rodgers, 1997; Seaman *et al.*, 1999). Where inter-study comparisons are to be made the analysis software and analysis options therefore need to be clearly stated and comparable in each study.

Non-statistical techniques for range analysis include the use of minimum concave polygons (Harvey and Barbour, 1965) and minimum convex polygons (Mohr, 1947). Minimum concave polygons (MCVPs) connect peripheral location fixes so that each edge is shorter than a selected fraction of the range width. Where the gaps between edge fixes are large the resulting polygons will describe a concave range, hence this method can often eliminate non-utilised areas from range estimates. This is a simple technique, however MCVPs frequently overestimate home range areas because they describe the largest possible polygon derived from connected points or locations. They also provide no description of the internal anatomy of ranges or otherwise highlight areas of differential use.

The minimum convex polygon (MCP) is the oldest and most widely-utilised non-statistical method for home range calculation (Beckoff and Mech, 1984). MCPs connect the peripheral locations of an animal's range in such a way that the internal angles of the resulting polygon do not exceed 180°. This is the simplest and most intuitive estimator and the least sensitive to non-independent data and choice of analysis software (Lawson and Rodgers, 1997). The resulting polygons are strongly influenced by small sample sizes however, and provide no descriptive information relating to the differential use of components within range boundaries (Macdonald *et al.*, 1980; Kenward, 1987; Harris *et al.*, 1990; Worton, 1987). In addition, minimum convex polygons are fitted to all data points irrespective of their actual distribution (Anderson, 1982). Where the spatial distribution of peripheral fixes is convex, these estimates will accurately exclude non-utilised areas, but where location data does not fit this pattern, fitted polygons may fail to exclude non-relevant areas (Anderson, 1982).

Unlike the above, statistical or 'probabilistic' estimators describe the differential utilisation of areas within individual distribution ranges. For any location within a home range there is an associated likelihood that the animal is present at that position (Jennrich and Turner, 1969; Anderson, 1982; Worton, 1989a, 1989b). Kernel range estimators construct probability contours or 'isopleths' to delineate regions of differential space use. The degree of smoothing applied to create these isopleths may be a single, fixed constant across all observations, or an adaptive value that allows local adjustments to individual kernel widths. Kernel estimations are relatively unbiased by small sample sizes and can generate densities of any shape (Worton, 1987; Worton, 1989a; Harris *et al.*, 1990; Seaman and Powell, 1996). Unlike parametric estimators, kernel methods can also identify areas of concentrated use, including multinuclear centres of activity. Inter-study comparisons between kernel range estimates are complicated, however, by the use of different software packages when these are based on alternative algorithms. Thus, outputs from different programs can lack concordance despite the use of identical data-sets (Lawson and Rodgers, 1997).

4.1.5 Core areas

Animals typically inhabit heterogeneous environments, where areas rich in resources are scattered throughout habitat that is comparatively depauperate (Cowie and Krebs, 1979). All parts of an animal's home range are hence not equally important to that individual and are used with varying intensity. Activity is often concentrated around resting sites, productive feeding areas or other essential resources (Samuel *et al.*, 1985; Bendel and Gates, 1987; Andrén, 1990; Powell *et al.*, 1997). These regions of intense or consistent utilisation are termed 'core areas' (Kaufmann, 1962; Adams and Davis, 1967; Ewer, 1968; Leuthold, 1977; Worton, 1989b).

Identification of core areas facilitates the description of those ecological factors that influence spatial use patterns. Core area location is identified using internal fixes; their delineation is therefore less affected by sample size and outliers than that of home range areas. Again there is no single method advocated for the description of core area, and the choice of estimator remains at the discretion of the researcher. Methods used to identify core areas have included: 50% convex polygons (Michener, 1979; Bowen, 1982), 55% and 50% adaptive kernel isopleths (Apps, 1992; Spong, 2002), 60% fixed kernel isopleths (Palomares *et al.*, 2001), and 70% fixed kernel isopleths (Dunstone *et al.*, 2002a; 2002b).

4.1.6 Temporal independence of spatial data.

Statistical inferences from home range estimates frequently require that sequential observations are independent of one another. Serial autocorrelation occurs when locations are recorded too close together in time and space to be considered independent, i.e. locational data does not represent an independent random sample of an animal's movements (Dixon and Chapman, 1980; Swihart and Slade, 1985; Worton, 1985; 1989a). Although strict independence is often difficult to achieve or prove, it is standard procedure to test for autocorrelation between successive locations (Swihart, 1981; Swihart and Slade, 1985; Harris *et al.*, 1990; Minta, 1992). Where significant autocorrelation occurs the most probable outcome is an underestimation of home range area, since the 'effective' sample size is then less than the number of locations recorded (Swihart and Slade, 1985a; Anderson, 1982).

When sampling intervals prove inadequate and data remain autocorrelated, locations considered too close together in time can be removed from the data set. Although the degree of temporal autocorrelation decreases with increasing inter-fix interval (Swihart and Slade, 1985b), in fixed duration studies a trade-off occurs between sample size and sampling interval. Increasing the time period between data points to achieve statistical independence potentially results in the underestimation of range areas and/or the sacrifice of other biologically important information (Reynolds and Laundré, 1990; Rooney *et al.*, 1998).

4.1.7 Spatial organisation of güiña

Minimal information is currently available regarding the spatial organisation of güiña. Sanderson *et al.* (2002) suggested that within the largely agricultural landscape of Isla Grande de Chiloé, the home ranges of male güiña (659 ± 397.89 ha, n = 5) were often larger than those of females (126 ± 41.25 ha, n = 2). These authors also reported home range exclusivity between same-sex neighbours and extensive inter-sexual overlap, suggesting the potential for intra-sexual resource defence through territoriality. This fits the pattern of intrasexual territoriality typical for small felids, whereby males are territorial towards other males and females towards females, but with extensive overlap between the territories of males and females. In contrast, Dunstone *et al.* (2002a; 2002b) reported high levels of intersexual spatial overlap based on data from the San Rafael population that is extended and reanalysed here.

4.1.8 Chapter Aims

In this chapter I examine further the social and spatial organisation of güiña within the Parque Nacional Laguna San Rafael (PNLSR) and Parque Nacional Queulat (PNQ) populations, two areas of minimal anthropogenic disturbance. Specifically the aims are to examine: (1) the size and stability of home ranges and core areas throughout the study period (spring 1997 to autumn 1999, PNLSR; spring 1999 to autumn 2001, PNQ), (2) the overlap between the ranges of neighbouring individuals and any dynamic interaction and (3) population densities within PNLSR and PNQ. The influence of season, sex and small mammal prey abundance on home range size and spatial organisation are also examined.

4.2 Methods

4.2.1 Temporal Independence of data.

The minimum inter-fix interval necessary to ensure serially independent data was calculated for each animal using the autocorrelations option in the RANGES V Interaction Analyses menu (Kenward and Hodder, 1996). To prevent intervals between tracking sessions being interpreted as an individual failing to move, each analysis was set to exclude gaps in the radio-telemetry data exceeding eight hours. Autocorrelation based on area use was high for a number of individuals but resampling for the removal of all sequential autocorrelation risked under-sampling the data set (Reynolds and Laundré, 1990; Rooney *et al.*, 1998). The data were instead resampled to separate consecutive locations by a minimum of five hours, an interval more than sufficient to allow any radio-collared güiña to traverse its entire home range. A five-hour inter-fix interval did not fully remove those problems associated with autocorrelation for all animals (see Lucherini and Lovari, 1996) but was sufficient however for the data sets of seven of the twelve focal animals, and provided an inter-fix interval comparable to that used by Sanderson *et al.* (2002) in their study on Isla Grande de Chiloé.

In accordance with Powell (1987) and Goodrich and Buskirk (1998), any residual autocorrelation was disregarded because it was accepted that movements are inevitably influenced to an extent by past experience and knowledge of the location of resources within the home range. The resampled data sets for all radio-monitored animals were used in subsequent analyses of range area unless otherwise stated.

4.2.2 Home ranges and core areas.

A multifaceted approach was used to examine home range and core area attributes in order to overcome the limitations of each single estimator method (White and Garrott, 1990) and to facilitate comparison with past and future studies (Voigt and Tinline, 1980). Total and seasonal home ranges were calculated for each animal using the RANGES V analysis program, where *total* range indicates a home range that incorporates all resampled locational data obtained for a particular animal and *seasonal* ranges correspond to individual field seasons. Ranges were approximated as: the minimum concave and convex polygons calculated using all resampled locations (MCVP100 and MCP100 ranges respectively); the minimum convex polygon including 95% of fixes closest to the harmonic mean centre (MCP95), and the fixed kernel isopleth including 95% of fixes closest to the harmonic mean centre (FK95). The exclusion of a pre-selected proportion of location fixes from range calculation is a standard method to remove non-typical movements from subsequent analyses (Michener, 1979; Bowen, 1982; Bekoff and Mech, 1984).

Core areas were estimated using the MCPs and fixed kernel isopleths that included the innermost 50% of location fixes (MCP50 and FK50 respectively). Kernel contours were calculated with a level of smoothing selected by least-squared cross-validation (Silverman, 1986; Worton, 1995; Seaman and Powell 1996; Seaman *et al.*, 1999) and a grid cell size of 40 m^2. The boundary limits of kernel contours were determined by the individual data sets.

The MCP method was selected for its simplicity, ease of plotting and comparability to other studies (Harris *et al.*, 1990). The fixed kernel estimator was used because it is a robust and reliable non-parametric technique capable of identifying the presence of multiple core areas where these occur within ranges (Worton, 1987, 1989a; 1995; Naef-Daenzer, 1993; Seaman and Powell, 1996). Fixed kernel estimates were utilised in preference to adaptive kernels, as these are considered more appropriate for large or spatially clumped data sets (Lawson and Rodgers, 1997). The choice of the MCP95 and FK95 contours was based on their widespread use in home range and habitat selection studies (Harris *et al.*, 1990; White and Garrott, 1990). MCVP100 ranges were calculated to permit comparison with those described by Sanderson *et al.* (2002) and were not analysed further. Differences between kernel and minimum polygon estimates (MCP95 vs. FK95, and MCP50 vs. FK50) were investigated using paired *t*-tests for each animal. The influence of age-class (adult or sub-adult) and gender on seasonal home range and core area estimates was evaluated using a univariate general linear model (GLM).

The influence of sample size on estimates of home range area was examined using the Incremental Area Analysis (IAA) option in the RANGES V software. This program draws an outline around the first three fixes in a data set then calculates the enclosed area according to the estimator method used. As successive fixes are added, cumulative increases in range size are plotted as an incremental area curve. The minimum number of locations required for the calculation of robust home range estimates is determined visually by calculating when this area estimate stabilises, i.e. when an asymptote or level area curve is reached (Odum and Kuenzler, 1955; Kenward, 1982; 1987; Parsh and Kruuk, 1982; Harris *et al.*, 1990; Wray *et al.*, 1992). Separate IAA plots were constructed for both the MCP95 and FK95 home range estimators.

For all subsequent analyses of range area, only those ranges with ≥ 30 independent locations and which reached a stable (asymptotic) area curve were included. Thirty locations is considered an adequate minimum threshold for fixed kernel home ranges (Seaman *et al.*, 1999) and is common in studies reliant on the MCP method (Fuller *et al.*, 1985; Litvaitis *et al.*, 1987; Lovallo and Anderson, 1996).

4.2.3 Static and dynamic interaction

Static interactions between neighbouring animals (*sensu* Macdonald *et al.*, 1980) were inferred within each study site from the spatial overlap of home ranges, assessed using the percentage overlap function in the RANGES V software (Kenward and Hodder, 1996). Home range and core area overlap between pairs of güiña was calculated as a percentage of each respective range. The influence of site, sex and age-class on home ranges and core area overlap was examined within each study site using three-way analyses of variance. Significant differences were identified using Fisher's LSD *post hoc* test.

Dynamic interactions (Macdonald *et al.*, 1980) were described by the 'cohesion' index outlined by Kenward *et al.* (1993), calculated using RANGES V. Location fixes for pairs of animals were considered to be simultaneous where they occurred within a 30 minute window. Because serial autocorrelation was not of concern here the original non-sampled data set was utilised in order to maximise the number of simultaneous recordings. RANGES V computes the mean observed distance between two individuals (D_O) from N pairs of simultaneous co-ordinates where (X_{1j}, Y_{1j}) is the location of animal 1 and (X_{2j}, Y_{2j}) the location of animal 2 at time j

$$D_O = \frac{1}{N}\sum_{j=1}^{N}\sqrt{(X_{1j} - X_{2j})^2 + (Y_{1j} - Y_{2j})^2} \qquad \text{Equation 4.2.1}$$

If both animals occupy each of their co-ordinates in a random manner, i.e. if animal 2 could have been at any (X_{2k}, Y_{2k}) of its N locations when animal 1 was at (X_{1j}, Y_{1j}), the expected mean distance is described by

$$D_E = \frac{1}{N^2}\sum_{j=1}^{N}\sum_{k=1}^{N}\sqrt{(X_{1j} - X_{2k})^2 + (Y_{1j} - Y_{2k})^2} \qquad \text{Equation 4.2.2}$$

To test the null hypothesis that there is no dynamic interaction between individuals, and that the movements of neighbours are random with respect to each other, random points are generated within the area of overlap and contrasted against the actual distribution of simultaneous locations. To determine whether animals with overlapping ranges showed temporal avoidance, the observed and possible distances are compared using Jacob's index (Jacob, 1974), which provides a single value J, for each neighbouring pair. A value of zero is returned if the observed and possible distances are the same, indicating that two movement paths are random with respect to each other. Positive values ($0 < J \leq 1$) arise when observed distances are small relative to those that are possible and indicate two animals are associated together. Negative values ($0 > J \geq -1$) indicate a tendency for pairs to avoid each other.

4.2.4 Number of güiña and population density

The minimum number of güiña present within each study area was determined from trap success and radio-telemetry. An approximate density estimate had previously been calculated for PNLSR (Dunstone *et al.*, 2002a). This value (0.97 güiña km^{-2} over 5.14 km^2) did not, however, account for transient animals or for the departure of previously resident animals from the study area. During the extended period over which this present study is based I estimated güiña density present inside the trapping area during each field season. The 'trapping area' was approximated after McLellan (1989) by the minimum convex polygon that included all successful trap locations. All individuals known to be present within the study area utilised this area (pers. obs.). The proportion of time spent by each within the trapping area was then estimated for each field season as the proportion of 'independent' fixes located within the trapping area.

Each individual was considered to contribute proportionally to the density estimate according to the percentage of its location fixes that fell within the trapping area as a measure of time spent within it (for example, an individual with 70% of locations inside the trapping area and recorded within the study area on 60 days during a given 3-month season contributed (0.70 × 60 days)/90 days = 0.47 individuals). Nine individuals trapped but not radio-tracked during the study period (three adults and three subadults, including one dependent kitten in PNLSR, two adults and one subadult in PNQ) were considered to be utilising the trapping area in a similar manner to the adults and subadults radio-tracked within the same area. The spatial behaviour of the dependent kitten (SAF9) was assumed to be similar to that of its mother (SAF7).

Two animals (QAM2 and QAM5) departed the PNQ study area within a few days of being radio-collared, and did not return at any stage during the remainder of the study period. Both were young adult males and were assumed to be transient individuals. The proportional contribution made by these animals to the density estimate was calculated in the same way as that of resident animals.

4.3 Results

4.3.1 Incremental Area Analysis

Incremental area curves generated for individual güiña indicated variable rates of home range stabilisation (Table 4.3.1, Figures 4.3.1 and 4.3.2). Asymptotes for utilised areas were achieved for 12 of the 14 animals, and absolute range areas were hence calculated for these 12 animals only. The mean fix number required for range stabilisation was 30.33 (range 14 – 45) for MCP95 and 29.75 (range 10 – 54) for FK95 area estimates. Consequently, range and core area estimates were only included in subsequent analyses where ≥ 30 location fixes were obtained and the respective cumulative area curve reached an asymptote. In the field, this corresponded with a period of not less than ten days of radio-tracking. Two transient animals (QAM2 and QAM5) did not remain long in the study area and had no defined range boundaries. No home range could be defined for these animals; the areas they utilised are described in Table 4.3.2 but were not included in subsequent analyses.

Table 4.3.1 Number of locations required for estimation of home range area.

		Home range estimator	
Site	Animal ID	MCP95	FK95
PNLSR	SSM1	34	37
	SSM2	36	18
	SAM3	20	10
	SJM4	45	54
	SAF7	26	52
	SAF8	31	27
PNQ	QAM1	30	27
	QSM3	30	25
	QSM4	27	20
	QAF10	14	24
	QSF11	26	18
	QAF12	45	45
	Mean [SE]	30.33 [2.61]	29.75 [4.08]

There was a positive correlation between the number of times individuals were located and the number of fixes required for the stabilisation of home range estimates (MCP95 $r = 0.77$, *d.f.* = 10, $P = 0.003$; FK95 $r = 0.60$, *d.f.* = 10, $P = 0.039$). This relationship was not significant however when home ranges were calculated across single seasons only (MCP95 $r = 0.42$, *d.f.* = 20, $P > 0.05$; FK95 $r = 0.30$, *d.f.* = 20, $P > 0.05$).

Figure 4.3.1 Incremental area curves calculated for MCP95 home range estimates.

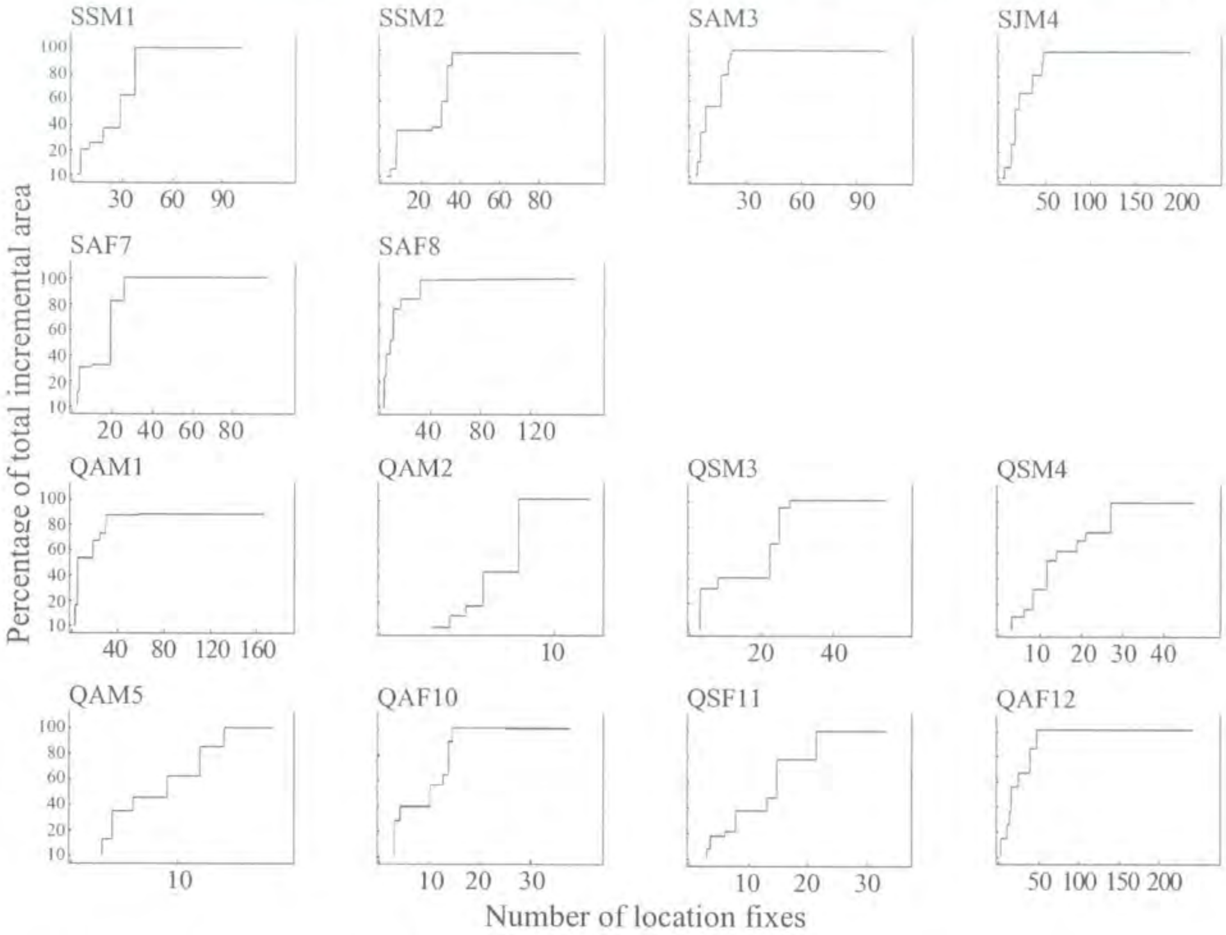


Figure 4.3.2 Incremental area curves calculated for FK95 home range estimates.

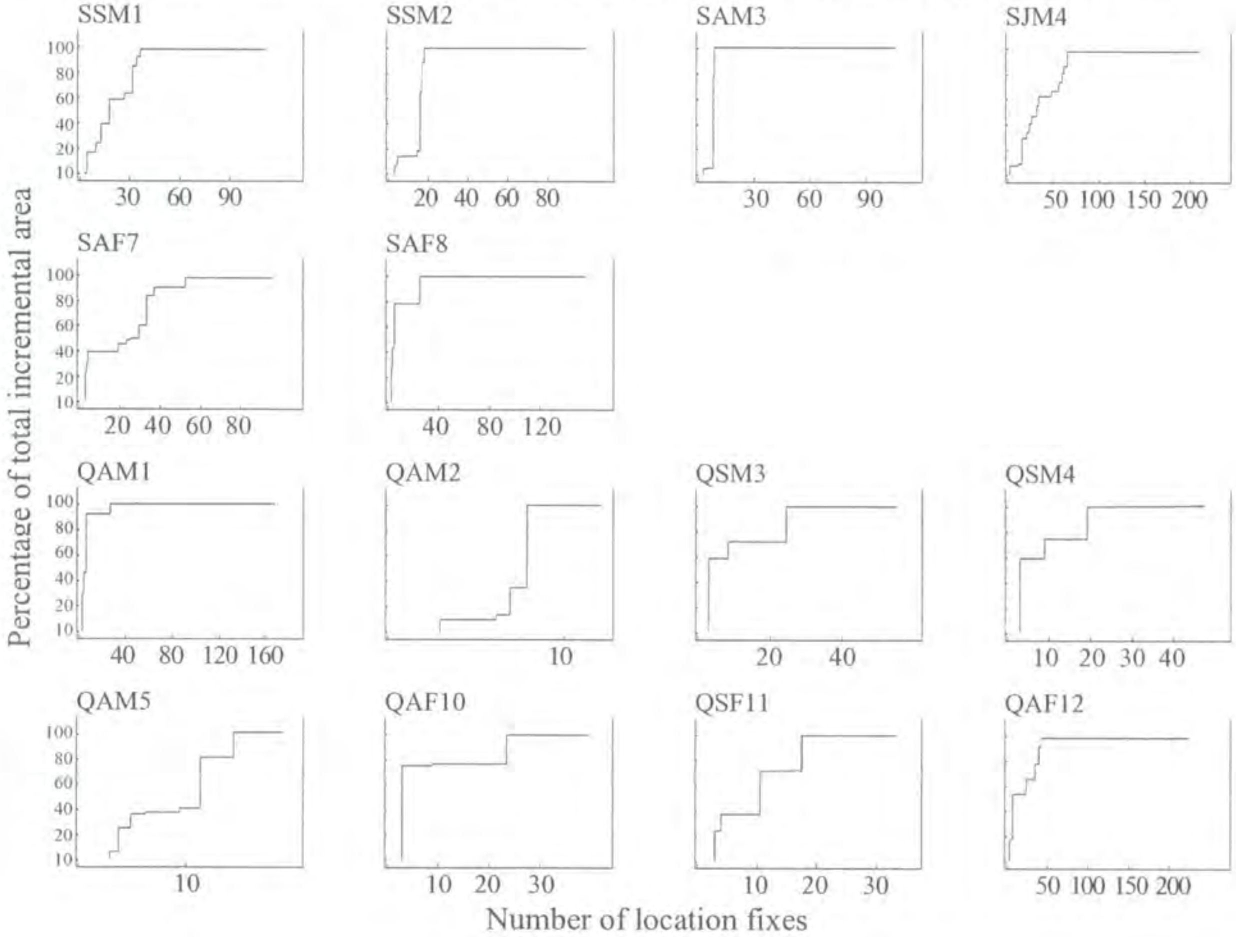


Table 4.3.2. Intensity of tracking and home range sizes of 14 güiña radiotracked in PNLSR and PNQ as calculated using the MCVP100, MCP100, MCP95 and FK95 range estimation models. Location data were resampled to ensure inter-fix intervals of ≥ 5 hours.

		Number of		Home range estimate (ha)			Core area estimate (ha)	
	Animal ID	location fixes	MCVP100	MCP100	MCP95	FK95	MCP50	FK50
PNLSR	SSM1	116	113.21	126.46	110.71	100.06	47.74	24.15
	SSM2	98	189.21	189.84	174.79	95.13	77.10	16.76
	SAM3	104	312.51	365.47	257.67	152.93	51.45	38.03
	SJM4	210	172.60	173.36	154.31	165.71	19.41	25.63
	SAF7	96	150.21	165.75	89.43	64.92	38.57	19.75
	SAF8	154	172.29	181.21	152.16	78.64	44.30	14.84
PNQ	QAM1	166	130.61	173.84	106.79	120.47	13.09	16.91
	QAM2	*12*	*32.34*	*37.99*	*35.76*	*184.17*	*12.41*	*27.30*
	QSM3	54	61.04	61.04	42.64	39.31	6.18	7.72
	QSM4	47	64.98	75.45	67.92	107.34	17.17	18.39
	QAM5	*19*	*63.96*	*63.96*	*53.09*	*76.18*	*10.59*	*19.68*
	QAF10	39	84.60	116.56	107.91	110.79	23.54	27.67
	QSF11	33	50.40	68.42	42.09	50.24	15.00	12.45
	QAF12	237	124.56	128.67	89.29	87.98	17.31	14.67

Animal in italics (*n* = 2) were excluded from analyses of total home range size due to insufficient location fixes.

Figure 4.3.3 Map of the PNLSR study area showing (a) minimum convex polygon home range (MCP95) estimates and (b) minimum convex polygon core area (MCP50) estimates.

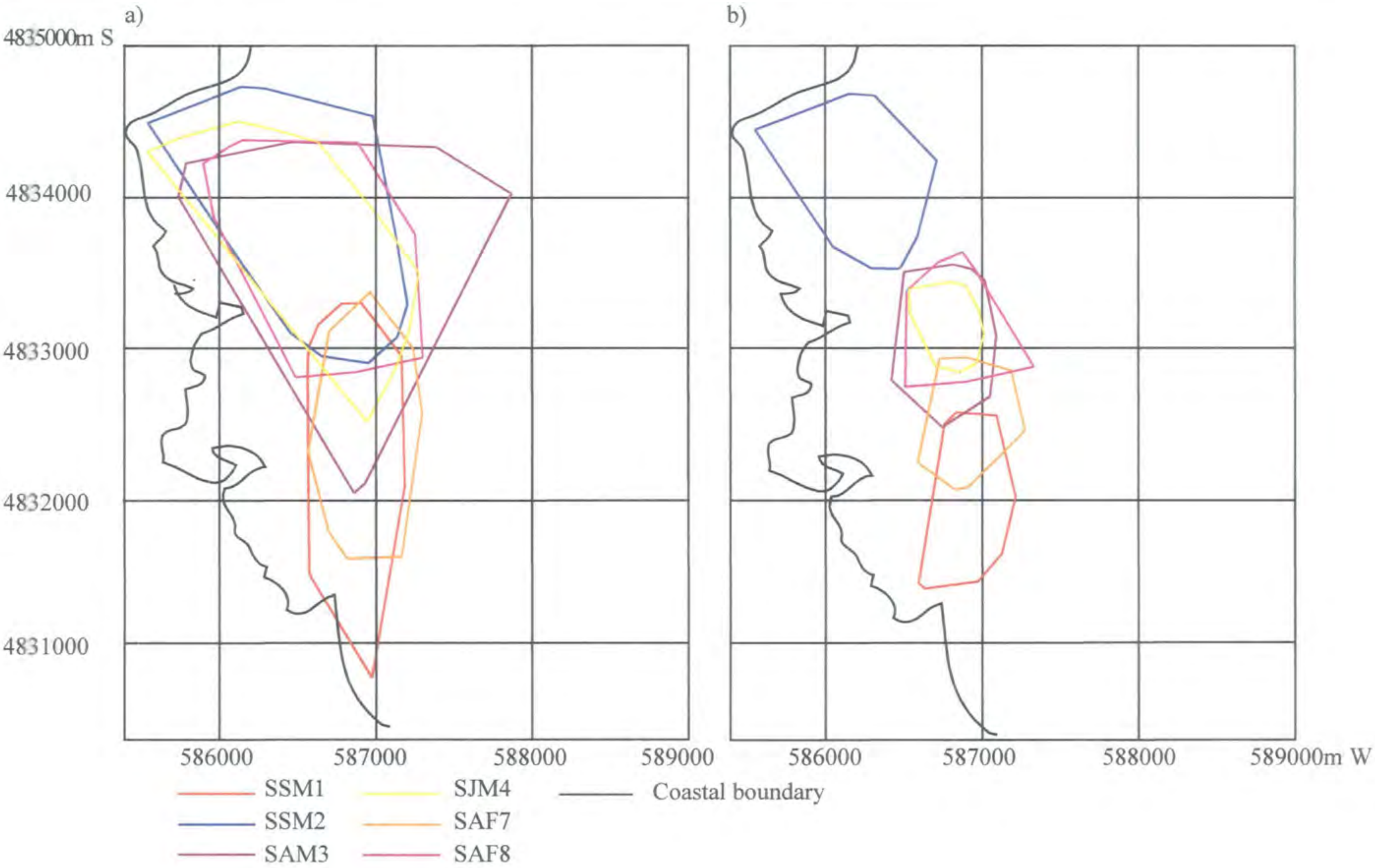


Figure 4.3.4 Map of the PNLSR study area showing (a) fixed kernel home range (FK95) estimates and (b) fixed kernel core area (FK50) estimates.

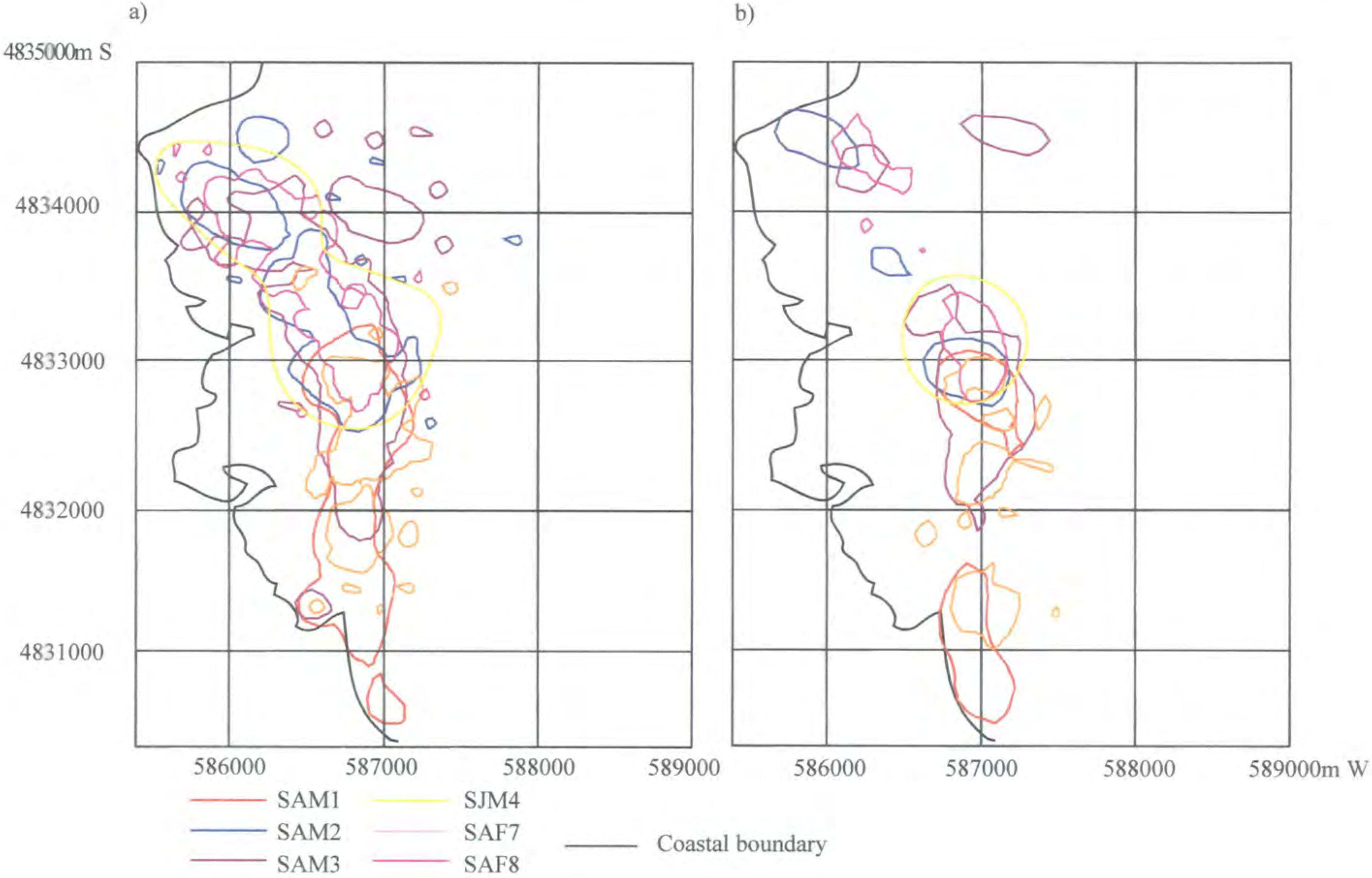


Figure 4.3.5 Map of the PNQ study area showing (a) minimum convex polygon home range (MCP95) estimates and (b) minimum convex polygon core area (MCP50) estimates.

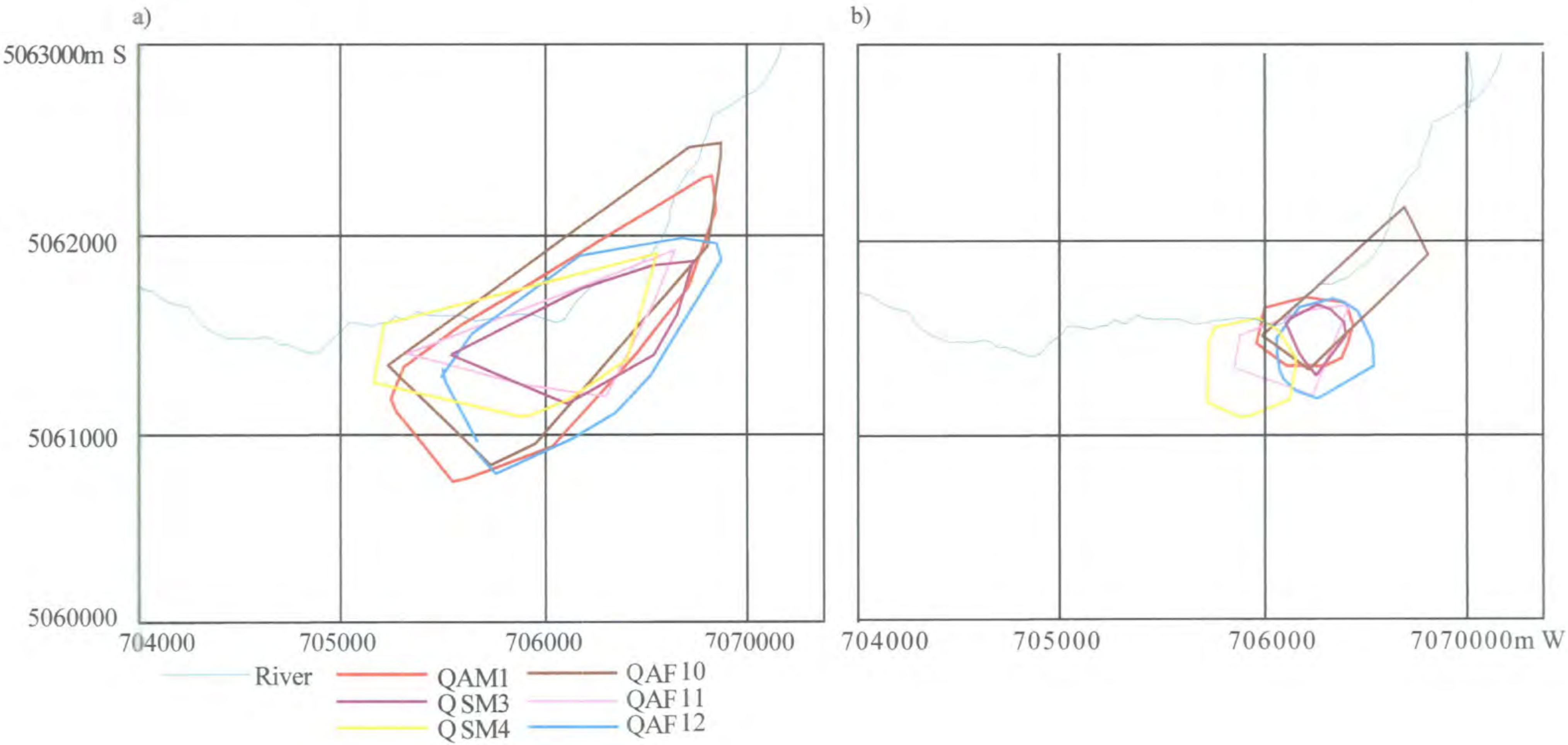
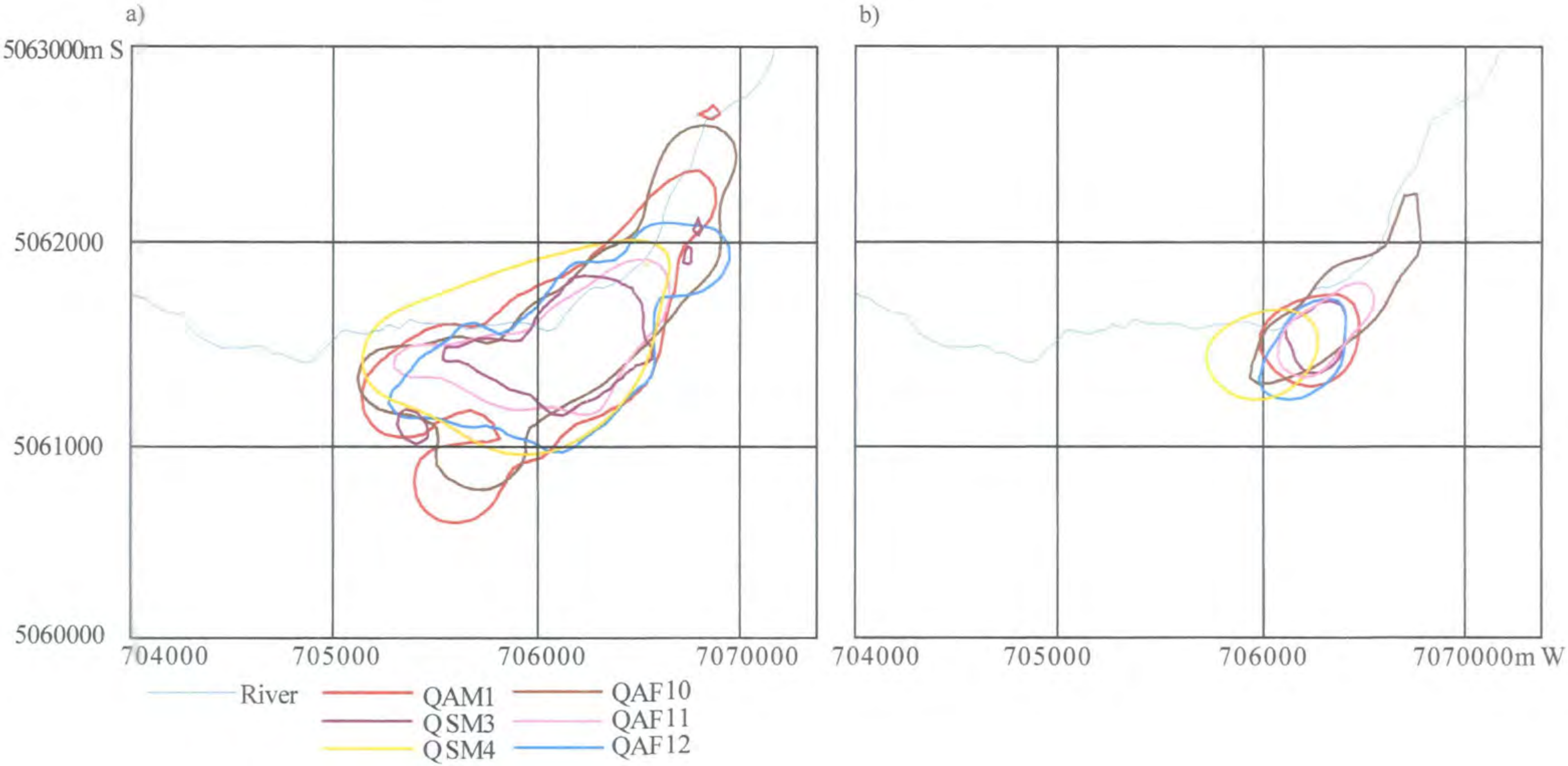


Figure 4.3.6 Map of the PNQ study area showing (a) fixed kernel home range (FK95) estimates and (b) fixed kernel core area (FK50) estimates.



4.3.2 Home range and core area estimates.

Home range areas were calculated for all radiocollared güiña using the MVP100, MCP100, MCP95 and FK95 estimators. Core areas were quantified using the smallest minimum convex polygon and fixed kernel isoline that encompassed 50% of location points (Table 4.3.2). MCP100 home ranges were consistently the largest; removal of the peripheral 5% of locations reduced these estimates by between 7.4 and 46.1%. The MCP50 core area estimates represented approximately 26.7% (range 12.26 - 44.11%) of MCP95 home ranges (Figures 4.3.3 and 4.3.5). Core areas calculated using FK50 isopleths represented approximately 20.72% (range 14.04 to 30.42%) of FK95 home range areas (Figures 4.3.4 and 4.3.6). Mean frequencies of core area occupation were close to twice that expected from their absolute sizes, had activity been equally distributed within home ranges. Half of all location fixes were concentrated within less than 27% of MCP95 home ranges and 21% of FK95 ranges.

Because the MCP95 and FK95 estimators are widely considered the most suitable for home range delineation (Harris *et al.*, 1990; Seaman and Powell, 1996; Kenward and Hodder, 1996) these were used in all subsequent analyses. Total home range sizes varied from 42.6 to 257.7 ha (MCP95 estimates) and between 39.3 and 165.7 ha (FK95 estimates). Despite some dissimilarity there was no significant disparity between minimum convex polygon and fixed kernel estimates of 95% home ranges or 50% core areas (paired *t*-tests: home range $t_{11} = 1.458$, $P > 0.05$; core area $t_{11} = 1.980$, $P > 0.05$). No significant relation was observed between number of location fixes obtained and the size of total home ranges calculated (MCP95 $r = 0.303$; FK95 $r = 0.415$) or core areas (MCP50 $r = 0.019$; FK50 $r = 0.047$, all *d.f.* = 10, $P > 0.05$).

Fixed kernel (FK95) home range estimates were not significantly influenced by site, age-class or gender, or by any interaction among these factors (all $P > 0.05$, Table 4.3.3). In contrast, minimum convex polygon home ranges were influenced by all three variables (Table 4.3.3). MCP95 estimates were larger within PNLSR than in PNQ (PNLSR $\bar{x} = 156.51 \pm 23.94$ ha; PNQ $\bar{x} = 76.11 \pm 12.21$ ha), adult animals utilised larger ranges than subadults (adults $\bar{x} = 133.88 \pm 26.48$ ha; subadults $\bar{x} = 98.74 \pm 23.32$ ha), and the MCP95 ranges of male güiña were more extensive than those of females (males $\bar{x} = 130.69 \pm 27.29$ ha, females $\bar{x} = 96.18 \pm 17.73$ ha). There was no interaction among any of these factors at $P < 0.05$ (Table 4.3.3).

Table 4.3.3 Univariate GLM to investigate the influence of site, age-class and gender on güiña home range areas. Significant *P* values (at $P < 0.05$) are given in bold.

Home range estimator	Factor	*d.f.*	Sum of Squares	Mean Square	*F* value	*P* value
MCP95	Site	1	15302.25	15302.25	16.623	**0.010**
	Age-class	1	11650.02	11650.02	12.656	**0.016**
	Sex	1	7041.57	7041.57	7.650	**0.040**
	Site × Age-class	1	1251.88	1251.88	1.360	0.296
	Site × Sex	1	5519.94	5519.94	5.997	0.058
	Age-class × Sex	1	8.33	8.33	0.009	0.928
	Site × Age-class × Sex	0	0.00			
	Error	5	4602.63	920.53		
	Total	11	41054.42			
FK95	Site	1	543.15	543.15	0.470	0.523
	Age-class	1	3459.15	3459.15	2.996	0.144
	Sex	1	3903.37	3903.37	3.380	0.125
	Site × Age-class	1	74.36	74.36	0.064	0.810
	Site × Sex	1	1202.60	1202.60	1.041	0.354
	Age-class × Sex	1	1.33	1.33	0.001	0.974
	Site × Age-class × Sex	0	0.00			
	Error	5	5773.56	1154.71		
	Total	11	15664.67			

Table 4.3.4 Univariate GLM to investigate the influence of site, age-class and gender on core area size. Significant *P* values (at $P < 0.05$) are given in bold.

Home range estimator	Factor	*d.f.*	Sum of Squares	Mean Square	*F* value	*P* value
MCP95	Site	1	2514.56	2514.56	7.142	**0.044**
	Age-class	1	28.13	28.13	0.080	0.789
	Sex	1	2.71	2.71	0.008	0.934
	Site × Age-class	1	1.34	1.34	0.004	0.953
	Site × Sex	1	100.34	100.34	0.285	0.616
	Age-class × Sex	1	5.36	5.36	0.015	0.907
	Site × Age-class × Sex	0	0.00			
	Error	5	1760.46	352.09		
	Total	11	4819.19			
FK95	Site	1	107.12	107.12	2.696	0.161
	Age-class	1	218.84	218.84	5.509	0.066
	Sex	1	109.34	109.34	2.752	0.158
	Site × Age-class	1	50.78	50.78	1.278	0.310
	Site × Sex	1	208.25	208.25	5.242	0.071
	Age-class × Sex	1	7.89	7.89	0.199	0.674
	Site × Age-class × Sex	0	0.00			
	Error	5	198.64	39.73		
	Total	11	717.60			

Fixed kernel estimates of core area were also unaffected by site, age-class and gender (all $P > 0.05$, Table 4.3.4), however MCP50 core area estimates did differ between the two study populations; güiña in PNLSR had larger core areas than those of PNQ (PNLSR: $\bar{x}$ = 46.43 ha ± 7.67, PNQ: $\bar{x}$ = 15.38 ha ± 2.33).

4.3.3 Seasonal ranges

Of the 28 seasonal ranges described, six did not meet the minimum criteria of 30 location fixes plus an asymptotic cumulative area curve and were therefore omitted from all analyses of seasonal home range. Of those animals included in seasonal analyses, each individual was radiotracked for between one and three seasons (Tables 4.3.5 and 4.3.6). There was no correlation between number of location fixes and home range sizes calculated across single seasons (MCP95 $r = -0.018$, $d.f = 20$, $P = 0.936$; FK95 $r = 0.098$, $d.f. = 20$, $P = 0.666$), and home ranges and core areas calculated across multiple seasons were no more extensive than those calculated across single seasons (MCP95: $t_{28} = 1.230$; FK95: $t_{28} = 2.444$; MCP50: $t_{28} = 1.040$; FK50: $t_{28} = 1.898$, all $P > 0.05$).

Site, age-class and sex had no significant influence on mean seasonal home range and core area values for individual güiña (Tables 4.3.7 and 4.3.8; all $P > 0.05$). There does appear to be some influence of site on MCP95 home range area (PNLSR $\bar{x}$ = 106.7 ± 10.2 ha; PNQ $\bar{x}$ = 68.3 ± 7.9 ha). Although the effect of site is not significant ($F_{1,11} = 5.174$, $P = 0.072$), this may be a consequence of the relatively small sample sizes.

Table 4.3.5 Intensity of tracking and seasonal home range sizes of six güiña radiotracked in PNLSR as calculated using the MCVP100, MCP100, MCP95 and FK95 range estimation models, and number of fixes required for range stabilisation.

Animal ID	Season	Number of days monitored	Number of location fixes	Range estimate for season (ha)				Core area estimate (ha)		Fixes for range stabilisation	
				MVP100	MCP100	MCP95	FK95	MCP50	FK50	MCP95	FK95
SSM1	Spring 1997	37	81	92.14	114.32	102.14	87.74	35.87	21.22	43	28
	Autumn 1998	17	35	46.99	51.86	49.82	44.65	9.62	10.59	26	16
SSM2	Spring 1997	20	49	93.24	105.84	99.89	33.70	53.28	8.47	16	20
	Autumn 1998	18	49	174.47	175.10	167.09	122.77	28.12	26.78	29	9
SAM3	*Spring 1997*	*4*	*11*	*47.47*	*134.49*	*108.28*	*133.30*	*10.03*	*65.66*	-	-
	Autumn 1998	17	54	149.47	186.13	143.76	93.85	22.70	27.01	24	7
	Spring 1998	*8*	*25*	*146.44*	*188.77*	*187.54*	*120.26*	*29.53*	*17.91*	-	-
	Autumn 1999	*7*	*14*	*25.17*	*42.87*	*31.17*	*20.60*	*3.61*	*7.63*	-	-
SJM4	Autumn 1998	11	50	119.58	119.58	108.13	115.02	23.43	25.47	28	34
	Spring 1998	19	81	104.80	138.65	95.15	114.61	1.92	4.46	49	22
	Autumn 1999	24	79	120.92	144.26	140.61	73.83	34.75	14.29	17	13
SAF7	Autumn 1998	22	63	135.31	148.31	83.10	45.34	21.73	10.60	23	28
	Spring 1998	10	30	63.50	83.88	79.83	14.34	7.20	8.17	18	5
	Autumn 1999	*2*	*3*	-	-	-	-	-	-	-	-
SAF8	Autumn 1998	22	56	154.73	163.60	143.95	35.24	66.25	11.50	31	26
	Autumn 1999	25	98	79.65	79.94	66.80	59.41	17.82	14.41	29	25

Seasons in italics ($n = 4$) were excluded from subsequent analyses due to insufficient fixes

Table 4.3.6 Intensity of tracking and seasonal home ranges of six güiña radiotracked in PNQ as calculated using the MCVP100, MCP100, MCP95 and FK95 range estimation models, and number of fixes required for range stabilisation.

Animal ID	Season	Number of days monitored	Number of location fixes	Range estimate for season (ha)				Core area estimate (ha)		Fixes for range stabilisation	
				MVP100	MCP100	MCP95	FK95	MCP50	FK50	MCP95	FK95
QAM1	Spring 1999	18	33	70.57	121.02	76.87	32.58	29.25	10.51	18	28
	Autumn 2000	34	94	70.56	86.55	72.78	48.61	6.96	8.51	32	23
	Spring 2000	44	39	86.34	106.28	102.68	96.05	22.78	22.89	20	18
QAM2	*Spring 1999*[1]	*3*	*12*	*32.34*	*37.99*	*35.76*	*184.17*	*12.41*	*27.30*	-	-
QSM3	Autumn 2000[1]	13	54	61.04	61.04	42.64	39.31	6.18	7.72	30	25
QSM4	Spring 2000[1]	16	47	64.98	75.45	67.92	107.34	17.17	18.39	27	20
QAM5	*Autumn 2001*[1]	*7*	*19*	*63.96*	*63.96*	*53.09*	*76.18*	*10.59*	*19.68*	-	-
QAF10	Spring 1999[1]	14	39	84.60	116.56	107.91	110.79	23.54	27.67	14	24
QSF11	Spring 1999[1]	12	33	50.40	68.42	42.09	50.24	15.00	12.45	26	18
QAF12	Autumn 2000	16	67	45.62	74.44	33.30	28.35	21.62	6.79	38	28
	Spring 2000	25	92	106.97	106.97	79.02	84.13	14.25	13.19	27	24
	Autumn 2001	23	78	72.08	88.00	57.64	52.10	11.37	14.66	13	23

Seasons in italics ($n = 2$) were excluded from subsequent analyses due to insufficient fixes.

[1] Data obtained for one season only

Table 4.3.7 Univariate GLM to investigate the influence of site, age-class and gender on güiña seasonal home range areas.

Home range estimator	Factor	*d.f.*	Sum of Squares	Mean Square	*F* value	*P* value
MCP95	Site	1	3764.60	3764.60	5.174	0.072
	Age-class	1	2543.32	2543.32	3.495	0.120
	Sex	1	1230.37	1230.37	1.691	0.250
	Site × Age-class	1	16.79	16.79	0.023	0.885
	Site × Sex	1	784.25	784.25	1.078	0.347
	Age-class × Sex	1	43.02	43.02	0.059	0.818
	Site × Age-class × Sex	0	0.00			
	Error	5	3638.15	727.63		
	Total	11	12339.69			
FK95	Site	1	143.79	143.79	0.154	0.711
	Age-class	1	437.12	437.12	0.469	0.524
	Sex	1	1309.41	1309.41	1.404	0.289
	Site × Age-class	1	242.86	242.86	0.260	0.632
	Site × Sex	1	2080.86	2080.86	2.232	0.195
	Age-class × Sex	1	731.02	731.02	0.784	0.416
	Site × Age-class × Sex	0	0.00			
	Error	5	4661.52	932.303		
	Total	11	8486.88			

Table 4.3.8 Univariate GLM to investigate the influence of site, age-class and gender on güiña seasonal core areas.

Home range estimator	Factor	*d.f.*	Sum of Squares	Mean Square	*F* value	*P* value
MCP50	Site	1	296.03	296.03	2.047	0.212
	Age-class	1	3.84	3.84	0.027	0.877
	Sex	1	23.33	23.33	0.161	0.705
	Site × Age-class	1	60.68	60.68	0.420	0.546
	Site × Sex	1	10.34	10.34	0.072	0.800
	Age-class × Sex	1	3.72	3.72	0.026	0.879
	Site × Age-class × Sex	0	0.00			
	Error	5	723.07	144.61		
	Total	11	1181.10			
FK50	Site	1	0.54	0.54	0.014	0.911
	Age-class	1	107.07	107.07	2.711	0.161
	Sex	1	54.96	54.96	1.392	0.291
	Site × Age-class	1	35.31	35.31	0.894	0.388
	Site × Sex	1	153.73	153.73	3.893	0.106
	Age-class × Sex	1	13.00	13.00	0.329	0.591
	Site × Age-class × Sex	0	0.00			
	Error	5	197.45	39.49		
	Total	11	424.82			

4.3.4 Site fidelity across seasons

The extent by which consecutive seasonal ranges overlapped was calculated for each individual monitored for more than a single season (Table 4.3.9). Each pair-wise comparison required the calculation of two overlap values, the percentage of range in season A overlapped by the range in season B, and the percentage of range in season B overlapped by that in season A. Consecutive field seasons were categorised as either summer-autumn or autumn-summer pairs. For example, animal SJM4 was radio-tracked during autumn 1998, spring 1998 and autumn 1999, therefore two pairs of consecutive field seasons were considered: autumn 1998 – spring 1998, and spring 1998 – autumn 1999.

Table 4.3.9 Percent overlap between home range and core area estimates (mean ± SE) calculated for consecutive field seasons.

		Range estimator							
	Animal ID	MCP95		FK95		MCP50		FK50	
		a	*b*	*a*	*b*	*a*	*b*	*a*	*b*
a) Summer-Autumn									
PNLSR	SSM1[1,2]	79.5	38.5	79.5	38.5	0.0	0.0	6.6	3.4
	SSM2[1,2]	49.4	82.8	26.2	93.4	0.0	0.0	18.3	56.1
	SJM4[3,4]	53.4	78.7	67.8	43.9	5.7	100	31.1	100
PNQ	QAM1[5,6]	81.6	77.1	40.9	60.7	89.5	21.3	51.4	41.6
	QAF12[7,8]	94.9	69.3	80.7	50.2	49.8	39.7	59.5	66.0
	$\bar{x}$ ± SE	70.5 ± 5.6		58.2 ± 6.9		30.6 ± 12.1		43.4 ± 9.4	
b) Autumn-Summer									
PNLSR	SJM4[2,3]	89.6	78.8	57.4	57.2	0.0	0.0	56.8	10.0
	SAF7[2,3]	82.9	79.4	54.7	18.1	0.0	0.0	19.8	14.5
PNQ	QAF12[6,7]	33.9	80.3	29.7	86.6	8.5	5.7	45.4	86.9
	$\bar{x}$ ± SE	74.2 ± 8.2		50.6 ± 9.8		2.4 ± 1.5		38.9 ± 12.2	

a Percent of the first range area that is overlapped by the second.
b Percent of the second range area that is overlapped by the first.
[1]Spring 1997 [2]Autumn 1998 [3]Spring 1998 [4]Autumn 1999
[5]Spring 1999 [6]Autumn 2000 [7]Spring 2000 [8]Autumn 2001

All consecutive seasonal home ranges overlapped (for example, see animal SJM4, Figure 4.3.7), though MCP95 ranges overlapped more extensively than the equivalent FK95 area estimates (paired $t_{15} = 3.228$, $P = 0.006$; Table 4.3.9). There was no difference in overlap between summer-autumn and autumn-summer pairs (MCP95 $t_{14} = 0.378$, $P = 0.711$; FK95 $t_{14} = 0.647$, $P = 0.523$), and güiña exhibited a similar degree of seasonal range overlap within each site (MCP95 $t_{14} = 0.161$, $P = 0.875$; FK95 $t_{14} = 0.378$, $P = 0.711$).

Core area overlap was similar between the two sites (MCP50 $t_{14} = 1.549$, $P = 0.144$; FK50 $t_{14} = 1.794$, $P = 0.095$) and between summer – autumn and autumn – summer consecutive season pairs (MCP95 $t_{14} = 1.776$, $P = 0.097$; FK95 $t_{14} = 0.415$, $P = 0.684$). Male and female güiña also demonstrated comparable levels of overlap between home ranges and core areas utilised in different seasons (MCP95 $t_{14} = 1.271$, $P = 0.225$; FK95 $t_{14} = 0.447$, $P = 0.661$; MCP50 $t_{14} = 0.160$, $P = 0.875$; FK50 $t_{14} = 0.085$, $P = 0.934$).

Three animals were radiotracked over two consecutive autumns: SJM4 and SAF8 (autumn 1998 and 1999), and QAM1 (autumn 2000 and 2001). High inter-annual home range and core area overlap values (home range: MCP95 $\bar{x} = 72.2\% \pm 7.79\%$; FK95 $\bar{x} = 53.68\% \pm 6.80\%$; core area: MCP50 $\bar{x} = 56.70\% \pm 13.86\%$; FK50 $\bar{x} = 43.67\% \pm 11.48\%$) indicate that fidelity to home range location persisted throughout the intervening years.

Linear shifts in seasonal home range geometric activity centre were examined using the RANGES V Interaction Analysis option for each of the güiña monitored across more than two consecutive seasons (SJM4, QAM1 and QAF12). All statistical outcomes were non-significant at $P < 0.05$ (random test $0.31 < t_{2\text{-}6} > 0.71$, randomised test $0.43 < t_{2\text{-}1000} > 1.22$) indicating that for these animals, range centres did not shift appreciably between seasons.

4.3.5 Static interactions

The total home range of each individual overlapped the ranges of all others radiotracked within the same study area, up to the maximum of 100% (Table 4.3.10, 4.3.11a and 4.3.11b; Figures 4.3.3 to 4.3.6). Overlap was variable, for example QAM1 shared between 79% and 100% of all neighbouring (FK95) home ranges, although no other range overlapped his by more than 75.2%. The FK95 home range of SAF7 covered no more than half that of any other in the same study area, but the home range of her male offspring SJM4 incorporated up to 94.2% of neighbouring ranges. Core area overlap was also extensive (Table 4.3.11a and 4.3.11); all but one of the radiotracked güiña shared regions of their MCP50 and FK50 'core' areas with animals of both sexes. Home range and core area overlap was more extensive between individuals in PNQ than in PNLSR (Table 4.3.10).

The influence of age-class and sex on the extent of overlap between total home ranges and core areas was examined within each study site using two-way GLMs. For each pair of güiña three sex combinations or dyads were possible: male-male, male-female and female-female, as well as three age-class combinations: adult-adult, adult-subadult, and subadult-subadult. The degree of overlap among MCP95 and FK95 home ranges and MCP50 and FK50 core areas was similar for each dyad and age-class category, indicating that neither age nor sex influenced the extent to which the ranges of neighbouring pairs of animals overlapped (all $P > 0.05$).

Figure 4.3.7 Seasonal home ranges and core areas of animal SJM4 described using (a) minimum convex polygon estimators (MCP95 and MCP50), and (b) fixed kernel isolines (FK95 and FK50). Dashed lines indicate home ranges, solid lines describe core areas.

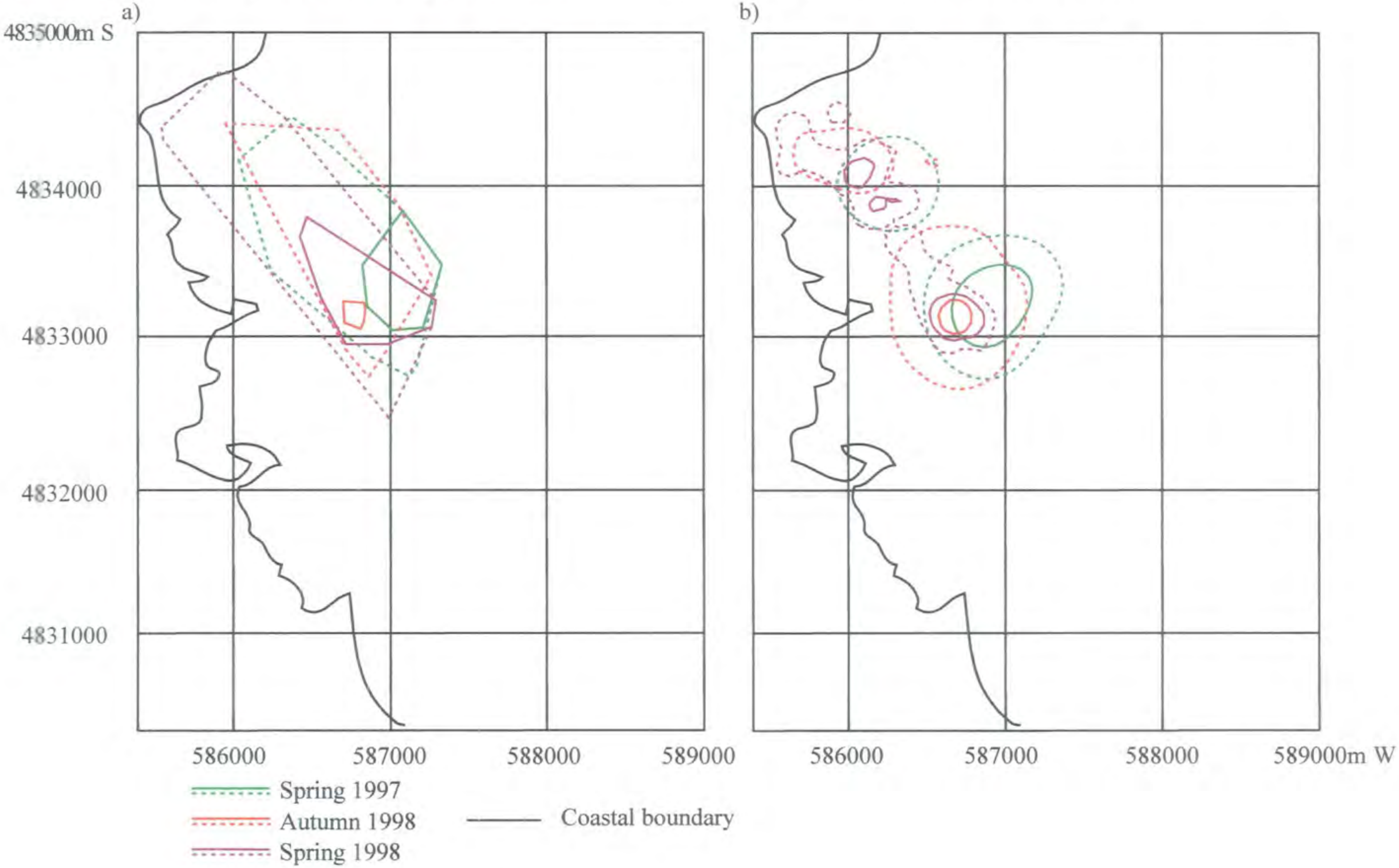


Table 4.3.10 Güiña home range and core area overlap within PNLSR and PNQ.

	Mean percentage overlap (SE)			
	MCP95	FK95	MCP50	FK50
PNLSR	46.51 (5.7)	43.72 (4.26)	20.05 (5.7)	32.98 (2.59)
PNQ	70.95 (3.81)	71.54 (3.98)	42.54 (5.2)	58.13 (4.46)
t ($d.f.$ = 58)	3.559	4.772	2.921	4.878
P	0.001	< 0.001	0.005	< 0.001

4.3.6 Static interactions within seasonal ranges

The seasonal home ranges of both sexes exhibited extensive overlap (Tables 4.3.12a and 4.3.12b and 4.3.13a, 4.3.13b). Seasonal ranges of male-female dyads overlapped by between 11.4% and 84.2% in PNLSR, and 22.8% and 94.6% in PNQ. Spatial overlap between same-sex home ranges was also considerable. Male home ranges overlapped by between 1.6% and 72.5% in PNLSR and 51.2% and 88.0% in PNQ. Fewer comparisons were possible for female dyads. The two PNLSR females shared 16.2% and 12.8% of their respective home ranges, in PNQ a second female-female pair overlapped by 43.2% and 94.8% (all overlap values quoted are for FK95 range estimates). The effect of dyad and age-class combination on range overlap was assessed using two-way analyses of variance for individuals monitored during autumn 1998 (PNLSR), and during spring 1999, autumn 2000 and spring 2000 (all PNQ) field seasons. Amongst seasonal home ranges, a significant difference occurred between dyad classes radiotracked in PNLSR in autumn 1998 when the seasonal FK95 home ranges of male-male dyads overlapped more than those of female-female pairs ($F_{2, 23} = 3.641$, $P = 0.042$). All other comparisons were non-significant at $P = 0.05$.

In all but one pair of overlapping seasonal FK95 home ranges, the core areas of these ranges also coincided (Tables 4.3.12a, 4.3.12b and 4.3.13a, 4.3.13b). There was greater concordance between male-male FK50 core areas during autumn 1998 than that between female-female or male-female pairs ($F_{2, 23} = 4.661$, $P = 0.020$). Overlap among FK50 core areas during this season was also influenced by age-class ($F_{2, 23} = 4.089$, $P = 0.030$): core areas of adult-adult dyads coincided by a lesser percentage (16.9 ± 5.0%) than those of subadult-subadult pairs (50.6 ± 10.8%). There was no significant interaction between dyad and age-class. In autumn 2000 male-male MCP50 core area overlap was significantly greater than that between male-female pairs ($F_{1, 2} = 169.29$, $P = 0.006$) and during spring 2000 adult-adult MCP50 core areas overlapped more than adult-subadult cores ($F_{1, 3} = 15.897$, $P = 0.028$). All other comparisons were non-significant at $P = 0.05$.

Table 4.3.11. Home range and core area overlap between güiña radiotracked in a) PNLSR and b) PNQ. Range areas in columns overlap range areas in rows. Values are expressed as percentages.

a)

	Home Range												Core Area											
	MCP95						FK95						MCP50						FK50					
	SSM1	SSM2	SAM3	SJM4	SAF7	SAF8	SSM1	SSM2	SAM3	SJM4	SAF7	SAF8	SSM1	SSM2	SAM3	SJM4	SAF7	SAF8	SSM1	SSM2	SAM3	SJM4	SAF7	SAF8
SSM1	-	11.7	46.0	22.6	68.4	16.9	-	26.2	55.2	30.7	49.2	15.9	-	0	0.6	0	31.0	0	-	24.8	40.6	25.5	37.1	15.6
SSM2	7.5	-	75.1	75.9	7.3	73.8	27.3	-	65.0	90.1	17.7	56.2	0	-	0	0	0	0	36.4	-	47.8	50.3	21.3	35.4
SAM3	19.8	51.0	-	54.1	19.8	58.2	35.8	40.7	-	61.7	27.0	40.0	0.7	0	-	37.7	24.1	71.9	25.8	21.3	-	38.1	24.6	25.2
SJM4	16.3	86.2	90.1	-	16.1	82.9	18.7	52.6	57.7	-	12.4	45.3	0	0	100	-	8.1	100	24.2	33.3	56.5	-	14.9	38.3
SAF7	84.8	14.3	56.9	27.7	-	20.7	74.3	26.3	63.1	31.3	-	17.4	38.4	0	31.8	4.2	-	13.6	44.4	17.9	45.5	19.0	-	13.7
SAF8	12.4	84.6	98.2	84.0	12.1	-	20.2	67.8	77.2	94.2	14.3	-	0	0	83.6	43.9	11.8	-	25.5	39.6	63.2	65.2	18.3	-

b)

	Home Range												Core Area											
	MCP95						FK95						MCP50						FK50					
	QAM1	QSM3	QSM4	QAF10	QSF11	QAF12	QAM1	QSM3	QSM4	QAF10	QSF11	QAF12	QAM1	QSM3	QSM4	QAF10	QSF11	QAF12	QAM1	QSM3	QSM4	QAF10	QSF11	QAF12
QAM1	-	38.9	51.7	82.1	39.4	74.3	-	32.4	70.3	75.2	42.0	64.4	-	46.1	23.8	61.6	69.4	74.4	-	45.8	44.4	77.1	62.0	71.8
QSM3	97.2	-	77.4	86.7	82.3	99.9	98.3	-	93.6	89.6	86.3	95.9	97.3	-	0	77.0	90.1	99.8	100	-	38.9	90.4	96.8	100
QSM4	81.5	49.2	-	87.5	55.6	73.5	79.0	34.8	-	67.7	46.6	70.4	18.1	0	-	4.9	41.2	11.6	40.8	16.5	-	45.3	23.9	39.9
QAF10	81.9	34.7	54.8	-	36.9	66.6	81.8	32.2	65.4	-	43.2	65.6	34.0	20.3	3.6	-	25.4	28.5	46.9	25.3	30.1	-	42.5	38.6
QSF11	98.8	83.6	88.6	93.3	-	95.3	100	67.8	99.0	94.8	-	95.5	60.9	37.3	47.0	40.1	-	65.2	83.8	60.2	35.1	94.2	-	73.5
QAF12	88.6	47.9	55.6	79.8	45.0	-	88.5	43.2	85.5	82.6	54.8	-	56.3	35.9	11.0	38.9	56.5	-	82.5	52.8	49.7	72.5	62.6	-

Table 4.3.12 Seasonal home range and core area overlap between güiña radiotracked in PNLSR. Range areas in columns overlap range areas in rows. Values are expressed as percentages as delineated by a) the minimum convex polygon home range estimator (MCP95) and b) the 95% fixed kernel home range estimator (FK95). Core area overlap (%) is given in parentheses.

a)

	Spring 1997 (October-December)		Autumn 1998 (January-March)						Spring 1998 (October-December)		Autumn 1999 (January-March)	
	SSM1	SSM2	SSM1	SSM2	SAM3	SJM4	SAF7	SAF8	SJM4	SAF7	SJM4	SAF8
SSM1	-	2.5 [0]	-	47.3 [87.3]	84.3 [84.3]	36.2 [0]	85.2 [20.8]	42.4 [89.8]				
SSM2	2.5 [0]	-	14.3 [30]	-	67.4 [64.4]	64.0 [30.7]	11.3 [7.6]	76.9 [95.1]				
SAM3			29.7 [35.9]	78.0 [79.7]	-	62.7 [14.7]	25.7 [27.2]	81.9 [76.0]				
SJM4			16.8 [0]	98.5 [36.7]	83.8 [14.4]	-	12.9 [0]	96.0 [98.0]	-	3.9 [0]	-	47.9 [48.7]
SAF7			51.3 [9.3]	22.8 [9.8]	44.2 [28.3]	16.8 [0]	-	17.5 [4.8]	4.6 [0]	-		
SAF8			14.8 [13.1]	88.9 [40.4]	82.0 [26.2]	72.2 [34.9]	10.1 [1.6]	-			100 [94.3]	-

b)

	Spring 1997 (October-December)		Autumn 1998 (January-March)						Spring 1998 (October-December)		Autumn 1999 (January-March)	
	SSM1	SSM2	SSM1	SSM2	SAM3	SJM4	SAF7	SAF8	SJM4	SAF7	SJM4	SAF8
SSM1	-	8.1 [1.0]	-	64.5 [96.5]	64.1 [92.2]	57.2 [26.6]	56.5 [16.8]	25.0 [36.7]				
SSM2	20.1 [2.1]	-	23.7 [38.6]	-	55.8 [67.6]	58.2 [34.6]	13.3 [6.0]	23.2 [29.9]				
SAM3			30.7 [36.4]	72.5 [66.5]	-	59.0 [27.9]	21.3 [10.7]	27.8 [21.8]				
SJM4			22.5 [11.0]	62.3 [36.4]	48.4 [29.5]	-	11.4 [2.0]	26.7 [16.9]	-	1.6 [0]	-	58.1 [50.5]
SAF7			55.2 [16.6]	35.3 [14.8]	42.5 [26.0]	28.2 [5.0]	-	12.8 [8.8]	12.3 [0]	-		
SAF8			30.9 [33.6]	77.8 [68.1]	72.2 [50.8]	84.2 [37.2]	16.2 [8.0]	-			72.0 [50.2]	-

Table 4.3.13 Seasonal home range and core area overlap between güiña radiotracked in PNQ. Range areas in columns overlap range areas in rows. Values are expressed as percentages as delineated by a) the minimum convex polygon home range estimator (MCP95) and b) the 95% fixed kernel home range estimator (FK95). Core area overlap (%) is given in parentheses.

a)

	Spring 1999 (October-December)			Autumn 2000 (January-March)			Spring 2000 (October-December)		
	QAM1	QAF10	QSF11	QAM1	QSM3	QAF12	QAM1	QSM4	QAF12
QAM1	-	85.2 [26.1]	41.6 [46.4]	-	51.2 [76.3]	43.3 [5.9]	-	53.8 [37.0]	61.1 [54.5]
QSM3				88.0 [85.6]	-	51.4 [1.8]			
QSM4							81.7 [48.9]	-	69.0 [13.2]
QAF10	61.3 [32.0]	-	36.9 [25.4]						
QSF11	75.7 [90.1]	93.3 [40.1]	-						
QAF12				94.6 [2.0]	66.0 [0.6]	-	80.3 [86.7]	59.2 [15.9]	-

b)

	Spring 1999 (October-December)			Autumn 2000 (January-March)			Spring 2000 (October-December)		
	QAM1	QAF10	QSF11	QAM1	QSM3	QAF12	QAM1	QSM4	QAF12
QAM1	-	75.7 [45.3]	52.6 [38.8]	-	62.9 [80.9]	49.3 [52.1]	-	67.4 [28.2]	61.9 [48.7]
QSM3				77.9 [89.2]	-	51.6 [56.7]			
QSM4							60.5 [35.1]	-	70.2 [36.0]
QAF10	22.8 [17.4]	-	43.2 [42.5]						
QSF11	34.7 [32.8]	94.8 [94.2]	-						
QAF12				83.4 [64.8]	71.2 [63.4]	-	70.6 [84.4]	89.1 [50.0]	-

4.3.7 Dynamic interactions and temporal spacing

Because both study populations exhibited considerable spatial overlap the potential for aggressive encounter was also assessed in relation to temporal spacing. Tables 4.3.14 and 4.3.15 detail the results obtained from analyses of simultaneously monitored güiña movements. The mean separation distance between 586 pairs of coincident locations varied between 106 and 1303 m, depending on pair-group, site and season. Two pairs of animals, SAF7/SAF8 and QAM1/QSF11 exhibited slight negative association. All other spatio-temporal relationships either indicated a positive association, implying some attraction between animals, or were neutral, implying the movement of a pair was random with respect to one other.

Some variation was apparent in the spatio-temporal behaviour of the three dyad combinations. Jacob's indices of dynamic interaction were higher between PNQ individuals, indicating these animals were more positively associated than those monitored in the PNLSR study site (t_{23} = 2.427, P = 0.023). Within each site, the most closely associated animals were mixed-sex pairs, for example SAF8/SJM4 (autumn 1999) and QAM1/QAF12. However, there was no significant trend for male-female dyads to have the highest indices for spatio-temporal overlap (PNLSR $F_{2,12}$ = 0.833, P = 0.458; PNQ $F_{2,7}$ = 0.825, P = 0.477) and the extent of home range overlap in spring did not differ from that during autumn (PNLSR $F_{1,13}$ = 0.086, P = 0.774; PNQ $F_{1,8}$ = 0.096, P = 0.765).

Table 4.3.14 Dynamic Interaction Analysis comparing observed and expected distances between simultaneously located pairs of (a) males, (b) females and (c) male and female güiña in PNLSR. All interactions quoted are from the Autumn 1998 tracking season unless otherwise indicated.

(a) Male pairs	SSM1/SSM2[1]	SSM1/SSM2	SSM1/SAM3	SSM2/SAM3	SSM2/SJM4	SAM3/SJM4		
Jacob's Index (*J*)	0.13	0.08	0.22	0.28	0.24	0		
Number of observed locations	42	29	15	8	2	1		
Number of randomised locations	1764	841	225	64	4	1		
Observed geometric mean dist (m)	454	1303	275	345	295	179		
Expected mean distance (m)	517	1419	344	460	375	179		
(b) Female pairs	SAF7/SAF8							
Jacob's Index (*J*)	-0.02							
Number of observed locations	62							
Number of randomised locations	3844							
Observed geometric mean dist (m)	1178							
Expected mean distance (m)	1151							
(c) Male – female pairs	SSM1/SAF7	SSM1/SAF8	SSM2/SAF7	SSM2/SAF8	SAM3/SAF7	SAM3/SAF8	SJM4/SAF8	SJM4/SAF8[2]
Jacob's Index (*J*)	0.30	0.19	0.07	0.22	0.31	0.03	0	0.78
Number of observed locations	26	23	13	19	21	10	3	119
Number of randomised locations	676	529	169	361	441	100	9	14161
Observed geometric mean dist (m)	284	619	612	407	203	858	608	164
Expected mean distance (m)	387	753	656	506	279	882	608	466

[1] Spring 1997
[2] Autumn 1999

Table 4.3.15 Dynamic Interaction Analysis comparing observed and expected distances between simultaneously located pairs of (a) males, (b) females and (c) male and female güiña in PNQ.

(a) Male pairs	QAM1/QAM2[1]	QAM1/QSM3[2]	QAM1/QSM4[3]
Jacob's Index (*J*)	0.13	0.26	0.43
Number of observed locations	4	45	6
Number of randomised locations	16	2025	36
Observed geometric mean dist (m)	444	118	255
Expected mean distance (m)	506	154	405

(b) Female pairs	QAF10/QSF11[1]
Jacob's Index (*J*)	0.31
Number of observed locations	5
Number of randomised locations	25
Observed geometric mean dist (m)	283
Expected mean distance (m)	391

(c) Male – female pairs	QAM1/QAF10[1]	QAM1/QSF11[1]	QAM1/QAF12[2]	QSM3/QAF12[2]	QAM1/QAF12[3]	QSM4/QAF12[3]
Jacob's Index (*J*)	0.70	-0.01	0.66	0.39	0.62	0.51
Number of observed locations	8	4	52	26	14	29
Number of randomised locations	64	16	2704	676	196	841
Observed geometric mean dist (m)	127	241	106	131	206	205
Expected mean distance (m)	299	237	236	197	422	358

[1] Spring 1999
[2] Autumn 2000
[3] Spring 2000

4.3.8 Number of güiña and population density.

Minimum convex polygons calculated from successful trap locations defined a trapping area of 290 ha inside PNLSR and 52 ha in PNQ. The mean proportion of radio-telemetry fixes located within these areas was 81.80 ± 4.76% for seasonal home range areas (FK95 ranges) in PNLSR (n = 12, range = 40.74 to 98.98%), and 63.14 ± 4.63% (n = 10, range = 38.46 to 80.60%) in PNQ (Table 4.3.16). Not all residents were recorded present in every season (Table 4.3.17). Two additional güiña (SAM6 and SJF10) were captured inside the PNLSR study area but were not monitored, as were a further five animals (QAM6, QAM7, QAM8, QAM9 and QAF13) captured within the PNQ study area.

The number of güiña radiotracked within the PNLSR study site each season included up to two adult females ($\bar{x}$ = 1.00 ± 0.41) and between one and four males ($\bar{x}$ = 2 ± 0.71), of which up to three were subadults ($\bar{x}$ = 1.5 ± 0.65). The number of güiña radiotracked within PNQ included up to two adult females ($\bar{x}$ = 1.25 ± 0.25) and two males ($\bar{x}$ = 1.5 ± 0.29) (Table 4.3.18). When all animals known to be present in a study area were included within population estimates, i.e. not just those individuals that were radiotracked, the mean seasonal density increased from 0.46 to 0.77 güiña km^{-2} in PNLSR and from 2.24 to 2.92 km^{-2} within PNQ (Table 4.3.19). The density of adult güiña each season ranged between 0.15 and 0.62 animals km^{-2} in PNLSR (spring 1997 and autumn 1999 respectively), and between 0.87 (autumn 2001) and 2.70 (spring 1999) km^{-2} in PNQ. The density of subadult animals throughout the study period varied between 0.30 to 0.45 km^{-2} within the PNLSR site (spring 1997, autumn and spring 1998) and in PNQ between 0.87 km^{-2} (spring 1999) and 1.83 km^{-2} (autumn 2001). Inclusive estimates indicate males were more numerous than females in each area, and also that numbers of adult animals were similar to those of subadults (Table 4.3.19).

Within the 5.3 km^2 PNLSR study area the estimated (inclusive) güiña population size varied from between two and three animals in spring 1997 to five in autumn 1999 (calculated as population density × area). In PNQ the estimated number present inside the 3.1 km^2 study area varied from a low of approximately eight animals in spring 1999 to eleven in each of the autumn 2000, spring 2000 and autumn 2001 field seasons. Removal of the two presumed transients from calculations of population size reduced the number of residents estimated present in the PNQ study area to between five and eight animals per season monitored, or 1.79 to 2.70 animals km^{-2}. No transient animals were identified inside PNLSR.

Table 4.3.16 Contribution from radio monitored animals to population density estimates. For explanation of column headings see text.

Site	Animal ID	Season	Proportion of fixes inside trap area	Days tracked / total days radio-tracking	Contribution to density estimate for season
PNLSR	SSM1	Spring 1997	0.407	0.927	0.378
		Autumn 1998	0.829	0.326	0.270
	SSM2	Spring 1997	0.980	0.488	0.478
		Autumn 1998	0.816	0.435	0.355
	SAM3	Autumn 1998	0.889	0.370	0.329
	SJM4	Autumn 1998	0.840	0.283	0.237
		Spring 1998	0.938	0.769	0.722
		Autumn 1999	0.886	0.774	0.686
	SAF7	Autumn 1998	0.714	0.478	0.342
		Spring 1998	0.633	0.385	0.244
	SAF8	Autumn 1998	0.893	0.478	0.427
		Autumn 1999	0.990	0.871	0.862
PNQ	QAM1	Spring 1999	0.515	0.818	0.421
		Autumn 2000	0.787	0.947	0.746
		Spring 2000	0.436	0.533	0.232
	QSM3	Autumn 2000	0.741	0.395	0.292
	QSM4	Spring 2000	0.723	0.600	0.434
	QAF10	Spring 1999	0.385	0.682	0.262
	QSF11	Spring 1999	0.697	0.545	0.380
	QAF12	Autumn 2000	0.806	0.526	0.424
		Spring 2000	0.609	0.967	0.588
		Autumn 2001	0.615	1.000	0.615

Table 4.3.17 Number of güiña recorded present each season. * Denotes seasonal datasets when ≥30 radiolocation fixes (of ≥5 hours inter-fix interval) were obtained during a particular field season, ※ denotes radiotracked individuals for which < 30 radiolocation fixes were obtained. ☆ Signifies güiña that were trapped or sighted, but not radiotracked.

PNLSR	Spring 1997	Autumn 1998	Spring 1998	Autumn 1999
SSM1	*	*	☆	
SSM2	*	*	☆	
SAM3	※	*	※	※
SJM4		*	*	*
SSM10				☆
SAF7		*	*	※
SAF8		*		*
SJF9				☆
PNQ	**Spring 1999**	**Autumn 2000**	**Spring 2000**	**Autumn 2001**
QAM1	*	*	*	
QAM2	※			
QSM3		*		☆
QSM4			*	
QAM5				※
QAF10	*			
QSF11	*			
QAF12		*	*	*

Table 4.3.18 Mean number of collared güiña recorded present each season. Values in brackets are standard errors. For explanation of column headings see text.

Site	Age-class	Mean number present/season	Contribution to population estimate in trap area	Individuals km^{-2}
PNLSR	Adult males	0.50 (0.29)	0.22 (0.12)	0.07 (0.04)
	Subadult males	1.50 (0.65)	0.65 (0.28)	0.22 (0.10)
	Adult females	1.00 (0.41)	0.47 (0.19)	0.16 (0.07)
	Subadult females	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
	All animals	3.00 (1.00)	1.33 (0.44)	0.46 (0.15)
PNQ	Adult males	0.75 (0.25)	0.36 (0.12)	0.69 (0.23)
	Subadult males	0.50 (0.29)	0.24 (0.14)	0.46 (0.26)
	Adult females	1.00 (0.00)	0.45 (0.00)	0.87 (0.00)
	Subadult females	0.25 (0.25)	0.11 (0.11)	0.22 (0.22)
	All animals	2.50 (0.50)	1.16 (0.24)	2.24 (0.45)

Table 4.3.19 Mean total number of güiña (collared, trapped, and observed) recorded present each season. Values in brackets are standard errors.

Site	Age-class	Mean number present/season	Contribution to population estimate in trap area	Individuals km^{-2}
PNLSR	Adult males	1.25 (0.25)	0.54 (0.11)	0.19 (0.04)
	Subadult males	2.25 (0.48)	0.97 (0.21)	0.34 (0.07)
	Adult females	1.25 (0.48)	0.59 (0.22)	0.20 (0.08)
	Subadult females	0.25 (0.25)	0.12 (0.12)	0.04 (0.04)
	All animals	5.00 (0.71)	2.21 (0.33)	0.77 (0.11)
PNQ	Adult males	1.00 (0.41)	0.47 (0.19)	0.91 (0.37)
	Subadult males	1.00 (0.41)	0.47 (0.19)	0.91 (0.37)
	Adult females	1.00 (0.00)	0.45 (0.00)	0.87 (0.00)
	Subadult females	0.25 (0.25)	0.11 (0.11)	0.22 (0.22)
	All animals	3.25 (0.25)	1.52 (0.11)	2.92 (0.22)

4.4 Discussion

4.4.1 Spatial patterns of güiña distribution

This study found evidence of spatial overlap between neighbouring güiña home ranges well in excess of the 10% threshold value proposed as the maximum for considering two ranges exclusive (Sandell, 1989), indicating a lack of territorial behaviour highly unusual among small felids (Gittleman and Harvey, 1982). No avoidance of neighbouring core areas was apparent, despite these areas frequently representing sites of heightened territoriality and resource partitioning among solitary carnivores (Horner and Powell, 1990; Nielsen and Woolf, 2001).

Patterns of spatio-temporal overlap were similar between dyad categories and across seasons. The majority of these interactions were positive (indicated by a positive Jacob's Index) implying these pairs were to some degree associated. Only two Jacob's index values were negative and both failed to indicate a significant departure from zero, suggesting no active avoidance or temporal partitioning of shared areas occurred between neighbouring güiña.

From the approximate age of kittens captured during this study, and the timing of reproduction among captive Geoffroy's cats (Law and Boyle, 1984), the mating period of güiña in southern Chile most probably occurs in the early spring, centring on August and September. No seasonal variation in home range size or core area utilisation was determinable however for either sex. Males were no closer to females during spring, and females were no farther from other females during this time, as might be expected for a solitary carnivore (Sandell, 1989).

The potential for interspecific aggression is predicted to be high when population densities are high and when home ranges are exclusive, or when densities are intermediate and overlap is extensive (Nielsen and Woolf, 2001). Despite the widespread coincidence of home range areas, instances of aggressive encounter were nevertheless observed only twice during the study period; the first was between a subadult male (SSM1) and an adult male (SAM3), the second occurred a year later between the then young adult SSM1 and a subadult male (SJM4). The older animal appeared to win on both occasions; each fight lasted no more than two to three minutes when both cats quickly disappeared into the undergrowth. After each incident the younger individual remained present in the vicinity during the subsequent days.

The monopolisation of a home range requires that a resident animal or social group is able to both control and defend such an area from potential competitors. When resources are dispersed and/or occur unpredictably in space and time however, it can be uneconomic for animals to maintain effective control (Emlen and Oring, 1977; Davies, 1978; Davies and Houston, 1984; Grant, 1993; Elchuk and Wiebe, 2003). Sunquist and Sunquist (1989) suggest that sedentary, predictable prey resources are often associated with small, exclusive predator ranges or territories. When resources are abundant and favourably distributed however, an alternative strategy by which common areas are shared may prove to be the more economically efficient (Rabinowitz and Nottingham, 1986), provided there is some mechanism in place to facilitate mutual avoidance. In circumstances when the costs associated with territorial defence outweigh benefits gained through exclusive access territoriality may therefore be abandoned completely.

Sanderson *et al.* (2002) noted consistent inter-sexual home range exclusivity among güiña on Isla Grande, and suggested that radiotracked males actively patrolled their home range boundaries. Such behaviour was clearly absent from both the PNLSR and PNQ populations. The Isla Grande güiña inhabit an anthropomorphically modified environment within an agricultural region. Although no data are available that describe the availability and distribution of prey and other potential resources on Isla Grande, the study area was markedly dissimilar to those within the Laguna San Rafael and Queulat National Parks. Güiña home range areas were of similar size in each of these three sites, however the contrasting patterns of social spacing described by this study and that conducted on Isla Grande indicate a capacity for flexibility in the güiña social system, and suggest that territoriality may be facultative for this species.

4.4.2 Home range area and population densities

The minimum concave estimates of güiña home range area detailed in Table 4.3.2 are similar to those calculated for güiña radiotracked by Sanderson *et al.* (2002) on Isla Grande between November 1997 and April 1998 (males $t_{10} = 1.54$, $P = 0.155$; females $t_5 = 0.23$, $P = 0.830$) and are comparable also to home range areas reported for other small neotropical felids such as the leopard cat (150 to 750 ha, Rabinowitz, 1990; Grassman, 1998a), Geoffroy's cat (370 to 920 ha, Johnson and Franklin 1991), and margay (*Leopardus wiedi*) (1095 ha, Konecny, 1989).

No consistent influence of age-class or gender on home range size or overlap could be determined. Sanderson *et al.* (2002) in contrast, reported larger MCVP range estimates for male güiña than for females on Isla Grande de Chiloé (males 659 ± 397.89 ha, $n = 5$; females 126 ± 41.25 ha, $n = 2$) and an absence of intra-sexual range overlap. This possibly reflects genuine dissimilarity between the mainland and island populations, though may also be an artefact of the differing survey procedures or numbers of animals monitored. The Chiloé study for instance included behavioural data for only two females, the ranges of which were encompassed by that of a single male. The spatial behaviour of neighbouring females was not ascertained.

Increases in range size in response to low or patchy food availability, and conversely decreases in range size in response to plentiful prey are widely recorded for carnivore populations (for example Sunquist, 1981; Jones and Theberge, 1982; Kruuk, 1986; Sandell, 1989), and among felids in particular (Genovesi *et al.*, 1985; Poole, 1995; du Bothma *et al.*, 1997). However, some carnivore studies have also shown little change in home range size after declines in abundance of their staple prey (Lockie, 1966; Breitenmoser *et al.*, 1993; White and Ralls, 1993). That mean home range sizes described by this study are no larger than those reported from the largely agricultural landscape of Isla Grande possibly reflects a similarity in patterns of prey availability in both locations (Macdonald, 1983, Genovesi *et al.*, 1995).

The results of this study indicate that site, age-class and gender all exert an influence on long term MCP95 home ranges, however these results were not reflected by FK95 estimates derived using the same spatial data, or by seasonal home range estimates (Tables 4.3.3 and 4.3.4). Minimum convex and fixed kernel estimators of activity area are based on fundamentally different computational procedures and their outputs are differently sensitive to factors such as sample size and outlying data points. That the two methods were influenced differently by site, age and sex highlights the need for methodological consistency wherever possible, and for caution when contrasts must be made between estimates of area obtained using different estimation techniques.

The radio-tracking data, in conjunction with records of sightings and captures indicated seasonal population densities of between 0.45 and 3.58 güiña km^2. Because dispersing animals present only temporarily within the study areas were successfully captured, and all resident animals were trapped repeatedly, it was assumed all güiña present in each site had been captured at least once. In PNLSR this equated to between one and four adults plus two to three subadults present concurrently. In the PNQ study area no more than two adults and one subadult were present simultaneously.

Summary

Similar home range and core area sizes were described for resident güiña within each of the PNLSR and PNQ study areas. The extent of these activity areas also resembled those estimated for güiña living within the largely agricultural landscape of Isla Grande de Chiloé (Sanderson *et al.*, 2002). In this study several adult and subadult güiña were radiotracked across several seasons. Home range locations varied little during this time, indicating that the home ranges of resident güiña may be stable across multiple years.

In contrast to the system of inter-sexual territoriality described by Sanderson *et al.* (2002), this study revealed high levels of home range and core area overlap among neighbouring güiña of both sexes, indicating a lack of territorial behaviour unusual in a solitary felid (Gittleman and Harvey, 1982). Güiña did not attempt to minimise the simultaneous use of shared areas, implying that no benefit was to be gained by reducing competition among conspecifics for resources within these areas. Thus, this study indicates that the maintenance of exclusive home ranges is not characteristic of all güiña populations, and that the güiña has a flexible spatial organisation that is likely to reflect local environmental quality.

Chapter 5

Daily Movement and Activity Patterns

5.1 Introduction

Flexible activity patterns represent part of the suite of adaptations animals utilise to track a variable environment. Local modifications are made to time budgets and movement patterns in response to changes in factors such as climate, season, prey availability, and social status (Cloudsley-Thompson, 1961; Aschoff, 1964; Enright, 1970; Curio, 1976; Daan and Aschoff, 1975; 1982; Nielsen, 1983).

The adaptive value of flexible activity patterns has been well documented for a variety of carnivores including black bears (*Ursus americanus*) (Garshelis and Pelton, 1980); red fox (Ables, 1969); pine marten (*Martes americana*) (Zielinski *et al.*, 1983); Eurasian lynx (Reinhardt and Halle, 1999); and Iberian lynx (Beltrán and Delibes, 1994). The timing of activity is an important consideration for predatory animals, particularly when prey animals are more readily detected or vulnerable when active. Zielinski *et al.* (1983), for example, demonstrated that the active behaviour of pine marten coincided with the active periods of small mammal prey, resulting in nocturnal hunting behaviour in winter and diurnal activity in summer. Ferguson *et al.* (1988) noted changes in the hunting activities of black-backed jackals (*Canis mesomelas*) in response to bright moonlight, which afforded prey animals greater visibility and hence made them less vulnerable to predation. Jackals responded by investing proportionally less time in predatory activities during these periods of reduced hunting efficiency.

Among the Felidae the timing of active behaviour varies among and often within species (Gittleman, 1989; Konecny, 1989; Beltrán and Delibes, 1994; Schmidt, 1999; Weller and Bennet, 2001). Many cats are primarily nocturnal and/or crepuscular, for example tiger (Sunquist, 1981), African lion (Schaller, 1972; Stander, 1992), leopard (Bailey, 1993), Geoffroy's cat (Cabrera and Yepes, 1960; Johnson and Franklin, 1991), margay (Koneny, 1989), bobcat (Hall and Newson, 1976) and ocelot (Emmons, 1988; Konecny, 1989; Sunquist *et al.*, 1989). Less common are felid species that are predominantly diurnal such as cheetah (Eaton, 1974; Eisenberg, 1986), leopard cat (Rabinowitz, 1990) and jaguarundi *Felis yaguaroundi* (Kiltie, 1984).

Early reports depicted the güiña as a predominantly nocturnal predator (Cabrera and Yeppes, 1960; Greer, 1965; Guggisberg, 1975; Miller and Rottmann, 1976). More recently Iriarte and Sanderson (1999) and Sanderson *et al.* (2002) found individuals radiotracked on Isla Grande de Chiloé to be less active during daylight hours (48.4% of observations active) than at other times (75.4% active), and described a slight tendency towards crepuscular behaviour. The same study also indicated that female güiña were located active more often than males. Sanderson *et al.* (2002) speculated that predawn peaks in active behaviour might correlate with stalking behaviour directed towards avian prey, and that the observed increase in activity during the early hours of darkness might reflect peaks in rodent activity.

5.12 Chapter Aims

The purpose of this chapter is to provide the first description of güiña activity patterns within a largely pristine habitat. Daily variation in the frequency and timing of the active behaviour of güiña is described for each of the Parque Nacional Laguna San Rafael and Parque Nacional Queulat populations, and is further examined in relation to site, sex, age-class and season.

5.2 Methods

5.2.1 Daily activity

Behaviour was categorised at the time of radiolocation as either active or inactive through interpretation of radio transmitter signal consistency and pulse frequency. Güiña were considered active if the strength of the transmitter signal was variable and the pulse rate was of the faster rate of 75 ppm. Inactive behaviour was recorded when the signal was of constant strength and/or at the slower pulse rate of 50 ppm.

Because variable numbers of location fixes were obtained for different animals, activity was expressed as the average of all fixes recorded during each hour of the 24-hour day for every individual and season. In order to investigate the influence of light level on active behaviour, each day was then partitioned into four periods: dusk and dawn (two hours duration each, centred on the mean monthly sunrise and sunset time respectively), day and night. Seasonal variation in the duration of daylight was incorporated into the diel categories (Table 5.2.1). At the latitudes of the two study sites the nightly period of darkness varied during the study period from less than five hours in December to over eight hours during March.

Table 5.2.1 Daylight, nocturnal and crepuscular period duration and monthly variation at latitudes 44-46°S (derived from data provided by the Direccíon General de Aeronautica Civil de Chile).

Season	Month	Dawn	Daylight	Dusk	Night
Spring	October	05:14 - 07:14	07:15 - 19:56	19:57 - 21:57	21:58 - 05:13
	November	04:20 - 06:20	06:21 - 20:52	20:53 - 22:53	22:54 - 04:19
	December	04:09 - 06:09	06:10 - 21:26	21:27 - 23:27	23:28 - 04:08
Autumn	January	04:40 - 06:40	06:41 - 21:10	21:11 - 23:11	23:12 - 04:39
	February	05:30 - 07:30	07:31 - 20:25	20:26 - 22:26	22:27 - 05:29
	March	06:06 - 08:06	08:07 - 19:44	19:45 - 21:45	21:46 - 06:05

The influence of site, sex, season, age and time of day (dawn, daylight, dusk and night) on the intensity of active behaviour (where intensity is defined as the mean proportion of radiotelemetry signals active each hour) was examined using one-way and multi-factorial generalised linear models (GLMs). Significant results were identified using *t*-tests or Fisher's test for least significant difference as appropriate. Small sample sizes for some site-season combinations necessitated that seasonal data within sites were grouped across years to permit analyses involving seasonal effects.

5.2.2 Daily distance travelled and movement rates

Net daily movement was calculated by measuring the straight-line distance between locations obtained for individual güiña radiotracked across successive days. When more than one location was recorded in a given day, only the first location was included in the analyses.

Cumulative daily distance travelled was described for all continuous radio tracking sessions of 24 hours duration. The straight-line distances between consecutive location points were then summed to provide an estimate of the total distance travelled each day.

Rate of movement (km h^{-1}) between consecutive locations was estimated by dividing inter-fix distances by the intervening time interval. The entire data set was utilised for this purpose, however to reduce error due to possible variation of speed with time and to ensure that distances between locations were associated with actual distances moved, linear distances were calculated from sequential fixes only for those occasions when no more than 45 minutes had elapsed between consecutive readings (Reynolds and Laundré, 1990).

The influence of site, sex, age, season and time of day (dawn, daylight, dusk and night) on distances travelled and rate of movement were examined using one-way and multi-factorial GLMs. For each population, seasonal data were grouped across years. Dependent variables were log-transformed to normalise non-normal distributions (Krebs, 1989).

The active behaviour recorded for animal QAM2 was noticeably different to that of other individuals (all 52 activity recordings were in the 'active' state). Because a malfunctioning activity sensor was suspected these data were excluded from further analyses of behaviour.

5.3 Results

5.3.1 Patterns of active behaviour

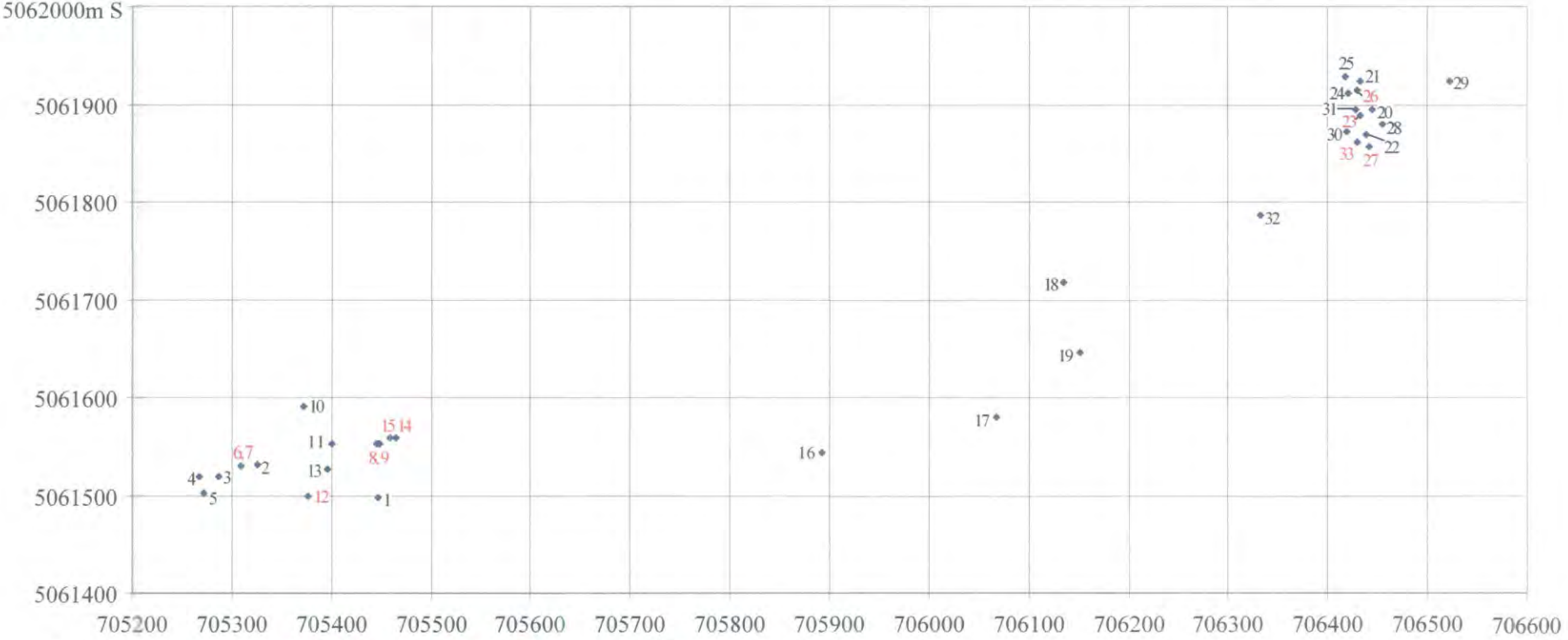
3812 activity samples were obtained from güiña radiotracked within PNLSR, and 1974 from PNQ (Table 5.3.1). Across both sites, most güiña activity ($\bar{x}$ = 84.3% of active fixes each hour, range 0 - 100%) occurred within small areas or patches. This activity was interspersed with almost linear movements or deslocations between patches, characteristically accompanied by an increase in speed. Figure 5.3.1 displays an example of the movements of animal QAM1, as determined via radio-telemetry during 24 hours of continuous tracking.

Male güiña were active during 55.3% of all activity readings, female güiña were active during 60.8% of readings. Bouts of active and inactive behaviour during periods of continuous radiotracking were often relatively short. Most bouts lasted less than three hours (219 of 341 active bouts (64%), 257 of 330 inactive bouts (78%), Figure 5.3.2), and only 17% of active and 8% of inactive bouts lasted more than five hours. The duration of active bouts was similar among male and female güiña (males 2.90 ± 0.16 hours; females 2.85 ± 0.18 hours, $F_{1,\,340} = 0.087$, $P = 0.768$). In contrast, the duration of inactive bouts was often longer among male güiña (males: 2.32 ± 0.14 hours; females 1.96 ± 0.14 hours), this difference between the sexes approaching significance ($F_{1,329} = 3.340$, $P = 0.069$).

Table 5.3.1 Güiña activity during different parts of the day, as determined from activity sensitive radio transmitters and magnitude of location shifts between consecutive fixes.

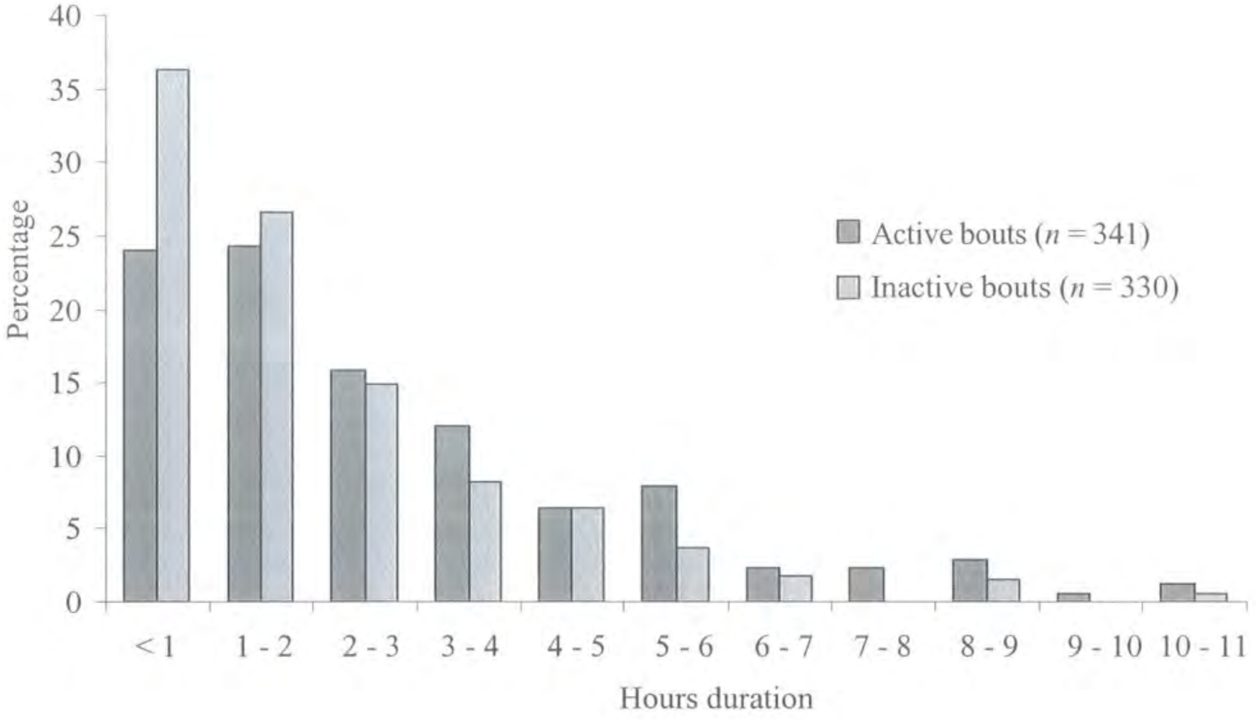
Variable	Whole day	Dawn (2 h)	Daylight	Dusk (2 h)	Night
PNLSR 1997-1999 (*n* = 6)					
Active fixes (%)	55.36	54.61	55.58	63.64	52.92
Static fixes (%)	44.65	45.39	44.41	36.37	47.08
Mean active bout length (h)	2.76				
Mean inactive bout length (h)	2.08				
Number of activity fixes	3812	277	2109	281	1075
PNQ 1999-2001 (*n* = 6)					
Active fixes (%)	60.29	67.50	55.68	77.33	63.19
Static fixes (%)	39.72	32.50	44.33	22.67	36.81
Mean active bout length (h)	3.22				
Mean inactive bout length (h)	2.33				
Number of activity fixes	1974	160	1137	150	527

Fig. 5.3.1 Movement distances and times for animal QAM1 as described by continuous radio-telemetry data recorded on 10th February 2000. Static location fixes are highlighted in red.



Time
1. 00:00
2. 00:30
3. 01:20
4. 02:00
5. 02:30
6. 03:00
7. 03:35
8. 04:35
9. 05:05
10. 05:40
11. 06:35
12. 07:08
13. 07:38
14. 08:26
15. 09:20
16. 10:20
17. 11:20
18. 12:10
19. 13:05
20. 14:05
21. 14:50
22. 15:50
23. 16:48
24. 17:18
25. 17:50
26. 18:20
27. 19:15
28. 20:10
29. 20:54
30. 21:55
31. 22:50
32. 23:25
33. 23:55

Figure 5.3.2 Frequency distribution for the duration of active and inactive behaviours of 12 güiña radiotracked within PNLSR and PNQ.



Mean hourly activity levels varied between individual animals ($F_{11, 276} = 7.029$, $P < 0.001$). Intensity of activity also varied with time of day and light level ($F_{3, 72} = 3.091$, $P = 0.032$); güiña were active more often at dusk then during any other period (71.56 ± 3.76%, Fisher's LSD test, $P = 0.01$). No direct influence of sex or site was identified, nor was any interaction detected between these two factors (all $P > 0.05$, Figure 5.3.3), however intensity of activity was influenced by age-class and season. Adult güiña were active for a greater part of the day during spring than in autumn ($F_{1, 8} = 7.00$, $P = 0.029$), and were also significantly more active than subadult animals during the spring months ($F_{1, 8} = 11.395$, $P = 0.010$, Figure 5.3.4).

Figure 5.3.3 Daily patterns of activity for male and female güiña. Values are mean percentage of activity data recorded in an active state. The seasonal ranges of dusk and dawn are underlined on the 24-hour abscissa.

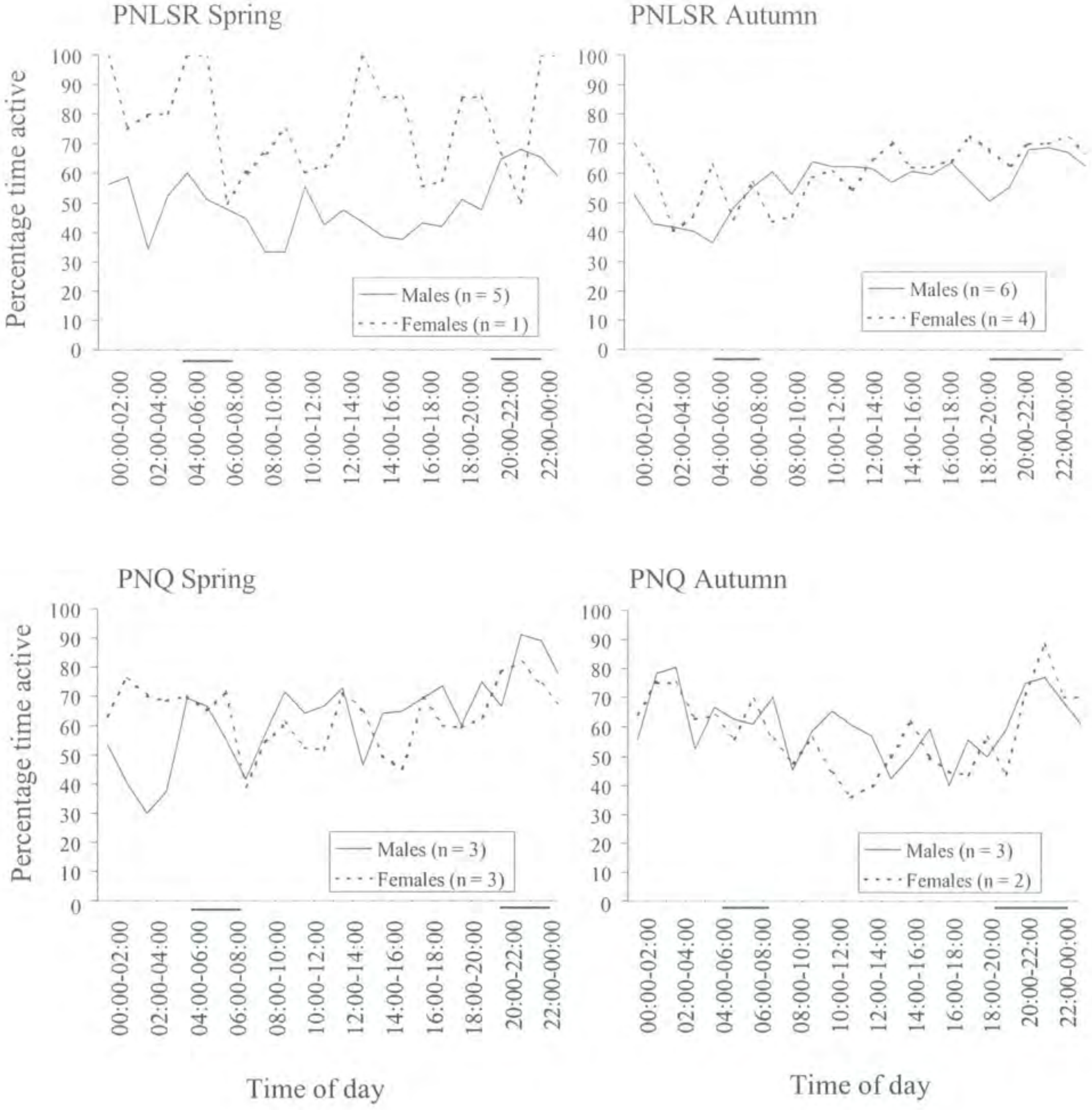
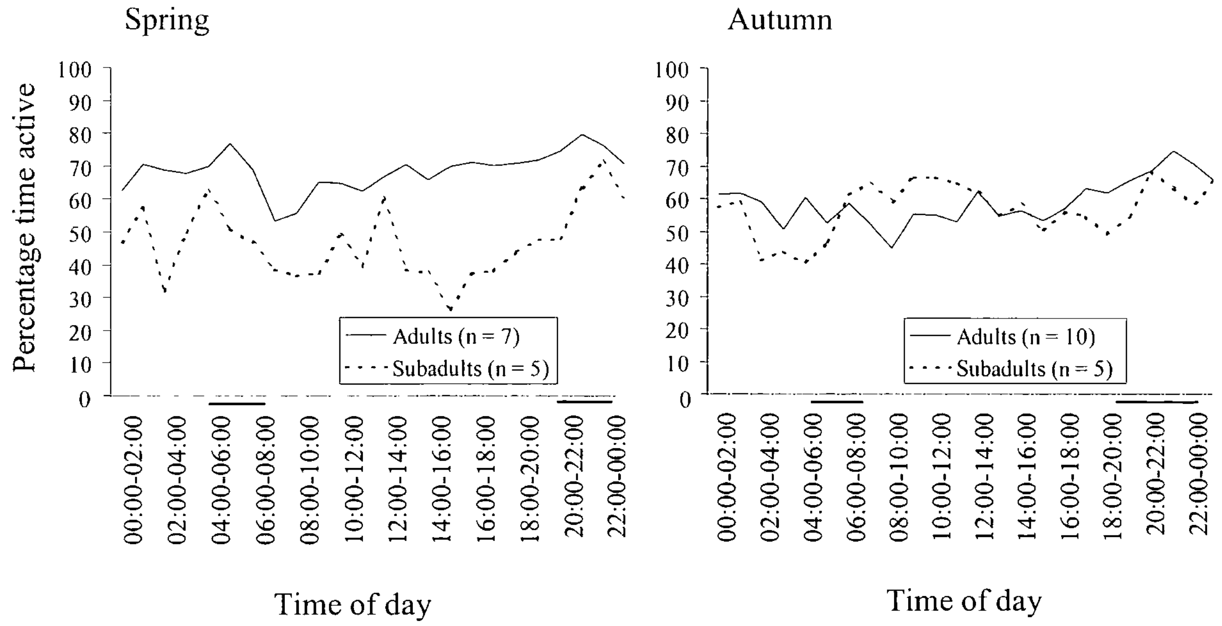


Figure 5.3.4 Daily patterns of activity for adult and subadult güiña. Values are mean percentage of activity data recorded in an active state. The seasonal ranges of dusk and dawn are underlined on the 24-hour abscissa.



5.3.2 Distances travelled and movement rates

5.3.2.1 Net daily movement

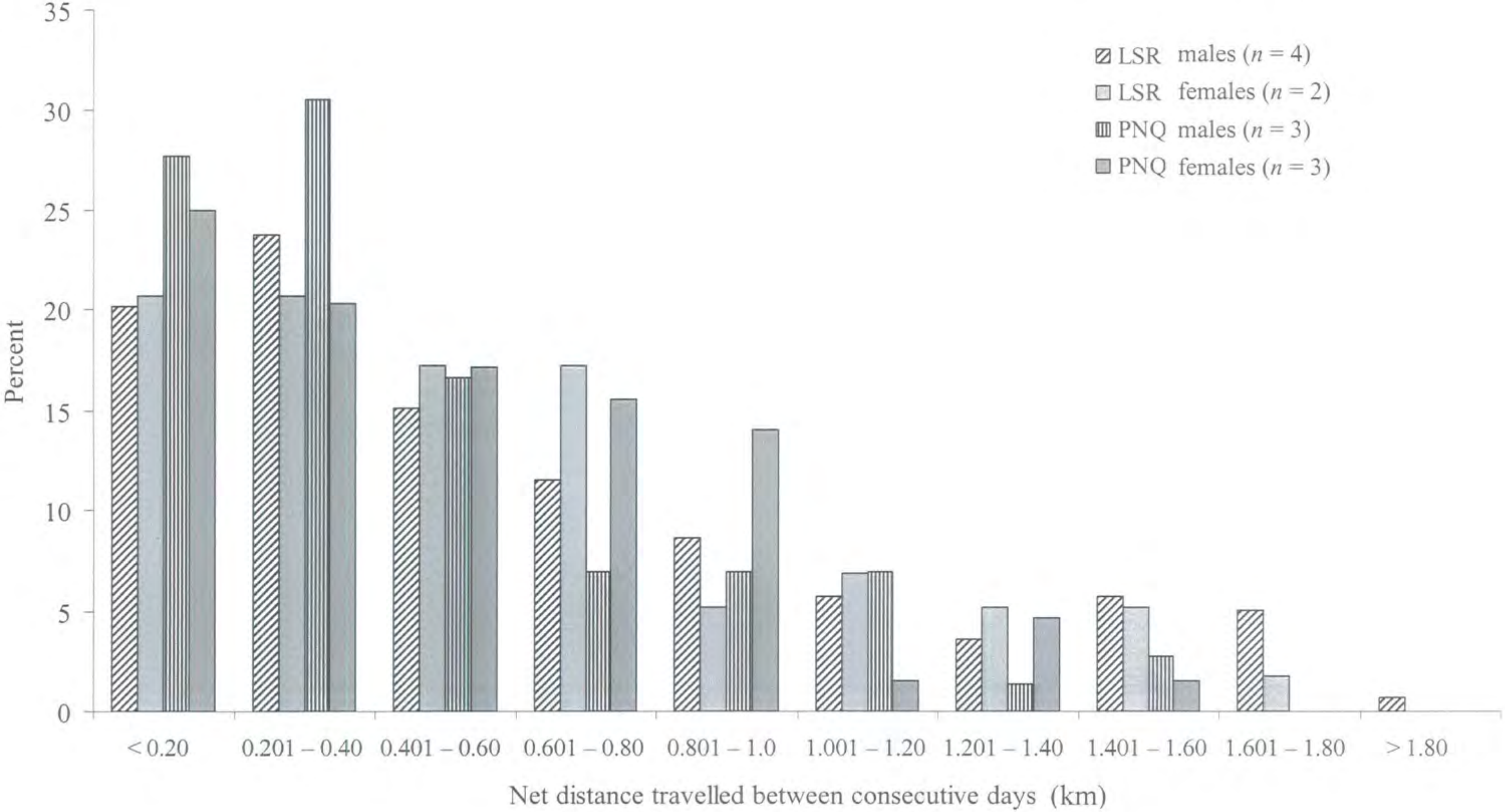
Radiocollared güiña moved straight-line distances of between 0.01 and 1.83 km between the first location fixes recorded on consecutive days (Table 5.3.2, Figure 5.3.5). The mean net daily movement was 0.56 km (± 0.03 km SE), equivalent to approximately 30% of maximum home range widths. 82% of net daily movements made by male güiña and 87% of those made by females were less than 1 km distance.

Net distances travelled between consecutive days were unaffected by sex ($F_{1,10} = 0.635$, $P > 0.05$) and age-class ($F_{1,10} = 1.386$, $P > 0.05$). There was, however, a significant interaction of site and season ($F_{1,19} = 11.044$, $P = 0.004$): radiotracked güiña from the PNLSR population moved further between consecutive days during autumn than during spring; the opposite was true at PNQ, where animals moved greater net daily distances during spring.

Table 5.3.2 Straight-line distance (km) travelled between consecutive day locations.

Site	Age/sex category	No. of consecutive day locations	Mean distance ± SE (km)	Maximum distance (km)	Frequency distribution (%)		
					< 0.50 km	0.50 to 1.0 km	≥1.0 km
PNLSR	Adult males	20	0.80 ± 0.13	1.67	35.00	40.00	25.00
	Subadult males	119	0.58 ± 0.04	1.83	18.49	53.78	27.73
	Adult females	58	0.59 ± 0.06	1.66	18.96	48.28	32.76
	Subadult females	-	-				
	All males	139	0.62 ± 0.21		20.86	51.80	27.34
	All females	58	0.59 ± 0.06		18.96	48.28	32.76
	All animals	197	0.61 ± 0.03		50.76	28.93	20.30
PNQ	Adult males	48	0.47 ± 0.05	1.52	12.50	60.42	27.08
	Subadult males	24	0.38 ± 0.07	1.14	8.34	70.83	20.83
	Adult females	54	0.50 ± 0.05	1.43	5.56	53.70	40.74
	Subadult females	10	0.62 ± 0.13	1.24	20.00	40.00	40.00
	All males	72	0.44 ± 0.04		11.11	63.89	25.00
	All females	64	0.52 ± 0.05		7.81	51.56	40.63
	All animals	136	0.48 ± 0.03		58.09	32.35	9.56
All animals both sites		333	0.56 ± 0.03		53.75	30.33	15.92

Figure 5.3.5 Frequency distribution of distances moved by güiña between consecutive days.



5.3.2.2 Cumulative daily dances travelled

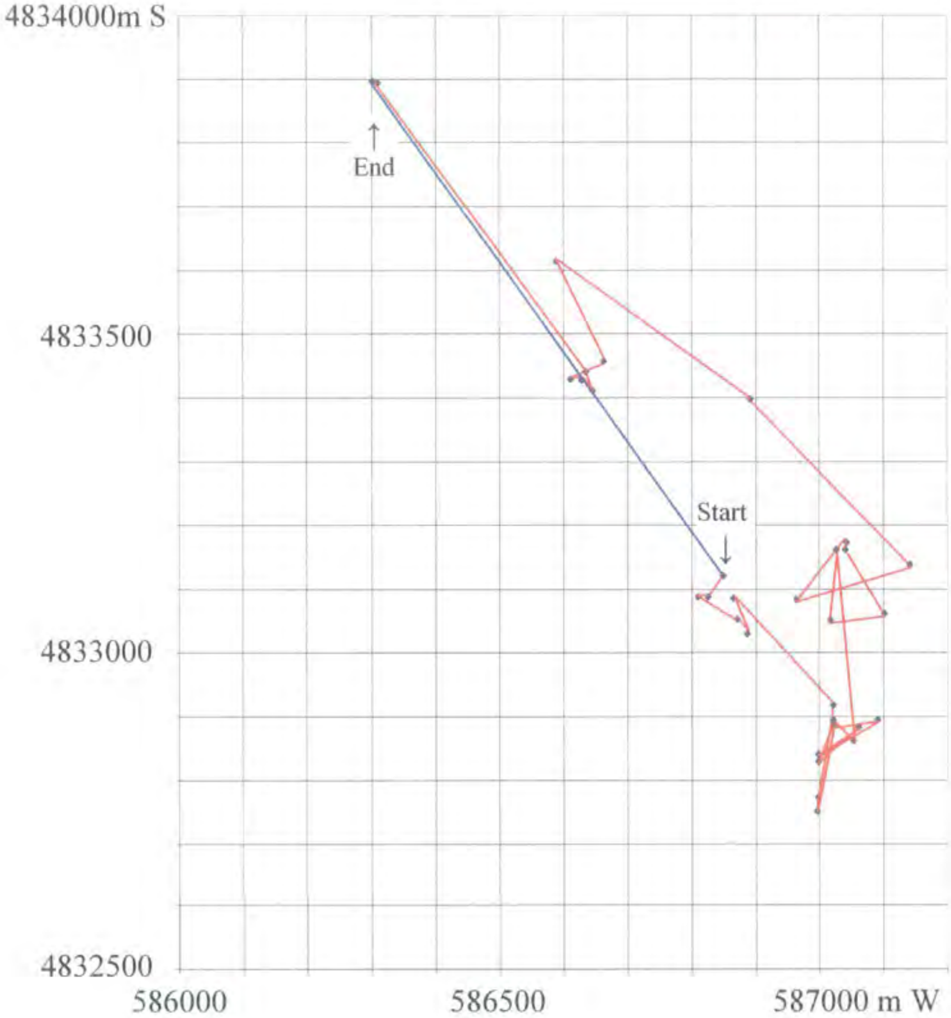
Although the net distances travelled between consecutive days provide an index of daily movement, they do not accurately depict actual distance moved. Total or cumulative daily distances travelled by güiña were therefore described using 71 continuous 24-hour radio-tracking sessions (Table 5.3.3). These data represent the cumulative distances of all linear movements between sequential radiolocations, and have not been corrected for additional non-linear movement between these locations (Bailey, 1974). Cumulative distances were considerably greater than net daily distances (for example see Figure 5.3.6).

Cumulative distances travelled across a 24-hour period varied between 1.21 and 9.00 km. The mean cumulative daily distance travelled (4.34 ± 0.21 km) represents approximately eight times that calculated using only the first radiolocation recorded each day. Güiña tracked in PNLSR travelled greater cumulative distances per day than those in PNQ (PNLSR: 4.91 ± 0.54 km; PNQ: 3.62 ± 0.54 km) this difference was not significant however ($F_{1,10} = 2.930$, $P > 0.05$). Mean daily distance travelled by males (4.24 ± 0.29 km) was similar to that travelled by females (4.48 ± 0.30 km, $F_{1,10} = 0.046$, $P > 0.05$) and there was no difference between the age-classes in cumulative daily distance travelled ($F_{1,10} = 1.273$, $P > 0.05$). Season also had no determinable effect on cumulative daily distance travelled ($F_{1,14} = 0.169$, $P > 0.05$) and there was no significant interaction between any of age, sex, site or season.

Table 5.3.3 Mean linear distance (km ± SE) travelled in 24 hours. Sample sizes are provided in parentheses.

Site	Class	Mean linear distance travelled ± SE (number of 24 hr sessions)		
		Spring	Autumn	All seasons
PNLSR	Adult males	-	6.37 ± 0.42 [6]	6.37 ± 0.42 [6]
	Subadult males	3.56 ± 0.54 [9]	4.78 ± 0.38 [13]	4.28 ± 0.33 [22]
	Adult females	4.77 ± 0.13 [3]	5.09 ± 0.45 [15]	5.04 ± 0.38 [18]
	Subadult females	-	-	-
	All males	3.56 ± 0.54 [9]	5.28 ± 0.35 [19]	4.73 ± 0.37 [28]
	All females	4.77 ± 0.13 [3]	5.09 ± 0.45 [15]	5.04 ± 0.38 [18]
	All animals	3.86 ± 0.43 [12]	5.20 ± 0.27 [34]	4.85 ± 0.25 [46]
PNQ	Adult males	-	2.46 ± 0.32 [5]	2.46 ± 0.32 [5]
	Subadult males	5.04 ± 1.22 [3]	2.44 ± 0.42 [4]	3.55 ± 0.73 [7]
	Adult females	4.30 ± 0.82 [5]	3.65 ± 0.42 [6]	3.95 ± 0.43 [11]
	Subadult females	2.36 ± 0.52 [2]	-	2.36 ± 0.52 [2]
	All males	5.04 ± 1.22 [3]	2.45 ± 0.24 [9]	3.10 ± 0.46 [12]
	All females	3.75 ± 0.68 [7]	3.65 ± 0.42 [6]	3.70 ± 0.40 [13]
	All animals	4.13 ± 0.59 [10]	2.93 ± 0.26 [15]	3.41 ± 0.30 [25]
All animals both sites		3.98 ± 0.35 [22]	4.51 ± 0.25 [49]	4.34 ± 0.21 [71]

Figure 5.3.6 Example of net (blue) and cumulative (red) daily distance travelled. Movement behaviour of animal SJM4 recorded between 00:00 hours 19th March to 00:00 hours 20th March 1998. Net distance travelled = 0.92 km, cumulative distance travelled = 3.68 km.



5.3.2.3 Rate of movement

Mean rate of movement differed significantly between individual güiña ($F_{11, 36} = 4.400$, $P < 0.001$) but there was no consistent influence of sex, age, season, light level (dawn, day, dusk and night) or site on distances travelled per hour (all $P > 0.05$). Fisher's test for least significant difference did however indicate that greater distances were travelled per hour during dusk than at dawn (dusk: 0.22 ± 0.03 km^{-1}; dawn, 0.16 ± 0.03 km^{-1}).

A two-way interaction was noted between the sex and age-class factors ($F_{1, 44} = 7.851$, $P = 0.008$). Adult male güiña travelled greater mean distances per hour than subadult males (adults: 0.28 ± 0.02 m; subadults: 0.17 ± 0.01 km^{-1}, $t_{26} = 4.367$, $P < 0.001$) whereas adult and subadult females moved at similar speeds (adults 0.17 ± 0.02 km^{-1}; subadults: 0.17 ± 0.03 km^{-1}, $t_{18} = 0.158$, $P > 0.05$).

5.4 Discussion

5.4.1 Güiña movement patterns

Radiotracked güiña were relatively mobile and changed their location from one day to the next. Individuals travelled straight-line distances of up to 1.80 km between consecutive days, however approximately 50% of these deslocations were less than 0.40 km and the mean net distance travelled represented no more than one third of maximum home range dimensions. Radio-monitored animals did not visit all areas of their range on a regular basis, and no patrolling of home range boundaries was apparent. This is consistent with the absence of territoriality indicated by extensive home range overlap (Chapter 4). It is in contrast however to observations made by Sanderson *et al.* (2002), who found male güiña regularly visited their home range boundaries. These males expanded their home ranges only when resident males first vacated neighbouring areas, indicating a reluctance to share a common area.

The general pattern of güiña movement within the two study sites was one of relatively slow movement within localised areas, interspersed with comparatively faster and more linearly directed movement between these patches, plus frequent short bouts of inactivity (for example, see Figure 5.3.1). The circuitous activity of güiña within small areas was interpreted as deliberate movement and systematic foraging. This within-patch movement typically occurred at speeds less than 17% of the fastest travel speed recorded during this study (mean speed = 0.19 km^{-1}, range 0.02 to 1.13 km^{-1}). The general felid hunting strategy in open habitats is one of ambush and/or cursorial pursuit (for example see Kruuk and Turner, 1967; Delibes, 1980a; Kruuk, 1986) In contrast, felids that inhabit forest environments often maximise their rate of prey encounter through a strategy of extensive walking and searching (Emmons 1987; 1988; Konecny 1989). Dense vegetation can obscure visual contact with prey species, which are often more widely dispersed than in open habitat, and less likely to be located at predictable sites such as waterholes (Emmons, 1987).

Güiña appeared to adopt a strategy based on walking and searching, but also incorporated a spatial component within this whereby relatively small areas within the available landscape were searched more intensively. This spatial distribution of activity is reminiscent of a Lévy distribution or random walk (Lévy, 1947). This foraging strategy is advantageous when a resource such as prey species is randomly located and can only be detected by a foraging animal when it is in the close vicinity (for example see Viswanathan *et al.*, 1996, Atkinson *et al.*, 2002). If no prey is encountered within the animal's radius of detection it then chooses a direction at random and a distance l_j. As it moves towards the new point it searches for a prey within this radius. If no prey item is detected the animal stops after travelling distance l_j and chooses a new direction and a new distance l_{j+1}. Levandowsky *et al.* (1988) and Schuster and Levandowsky (1996) demonstrated how search strategies based on Lévy random walks are less likely to return to a previously visited site then purely random patterns of movement. Güiña movement patterns described as part of this study may therefore represent a behavioural adaptation to changeable or unpredictable resource availability. Further study of both the spatial and temporal distribution of potential prey items should establish whether prey is indeed a randomly distributed resource for güiña, or if the observed utilisation of 'patches' is a response to, for example, the spatial clumping of prey.

5.4.2 The timing of güiña activity

Radiocollared güiña were active during 57% of radiolocations (3300 of 5786 activity samples). This level of activity is in close agreement with that recorded among güiña on Isla Grande de Chiloé (Iriarte and Sanderson, 1999; 54% activity) and for forest-dwelling ocelot (46%, Crawshaw and Quigley, 1989), jaguar (57%, Rabinowitz and Nottingham, 1986) and the more similarly sized leopard cat (51%, Rabinowitz, 1990; 47%, Grassman, 2000).

Felids in general do not store large amounts of fat, unlike, for example ursids (Herminghuysen *et al.*, 1995; Farley and Robbins, 1995; Hissa *et al.,* 1998). Unless cats are able to hoard prey items, the absence of substantial energy reserves demands that they must hunt regularly to fulfil their energetic requirements. Large potential prey items were considered scarce in each of the two sites, and the small mammals and birds that dominated the diet were unlikely to provide more than a single meal each. Small mammal population densities as high as 100 animals ha^{-1} were recorded during this study (Table 3.3.1), yet despite this apparent abundance, güiña were active for approximately 12 hours each day, and presumed to be hunting for much of this time.

Güiña activity was essentially arrhythmic, though considerable variation was noted both between individuals and by the same individual in different seasons. Overall there were few consistent patterns among age/sex groups, between seasons or between sites to indicate that güiña modified their active behaviour according to any of these factors. Adult animals were significantly more active in spring than during autumn, and were also more active than subadults at this time. Adult males also moved further between consecutive days than subadult males. The increased level of activity observed among adult males during spring possibly resulted from searching behaviour for receptive mates.

The active periods exhibited by felids often reflect those of their prey (Schaller and Crawshaw, 1980; Rabinowitz, 1986; Emmons, 1987). Although predominantly arrhythmic, güiña were more active at dusk than at other times and dusk was also the time of day when the greatest rates of travel were recorded. No dawn or pre-dawn peak in the intensity of güiña activity was determined. This is in contrast to Sanderson *et al.* (2002) who described a slight increase in active behaviour between 06:00 and 08:00.

Although the periodicity of birds and small mammal species was not assessed during this study, the slight increase in güiña activity at dusk may coincide with the heightened activity and/or vulnerability of prey species. Studies conducted both in the field and under laboratory conditions indicate that the majority of small mammal species of the Northern Patagonian rainforests are predominantly nocturnal and/or crepuscular (Murúa *et al.*, 1978; Feito and Ortega, 1981; Iriarte *et al.*, 1989). *A. olivaceus, A. longipilis* and *A. micropus* for example, all display heightened activity at dusk, whereas *O. longicaudatus* is mostly active between 22:00 and 06:00 hrs. Although no comparable activity data were available for the resident avian species, Rozzi *et al.* (1996b) noted that within Chilean rainforests both the number of individuals and number of bird species active in the morning is generally higher than at midday. Furthermore, Lima (1988) suggested that vigilance levels among dark-eyed juncos (*Junco hyemalis*) were greatest when these birds foraged in dim light, due to the potential difficulty of detecting predators.

The lack of any pronounced seasonal variability in activity or distance travelled is most likely attributable to the relatively stable environment within the two study areas throughout the study period. Because data were only collected during spring, summer and autumn, activity during periods of extreme weather, as are common at this latitude during late winter, could not be included.

In southern Chile, mean daily temperatures frequently drop to below 4°C during winter, and may reach -15°C at night (Conama, 1999). This climatic seasonality influences spatial and temporal availability of prey species (Meserve, 1981), and is expected to increase the energetic demands for thermoregulation for the güiña. As foraging time is inversely proportional to prey abundance, güiña should therefore become more active when food availability is low, yet where possible restrict their activity to the warmest part of the day to minimise thermoregulatory costs (Chappell, 1980). This was indeed the case for Geoffroy's cats in Torres del Paine National Park in the extreme south of mainland Chile. Johnson and Franklin (1991) found radiotracked individuals to be primarily nocturnal, but became less nocturnal and commenced activity earlier in the day in winter months.

Female güiña were active more often than male güiña (percentage of activity data recorded in the active state: females 60.8%; males 55.3%). This difference was not significant but is similar to observations made of the Isla Grande population (Iriarte and Sanderson, 1999), where a significantly higher intensity of activity was recorded among female güiña than among males (females 64.1%; males 46.8%). Adult male güiña were approximately 25% larger than adult females, and as a result might be expected to have allometrically higher energetic requirements (McNab, 1989; 2000). That females were slightly more active than males was therefore unexpected, but may be a result of the energetic demands of reproduction and weaning. Animal SAF7 for example was twice observed with dependent kittens during the period of radio-tracking (spring 1997 and spring 1998). Alternatively, the smaller body size of female güiña may necessitate that they forage for longer, to meet the relatively greater costs of thermoregulation.

Summary

Güiña active behaviour was largely arrhythmic, except for a slight increase in frequency and speed of movement at dawn. Radio-collared individuals were active during approximately 57% of location fixes, and most bouts of activity and inactivity were of relatively short duration (< 3 hours). Although individuals travelled up to 9 km during a 24 hour period, both sexes were regularly relocated less than 1 km distance from location fixes of the preceding day. An apparent increase in the frequency of active behaviour among adult males in spring was attributed to mate searching behaviour.

Chapter 6
Habitat Utilisation and Associations

6.1 Introduction

6.1.1 Distributional behaviour

Spatial and temporal patterns of movement connect an animal to its environment as it travels in search of key resources. Habitat selection occurs when components of this landscape are used in proportions greater than their relative availability, and affects the fitness of individuals by influencing their foraging opportunities and exposure to predators and competitors (Wywialowski, 1987; Rangeley and Kramer, 1998; Kunkel *et al.*, 2002; Mauritzen *et al.*, 2003). Animal populations therefore do not necessarily occupy their entire potential range, even though dispersal into unoccupied areas is possible. Patterns of resource quality and availability as perceived by individuals consequently exert considerable influence on the spatial distribution of populations, and ultimately, species (Elton, 1927; Brown, 1984; Nix and Gillison, 1985; Harris *et al.*, 1990; Krebs, 1994).

Trends in habitat utilisation potentially provide information relating to population resilience in response to environmental change. Species that are closely associated with habitat features that provide specific requirements, such as accessibility to prey or shelter are more reliant upon the size, number, and spatial distribution of these features than animals with more generalist requirements (Wiens, 1996). The management implications of habitat selectivity are numerous (Saunders *et al.*, 1991; Kaiser, 1997); for example, the disciplines of wildlife management and conservation biology increasingly apply habitat selection theory to the description of both vulnerable and pest species requirements (Caughley and Sinclair, 1994; Noss and Csuti, 1997; Pulliam and Dunning, 1997). Habitat preferences can be used to predict population densities, highlight priority areas or anticipate species' responses to alternative management strategies. Indeed, predicted distributions based on habitat associations can provide a much higher level of resolution than the often incomplete distribution maps from which they are derived (Scott *et al.*, 1993; Csuti, 1996).

6.1.2 Habitat selection by felids

Many felids display a degree of plasticity in their utilisation of habitat (for example bobcat (Bailey, 1974; Fuller *et al.*, 1985; Koehler and Hornocker, 1989), and ocelot (Schaller *et al.*, 1984; Ludlow and Sunquist, 1987; Emmons, 1988; Konecny, 1989). Others, such as the sand cat (*Felis margarita*) appear to be strongly associated with and dependent upon specific habitat types (Abbadi, 1992; Nowell and Jackson, 1996). Consistent among quantitative studies however, is a preference for forested habitat or other dense vegetation (ocelot: Ludlow and Sunquist, 1987; Konecny, 1989; jaguar: Crawshaw and Quigley, 1991; Eurasian wildcat: Liberek, 1996; clouded leopard (*Neofelis nebulosa*): Austin and Tewes, 1999). Even among those species adapted for open areas, for example the caracal (*Caracal caracal*) and cheetah, dense vegetation is regularly utilised for hunting, resting, and travel (Weisbein and Mendelson, 1990; Purchase and du Toit, 2000).

Güiña are widely considered to be associated closely with the *Nothofagus* dominated temperate forests of southern Chile and Argentina (Miller and Rottmann, 1976; Melquist, 1984; Nowell and Jackson, 1996) and their geographic range closely maps the historic distribution of these forests. This species is also known however to utilise certain modified environments that have replaced native forest cover, including eucalyptus plantations (*Eucalyptus globule* and *E. nitens*), secondary forest and semi-open country, as well as habitat bordering cultivated areas (Greer, 1965; Udvardy, 1975; Melquist, 1984). Sanderson *et al.* (2002) found that güiña from Isla Grande de Chiloé incorporated isolated forest fragments; agricultural fields, pastures and other cleared areas within their home ranges, but noted that these habitats were rarely visited. Isla Grande güiña instead favoured more contiguous areas of forest, including steep coastal forest, and travelled through modified habitat using ravine systems and thick vegetation corridors as cover. These observations suggest a lack of specificity with regard to the utilisation of habitat types by güiña, although key components of landscape structure, such as the presence of trees and shrubs, appear critical.

6.1.3 Statistical examination of habitat preferences

The Chi-square goodness-of-fit test is the most widely implemented among the analytical techniques suitable for the examination of habitat utilisation. This test contrasts observed frequencies of habitat utilisation with expected levels based on the relative availability of each habitat (White and Garrott, 1990) and highlights significant differences (i.e. non-random habitat utilisation). Chi-square analysis does not, however, identify which habitats are avoided or preferred, nor can it be used to contrast the relative importance of each category, as their proportional use is not independent (Aebischer *et al.*, 1993). The proportions that describe habitat availability and use necessarily sum to one (the unit-sum constraint), consequently, any preference for one habitat category leads to an apparent avoidance of another (Aebischer *et al.*, 1993; Otis and White, 1999). Chi-square analysis is further undermined when serially correlated radiolocations are treated as independent sample points (Swihart and Slade, 1985, and see discussions in Aebischer *et al.*, 1993; Alldredge and Ratti, 1992; Alldredge *et al.*, 1998), violating the statistical assumptions of independence that underlie the test.

As an alternative to Chi-square, Johnson (1980) advocated the concept of a hierarchical order of selection processes that ranks both the utilisation and availability of each habitat, and then uses the difference between these ranks as a measure of preference. However this method does not identify habitat selection by individual animals. Each animal is instead used as a single observation in a population level test for relative habitat preferences.

To avoid many pitfalls inherent in alternative methodologies, Aebischer and Robertson (1992) and Aebischer *et al.* (1993) advocate the application of compositional analysis (Aitchison, 1986) to analyses of resource (for example habitat) selection. This non-parametric technique uses log-ratio analyses of proportional data to rank habitats according to relative utilisation:

$$\ln(x_{ij}/x_{ik}) - \ln(x_{hj}/x_{hk}) \qquad \text{Equation 6.1.1}$$

where x_{ij}, x_{ik}, are proportions of habitat use and x_{hj}, x_{hk}, are proportions of available habitat. Compositional analysis uses radio-tagged animals as the sampling unit rather than individual radiolocations, and considers all habitat types simultaneously. Problems such as autocorrelation among radiolocations and statistical problems arising from non-independence of category representations within a defined area are thus avoided (Aebischer and Robertson, 1992; Aebischer *et al.*, 1993). This approach also facilitates separation of within-animal and between-animal variation, and permits comparison between group means and other multiple-comparison statistical tests that assess habitat utilisation by age and sex across different spatial scales (Scheiner, 1993).

6.1.4 Scale of resolution

The physical and biological processes that determine resource distribution and availability can be considered as hierarchically scaled, both in space and time. Climate and competition for example operate at the level of individual animals through to the geographic distribution of species. An animal's utilisation of available habitat can therefore also be envisaged as a hierarchical process (Wiens, 1973; Johnson, 1980; Morris, 1987, 1992; Porter and Church, 1987; Orians and Wittenberger, 1991; Henschel and Lubin, 1997). Different forms of habitat selection occur at different scales, with animals adopting relevant proximal stimuli for decision-making from a variety of environmental cues at each scale. Dispersing predators, for example, might consider landscape patterns and terrain to be of primary importance when selecting home ranges, but assign greater significance to shelter or feeding sites when choosing among available habitat patches within such a range (for example, see Powell, 1994).

Miquele *et al.* (1999) considered, after Johnson (1980) that habitat selection by the Amur tiger (*P. t. altaica*) occurs at three spatial scales. First-order selection operates at the landscape scale. It describes the range and relative occurrence of habitats within a species' physical or geographic range, i.e. the key habitats that define species distribution. Within this distribution, selection at second-order resolution identifies those parameters that drive home range selection by contrasting home range composition by habitat type to the 'availability' of each within the more general landscape. Habitat selection at the third-order details the relative utilisation of habitats in relation to their proportional representation within individual home ranges. A particular habitat may not be important in terms of its proportion of a home range for example (second-order selection), but might be used more intensively than other categories present within the home range. At this local scale, selection is essentially at the level of habitat choice or "preference/avoidance" (Neu *et al.*, 1974; Leuthold, 1977) and should reflect the critical needs of the individual. Incorporation of two or more of these spatial scales into analyses of habitat selection enables consideration of both changes in resolution and the different constraints that act on populations and individuals at each scale.

Aebischer *et al.* (1993) reiterated the advantages of a hierarchical method such as that of Johnson (1980) and stressed its applicability to compositional analysis. Hierarchical compositional analysis has been applied to habitat selection studies for a diverse array of organisms and ecological questions. Mace *et al.* (1996) described the second- and third-order habitat selection processes operating on grizzly bears in the Swan Mountains, Montana. In their analyses of home range size and correlative habitat use by roe deer (*Capreolus capreolus*), Tufto *et al.* (1996) described second- and third-order selection patterns and Mills and Gorman (1997) and Sunde *et al.* (2000) recognised these two orders in their research on the distribution and habitat utilisation by African wild dogs (*Lycaon pictus*) and Eurasian lynx respectively. Miquele *et al.* (1999) examined the spatial distribution of Amur tigers and prey at first-, second-, and third-order scales of resolution.

6.1.5 Predictive spatial distribution models

Whereas generalised species distribution maps can often provide a useful starting point for the consideration of large-scale distribution patterns, maps at this scale provide little information about causal factors underpinning why species occur where they do. A more realistic approach, and one which is becoming increasingly recognised as an important element of conservation biology and management planning, is to assess landscapes from a species-centred perspective using survey data (Franklin, 1995; Austin, 1998; 2002; Guisan and Zimmermann, 2000; Elith and Burgman, 2002; Scott *et al.*, 2002). To this end, several multivariate statistical approaches have been developed that, when employed in conjunction with geographic information systems (GIS) are capable of predicting species distributions from the spatial arrangement of selected and non-selected habitat categories (Pereira and Itami, 1991; Fitzgerald and Lees, 1992; Aspinall and Veitch, 1993; Franklin *et al.*, 2000; Guisan and Zimmermann, 2000). Management strategies for focal endangered species (Sanchez-Zapata and Calvo, 1999; Palma *et al.*, 1999), species re-introductions (Mattson, 1996; Schadt *et al.*, 2002) and ecosystem restoration (Mladenoff *et al.*, 1997) increasingly refer to spatially explicit habitat-suitability models. These are particularly useful because areas lacking survey data for the focal species can be incorporated within a GIS output.

Among the most frequently employed of the spatial modelling approaches available are generalised linear models (GLMs) and generalised additive models (GAMs) (Ferrier and Pearce, 1996; Elith, 2000). These statistical analyses typically utilise survey data in the form of presence/absence data for focal species within a set of sampled locations (Guisan and Zimmermann, 2000). GLMs represent a generalisation of multiple regression analysis. They have a binomial distribution and are capable of fitting polynomials of higher degree than linear to describe the dependent variable (presence/absence of the species) in terms of a sum of weighted ecogeographical predictors. The weighting of each predictor is adjusted in order to generate the best fit between the model and a calibration data set (Nicholls, 1989). GAM models, in contrast, are a non-parametric interpretation of GLM models and fit predictor variables independently by smooth functions rather than by assumed linear or quadratic relationships (Hastie and Tibshirani, 1986).

Both GLMs and GAMs require that survey data for focal species be representative of the study population (Guisan and Zimmermann, 2000). However, whilst presence data (of individuals, tracks or droppings for example) may be definitely established by direct observation, absence data are notoriously difficult to obtain accurately (Leclercq, 1981).

Species distributions are susceptible to erroneous or 'false' absences when i) focal species are not detected despite being present within a study area (McArdle, 1990; Solow, 1993; Weckerly and Ricca, 2000), or ii) when species are absent from localities with suitable available habitat for reasons unrelated to habitat, for example persecution (Ménoni, 1994).

6.1.6 Ecological niche factor analysis

The compilation of reliable presence/absence data sets frequently requires that expensive, time consuming and/or labour intensive field surveys are undertaken. Systematically collected data are hence often of limited availability (Austin *et al.*, 1994; Ferrier and Watson, 1997; Franklin, 1998). In situations where absence data are not available, unreliable or meaningless (for example, in the case of invasive species with expanding distributions), Hirzel *et al.* (2002a) recommended the application of Ecological Niche Factor Analysis (ENFA). Based on Hutchinson's (1957) ecological niche theory, ENFA creates habitat suitability maps that indirectly predict the potential spatial distribution of species, yet does not require absence data as input. In accordance with Hutchison (1957), ecological niche is referred to here as the subset of the multidimensional space of ecological variables where the focal species has a reasonable probability to occur and maintain a viable population.

ENFA characterises each grid cell of a raster map by a series of *N* ecogeographical variables (EGV) (for example, habitat class, topographical or climatic data). From these, the factor analysis extracts *N* independent axes representing linear combinations of the original ecogeographical variables. The first to be extracted is the marginality factor (*M*), a measure of the ecological distance and direction by which the mean of the species distribution (m_S) differs from the mean of the global distribution (m_G), i.e. that within the wider reference area (see Figure 6.1.1).

$$M = \frac{|m_S - m_G|}{1.96 s_G} \qquad \text{Equation 6.1.2}$$

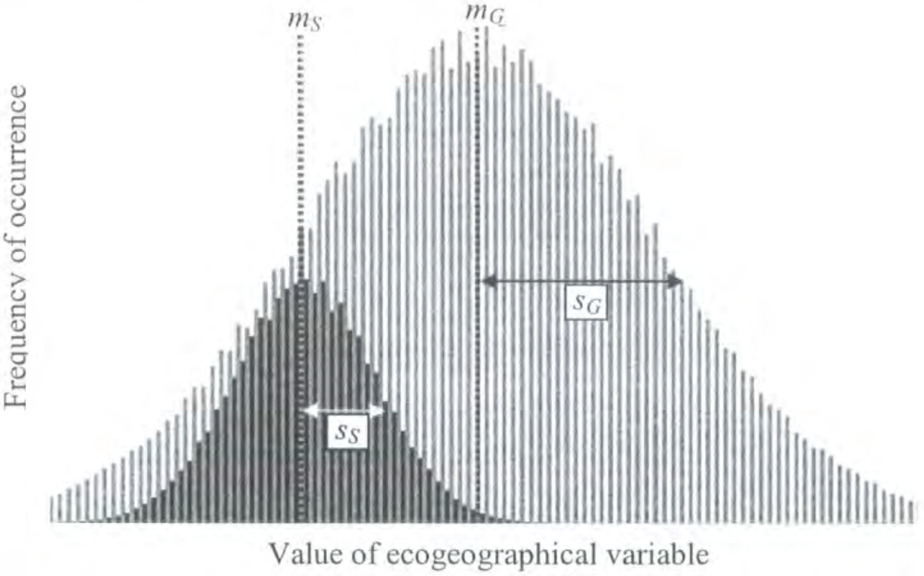
where s_G is the standard deviation of the global distribution.

ENFA utilises a multivariate extension of Equation 6.1.2 in order to describe the global marginality of a species:

$$M = \frac{\sqrt{\sum_{i=1}^{V} m_i^2}}{1.96} \qquad \text{Equation 6.1.3}$$

where m_i = the coefficient of the marginality of the focal species on ecogeographical variable *i*, and *V* = the number of eigenvectors extracted.

Figure 6.1.1 A graphical representation of marginality and specialisation factors. From Hirzel *et al.,* 2002a.



The distribution of a focal species on any ecogeographical variable (black bars) may differ from that of the whole set of cells within a reference area (gray bars) with respect to its mean ($m_S \neq m_G$), thus allowing marginality to be defined. A species' distribution on any ecogeographical variable may also differ to that of the reference area with respect to standard deviation ($s_S \neq s_G$), allowing specialisation to be defined.

The global marginality factor is most often a value between zero and one, but can be greater than one (Hirzel *et al.*, 2002a). High values indicate that a focal species lives in a very particular habitat in relation to the reference area. For each ecogeographical variable a coefficient relating to the marginality factor indicates the degree of correlation between that variable and the marginality factor. The higher the absolute marginality value of a coefficient, the further the species departs from the mean available habitat regarding the corresponding variable, and the more this variable contributes to the global marginality. A positive value indicates that the focal species has a preference for higher-than-mean values of the variable (with respect to the entire area), whilst negative coefficients indicate a preference for values that are lower than the mean of that variable over the entire study area.

Axes extracted subsequently are uncorrelated and describe how specialised the focal species is by reference to the available range of habitat in the study area. Eigenvalues computed for each ecogeographical variable express the ratio of the ecological variance of available habitat within the wider reference area to that of the observed species distribution on that axis, i.e. the amount of specialisation that factor accounts for (see Figure 6.1.1). The higher the absolute variable, the more restricted is the ecological tolerance and therefore range of the focal species on the corresponding variable. Only absolute values are of concern here, hence the signs of the values are arbitrary.

Each successive eigenvalue represents a decreasing amount of information specialisation and explained variance, from the second factor to the last. Because the majority of the information is accounted for by the first few factors the remainder of the analyses are typically restricted to those that explain the largest part of the variance. Only those eigenvalues shown to be significant, for example by comparison with MacArthur's Broken-stick distribution (Hirzel *et al.*, 2002a), are considered useful to the computation of habitat suitability and are retained.

The global specialisation coefficient (S) is mathematically defined as the ratio between the standard deviations of the species distribution (s_S) and global distribution (s_G).

$$S = \frac{s_S}{s_G} \qquad \text{Equation 6.1.4}$$

This coefficient varies from one to infinity.

The species niche as described by the derived eigenvalues can be used to construct habitat-suitability maps for the focal species. For maps of a raster format an overall suitability index is computed for each cell of the original map from a combination of its values for each of the independent axes. Suitability values are normalised in such a way that the resulting suitability index ranges from zero to 100% (Hirzel *et al.*, 2002a). This quantitative map may then be translated into a geographic representation of the reference area.

6.1.7 Chapter Aims

Habitat selection has been studied in more detail for carnivores than for most other groups, yet it remains a poorly understood process, particularly at the scale of individual home ranges. Minimal information is available at the present time on which to base an assessment of the current distribution range of the güiña. Nowell and Jackson (1996) had only ten locations from which to construct their estimate (see Figure 1.1.1), including a number of unsubstantiated sightings (Honacki *et al.*, 1982). Housse (1953), Cabrera and Yeppes (1960), Greer (1965), Miller and Rottmann (1976) and Sanderson *et al.* (2002) each describe some basic aspects of güiña ecology, but do not address the relative habitat preferences or requirements of this cat in any detail. A more comprehensive understanding of the habitat requirements of this species and of the probable effects of, for example, future habitat alteration, requires the quantitative assessment of selected and avoided habitat attributes, ideally across multiple spatial scales.

This chapter describes güiña habitat utilisation within a naturally fragmented habitat mosaic (PNLSR) and also a largely contiguous area of primary forest (PNQ). The study aims were to assess the utilisation of habitat by güiña in relation to habitat availability using two very different approaches: compositional analysis and Ecological Niche Factor Analysis. Compositional analysis was applied at both the second- and third-order scales of spatial resolution using radio-telemetry data and the habitat map created in Chapter 2. The ENFA was applied utilising the same habitat map and radiotelemetry data pooled for all individuals to further investigate the link between the güiña and its preferred habitat. Using the ENFA model I have attempted to represent the habitat of southern Chile from a species-centred perspective (Wiens, 1989; With, 1994). From the resulting habitat-suitability map the potential distribution and approximate population size of the güiña may be inferred.

The results of the two investigative approaches are discussed within the context of the availability of preferred habitat, the spatial arrangement of such habitat and the presence of potential barriers to güiña movement between these suitable areas.

6.2 Methods

6.2.1 Application of compositional analysis to güiña habitat utilisation data

6.2.1.1 Habitat availability

Habitat analyses were conducted for the same twelve güiña and 22 seasonal ranges described in Chapter 4. Nine habitat types and land cover categories were defined in Chapter 2: forest, forest-thicket, thicket, scrub, rock, scrub-thicket, open, saltmarsh and forested cliffs. Based on these, the availability of each category inside individual home ranges and the two study sites was approximated from proportional habitat coverages, calculated using the raster-based habitat map constructed in Chapter 2 (Figure 2.1.1) and the habitat analysis function of RANGES V. Field surveys determined no real difference between the forest and forested cliff vegetation categories. The distinction of two forest classes by the Idrisi software was attributed to shade cast by mountain slopes, affecting surface reflectance, and hence lower brightness values in the LANDSAT imagery. Consequently, these categories were pooled. The study site boundaries were defined by the minimum convex polygon that encompassed all radiolocations fixes recorded within each (Quinn, 1997). Total and seasonal home ranges were delineated using 95% fixed kernel isopleths and location fixes where inter-fix intervals were a minimum of five hours.

6.2.1.2 Habitat utilisation

Habitat utilisation was examined at two levels: the habitat composition inside 95% fixed kernel isopleth home ranges compared to availability within the appropriate study area (second-order selection), and habitat use within individual home ranges compared to habitat availability within those ranges (third-order selection). Because statistical analyses of habitat utilisation assume that habitat type is assigned correctly, location fixes were buffered to account for error in assigning each to a particular habitat category, and to ensure that analyses operated at a scale appropriate to the degree of relocation precision (Rettie and McLoughlin, 1999). For analysis at the third-order I assumed, therefore, that an animal used all classes within a 50 m radius of each location (a distance equal to the mean triangulation error) in proportion to the area of that class within the circle (Arthur *et al.*, 1996; Cooper and Millspaugh, 1999; Gros and Rejmánek, 1999).

6.2.1.3 Hierarchical habitat utilisation by güiña

Habitat selection was evaluated using compositional analysis (Aitchison, 1986) at both levels of resolution. Habitat availability and proportional utilisation by each animal was first converted to log-transformed ratios using the scrub habitat category as the denominator k.

$$Y_{ij} = \ln(x_{ij}/x_{ik}) \; (i = 1,\ldots, n; j = 1,\ldots, 7; j \neq k) \qquad \text{Equation 6.2.1}$$

where x_{ij} describes an individual i's proportional use of the j-th of the eight habitat types and n = number of individual animals. The (n-1)-dimensional point Y_{hj} similarly calculated from log-ratios from the available habitat composition is then subtracted from the point Y_{ij}. If habitat utilisation is random, then $Y_{ij} \equiv Y_{hj}$ or difference $d \equiv 0$ (Aebischer and Robertson, 1992). The results of such analyses are independent of the arbitrary choice of scrub habitat as the denominator in the log-ratio transformation (Aitchison, 1986).

Compositional analysis assumes that the habitat components derived for different animals are equally accurate, however this assumption may be invalid when the number of location fixes differ greatly between animals. I therefore weighted the log-ratio differences by the square root of the relevant sample size to adjust for inequalities between individual animals (Aebischer *et al.*, 1993). Because the minimum number of individuals for statistical inference from compositional analyses is six (Aebischer *et al.*, 1993), the sexes were pooled. Where a habitat was available but not used it was assigned a value of 0.001% to avoid division by zero. This substitution is necessary and does not affect the outcome of the category rankings (Aebischer *et al.*, 1993).

For each individual the log-ratio differences between used and available habitat form a single row of a matrix with (number of habitats – 1) rows and columns. To test the null hypothesis that utilisation is random over all habitats simultaneously (i.e. the difference matrix equates to zero), a residual matrix was also constructed. The significance of the original matrix of differences was then examined using Wilk's lambda (Λ), where

$$\Lambda = \frac{|R_1|}{|R_2|} \qquad \text{Equation 6.2.2}$$

and where R_2 is the original matrix of raw sums of squares and cross-products, and R_1 is the matrix of mean corrected sums of squares and cross-products. The value Λ was then transformed, following the procedure proposed by Aebischer *et al.* (1993), into the test statistic: $-n \ln \Lambda$. This approximates a Chi-square distribution with $k - 1$ degrees of freedom, where n is the number of individuals in the sample and k is the number of habitat categories considered.

When habitat utilisation was non-random ($P < 0.05$), mean pair-wise differences between matching log-ratios were calculated for each habitat combination to identify where utilisation deviated from random. The scrub category was again used as the denominator. For each study site and spatial scale, the ratio of mean log-ratio difference value to standard error described a t value (with n-1 degrees of freedom) that measured departure from random (signified by a t value of zero). Using the D^{th} element as the denominator a value of $d_i > 0$ would therefore imply that relative to habitat D, habitat i is used more than expected, likewise the utilisation of habitat D relative to habitat i is less than expected. If $d_i > 0$ for all $i = 1, \ldots, D\text{-}1$, then the use of habitat D relative to all other categories is less than expected, i.e., habitat D is the relatively least used habitat type. Conversely, $d_i < 0$ for all i would imply that habitat D was the relatively most used habitat. The available and utilised habitat compositions at the second-order were transformed to log-ratios (y_0 and y) for both sites and populations using the proportion of scrub as the denominator. The difference $d = y - y_0$ was then calculated and tested against zero by constructing a matrix of mean-corrected sums of squares and cross-products R_1 and a residual matrix R_2 comprised of the raw sums of squares and cross-products calculated from d.

For ease of interpretation, mean log-ratio differences were replaced by their sign (+ or −). A row of positives indicated that the particular habitat type was most preferred (highest rank), whilst a row of negatives indicated it was least preferred and therefore ranked lowest. Signs were tripled if the calculated t value exceeded the critical value for the appropriate degrees freedom, signifying a significant departure from zero. Each habitat was then ranked in order of preference at the second and third-order of resolution for each site according to relative utilisation (Aebischer *et al.*, 1993). Mean pairwise log-ratio differences were compared for the two study sites using a two-sided t-test. Because the minimum number of individuals for statistical inferences from compositional analysis is six (Aebischer *et al.*, 1993), the sexes and age classes were pooled for analyses of total home range.

Habitat diversity within each study site and range was examined using Levin's standardised index B_i (see Equation 3.2.2). The influence of age, sex, site and season on habitat selection at the second- and third-orders was examined using a series of univariate GLMs. The response variable was the log-ratio differences calculated for each animal and habitat type transformed by the square root of arcsine, and seasons were blocked by year.

6.2.2 Application of ecological niche factor analysis to güiña habitat utilisation data

Sample sizes (number of güiña radiotracked) were small within each site, and were the minimum size necessary for compositional analysis (minimum number = 6, Aebischer *et al.*, 1993). Because small sample sizes can prevent the drawing of firm conclusions a second analytical approach was sought to provide an alternative and independent analysis of güiña habitat utilisation. Since absence data were not collected as part of this study, ecological niche factor analysis was chosen as the most suitable analysis.

6.2.2.1 Formatting procedures for the ENFA model input data

The reference area classified according to habitat type in Chapter 2 corresponds to an area of 105,000 km^2 area, or approximately 117 million 30 × 30 m cells (Figure 2.2.1). Three of the eleven habitat categories within this coverage (snow, water and saltmarsh) were considered irrelevant for the assessment of güiña habitat utilisation and were hence excluded from subsequent analyses. The forest and forest-slope categories were merged into a single category (forest). Boolean images were constructed for each of the remaining categories using BioMapper (version 2.1, Hirzel *et al.*, 2002b), a Microsoft Windows program that can use Idrisi format images as input and output. These variables were then transformed into quantitative ones by calculating the proportion of cells from each of the seven variables within a circle of 540 m radius (an area corresponding to the mean güiña home range area (92 ha) (FK95 values), as identified in Chapter 4) centred on each cell in turn. The complete data set for the overall area thus comprised seven overlapping layers in raster format, referenced to the UTM-18 projection of the South American Datum 1969 co-ordinate system, one for each of the ecogeographical variables.

The field sampling procedures for güiña presence data are described in Chapter 2. This spatially referenced data set was rasterised using the Idrisi32 software then transformed using the CONVERT function of the BioMapper software into a boolean map. This process assigned each cell of the reference area a value of one if güiña presence data was recorded on that cell during the field research period (presence cell), or zero to signify an absence of presence data.

6.2.2.2 Ecological Niche Factor Analysis, the ENFA model

One marginality factor and six specialisation factors were computed within BioMapper, each representing a linear correlation of the contributing ecogeographical variables. The first two factors explained the majority of total variance by comparison with MacArthur's Broken-stick distribution and were retained within the ENFA (Hirzel *et al.*, 2002a), from which a habitat suitability map was constructed. Because false positives (where suitable habitat is predicted for areas for which there is no species presence data) provide no indication about the quality of the model, standard estimators such as the kappa index (Monserud and Leemans, 1992) which attribute the same importance to false positives and false negatives (unsuitable habitat is predicted in areas where the focal species is present), cannot be used in model validation. This model was therefore validated using Jack-knife cross-validation (Fielding and Bell, 1997) whereby the presence data were partitioned into ten subsets of equal sizes. The habitat-suitability map was calibrated using nine of these subsets; the tenth was used to evaluate the result. This process was replicated ten times using each subset in turn for validation, from which it was possible to compute mean and standard deviation values for the accuracy assessment.

6.3 Results

6.3.1 Compositional analyses of habitat utilisation

6.3.1.1 Habitat utilisation at the second-order

The two study sites were each defined by the minimum convex polygon that encompassed all location fixes obtained from all güiña radiotracked within that site. 3825 location fixes recorded in PNLSR corresponded to an area of 567 ha, with maximum dimensions of approximately 2.4 km by 4.2 km. In PNQ, 2033 location points corresponded to an area of 472 ha with a maximum range span of 3.8 km. The major habitat types and their relative representation within each study area and individual ranges are displayed in Table 6.3.1, and Figures 6.3.1 to 6.3.4.

Table 6.3.1 Habitat composition within the PNLSR and PNQ study sites and inside güiña home ranges. Individual ranges are delineated by 95% fixed kernel isolines. The most widely occurring habitat category within each range is given in bold.

	Habitat category (percentage composition)								
Individual	Forest	Thicket -forest	Thicket	Scrub	Rock	Scrub-thicket	Open	Saltmarsh	Levin's B_i
PNLSR									
Study site	27.37	19.60	24.64	9.16	1.71	9.86	0.46	7.20	0.5799
SSM1	**44.20**	26.33	22.58	2.13	1.49	1.67	0.50	1.10	0.3081
SSM2	13.46	28.11	**30.19**	3.55	0.41	12.03	0.45	11.8	0.5125
SAM3	19.91	30.51	**32.74**	5.11	1.00	9.82	0.35	0.56	0.4233
SJM4	13.70	34.46	**34.47**	3.73	0.42	12.01	0.37	0.84	0.3819
SAF7	**42.73**	25.46	22.80	2.38	1.62	4.37	0.13	0.51	0.3299
SAF8	19.41	**36.41**	27.95	3.09	1.61	10.04	0.26	1.23	0.4070
PNQ									
Study site	28.72	39.20	17.50	3.89	1.61	1.62	7.00	0.46	0.3790
QAM1	27.38	**45.61**	21.09	3.00	1.22	1.46	0.11	0.13	0.2917
QSM3	31.50	**44.89**	17.75	2.18	1.41	1.65	0.47	0.15	0.2859
QSM4	25.60	**46.20**	20.66	3.82	1.41	1.62	0.37	0.32	0.2986
QAF10	30.23	**42.38**	19.83	3.86	1.40	1.67	0.34	0.29	0.3146
QSF11	32.49	**41.06**	20.15	2.98	1.34	1.54	0.27	0.17	0.3091
QAF12	38.09	**41.06**	14.34	3.11	1.35	1.55	0.20	0.30	0.2828

The predominant habitats within the PNLSR study area are stands of forest, dense thicket and thicket-forest, bounded by coastal scrub, scrub-thicket and saltmarsh. Inland the terrain rises steeply through densely forested slopes (predominately *Nothofagus nitida* and *N. betuloides*). In comparison the PNQ study area is centred on a three-sided valley. The valley floor is dominated by thicket-forest and a central swampy region characterised by shorter thicket vegetation. The vegetation along the valley sides is again almost entirely comprised of stands of *Nothofagus* forest. Where the soil is thin or landslides have occurred, grassy open patches have replaced areas of forested slope.

Individual home ranges within each study site were principally comprised of thicket, thicket-forest and forest habitat (Table 6.3.1). No single category predominated among PNLSR home ranges, whereas thicket-forest was consistently the most prevalent class within PNQ home ranges, although thicket-forest was also the most common habitat throughout this site. Scrub, rock, scrub-thicket, open habitat and saltmarsh each represented a far lesser proportion of each site and of individual home ranges.

The difference between log-transformed ratios of available and utilised habitat compositions at the second-order was calculated for each site and tested against zero by constructing a matrix of mean-corrected sums of squares and cross-products R_1 and a residual matrix R_2 comprised of the raw sums of squares and cross-products (Appendix 4). Transformation of the Wilk's lambda statistic Λ to $-n \ln \Lambda$ yielded $P < 0.001$ in each case when compared to χ^2 at the appropriate degree of freedom. Despite some general similarities in composition therefore, the proportional representation of habitats inside home ranges differed from their availability in the wider study area, i.e. habitat utilisation was non-random.

6.3.1.2 Habitat selection, second-order resolution

Güiña utilised habitat in a non-random manner in both study areas (Table 6.3.1, Figure 6.3.5, Appendix 4). Comparison of site and home range compositions (analysis at the second-order scale of resolution) revealed that thicket-forest, thicket, forest and scrub-thicket were ranked first to fourth at both sites, thicket-forest being the most highly selected habitat (Tables 6.3.2 and 6.3.3). In PNLSR thicket-forest was significantly selected over all other habitat categories, but relative to one another the utilisation of thicket, forest and scrub-thicket habitat did not differ from random (Tables 6.3.2 and 6.3.4). Inside the PNQ study site relative preferences were similar, though in this site thicket-forest was not significantly selected over thicket or forest, ranked second and third respectively (Tables 6.3.3 and 6.3.4). At the second-order scale of resolution, areas of scrub-thicket were utilised approximately in accordance with their abundance within each site, whereas scrub, saltmarsh, rock and open habitat were under-utilised relative to all other categories (Figure 6.3.5).

Habitat utilisation at the second-order of resolution differed significantly between the two study sites ($F_{6, 83} = 8.859$, $P < 0.001$; two-way GLM). Log-ratio differences calculated for PNLSR güiña were greater than those for PNQ individuals for all habitat categories except saltmarsh, indicating that the pattern of habitat utilisation by PNLSR güiña diverged further from the proportional utilisation predicted for random habitat use. Age-class, sex and season did not affect the habitat composition of home ranges (all $P < 0.05$).

Figure 6.3.1 Habitat composition of the PNLSR study site and home ranges of male güiña used in the evaluation of habitat selection at the second-order. Home ranges are displayed as 95% fixed kernel isolines.

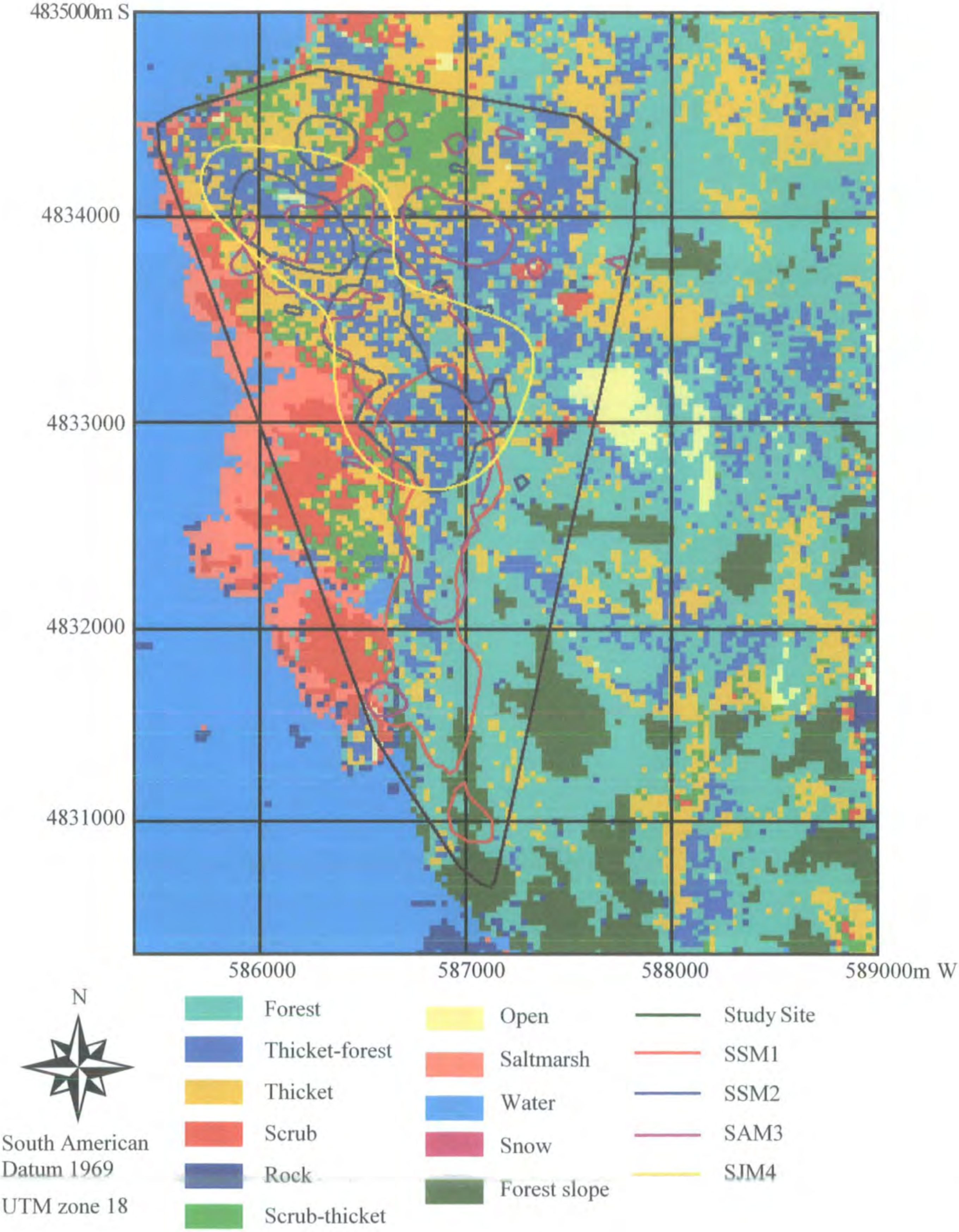


Figure 6.3.2 Habitat composition of the PNLSR study site and home ranges of female güiña used in the evaluation of habitat selection at the second-order. Home ranges are displayed as 95% fixed kernel isolines.

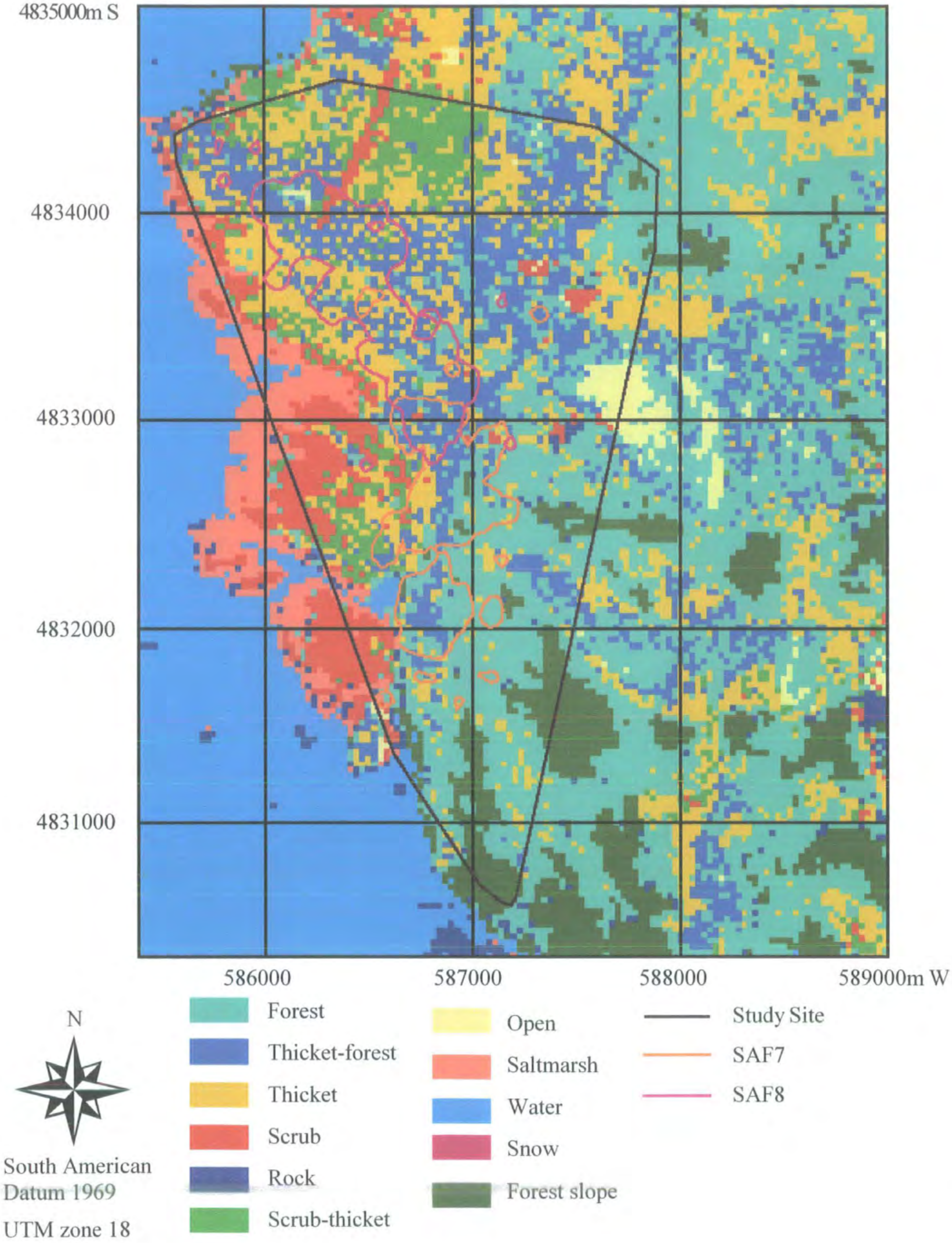


Figure 6.3.3 Habitat composition of the PNQ study site and home ranges of male güiña used in the evaluation of habitat selection at the second-order. Home ranges are displayed as 95% fixed kernel isolines.

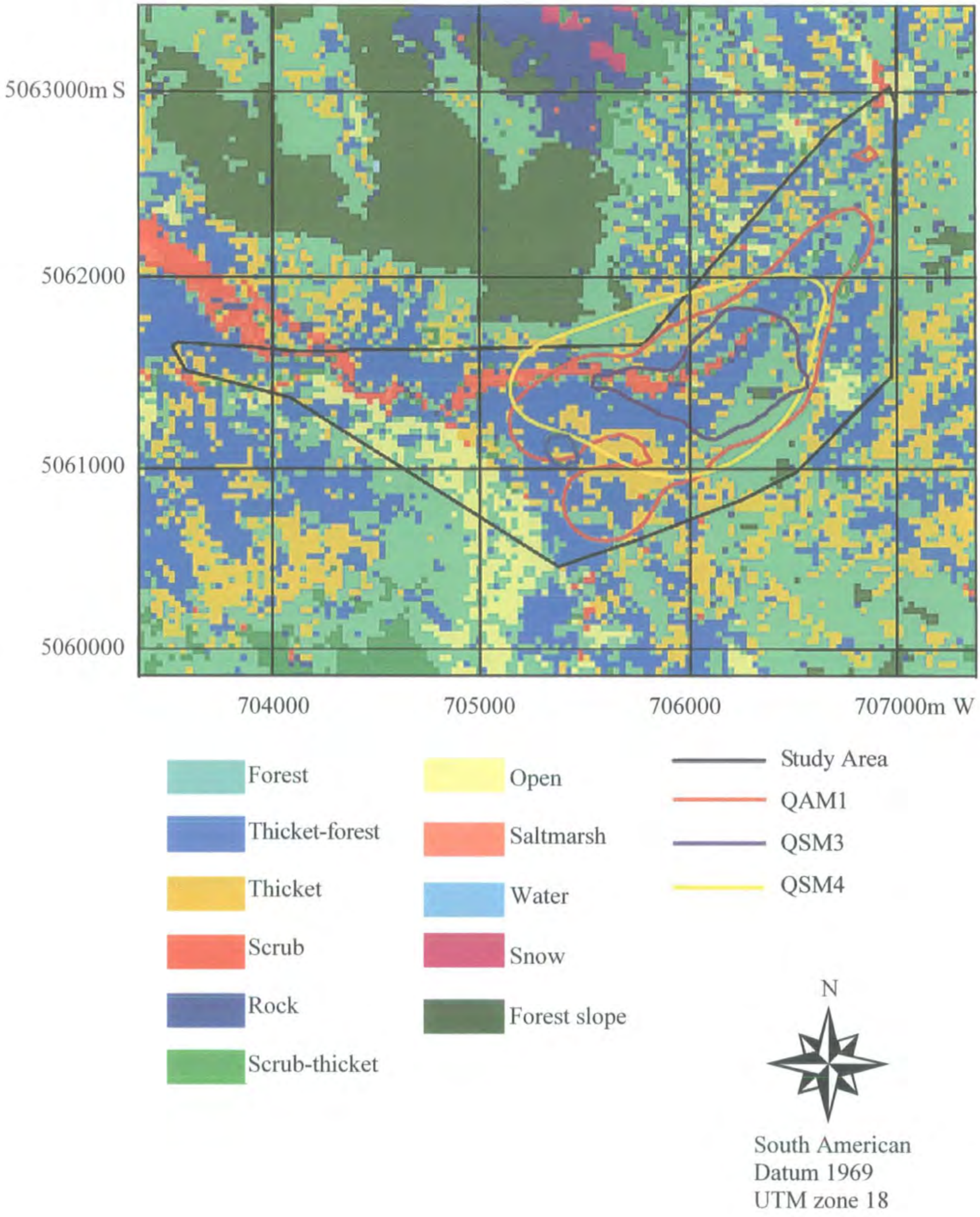


Figure 6.3.4 Habitat composition of the PNQ study site and home ranges of female güiña used in the evaluation of habitat selection at the second-order. Home ranges are displayed as 95% fixed kernel isolines.

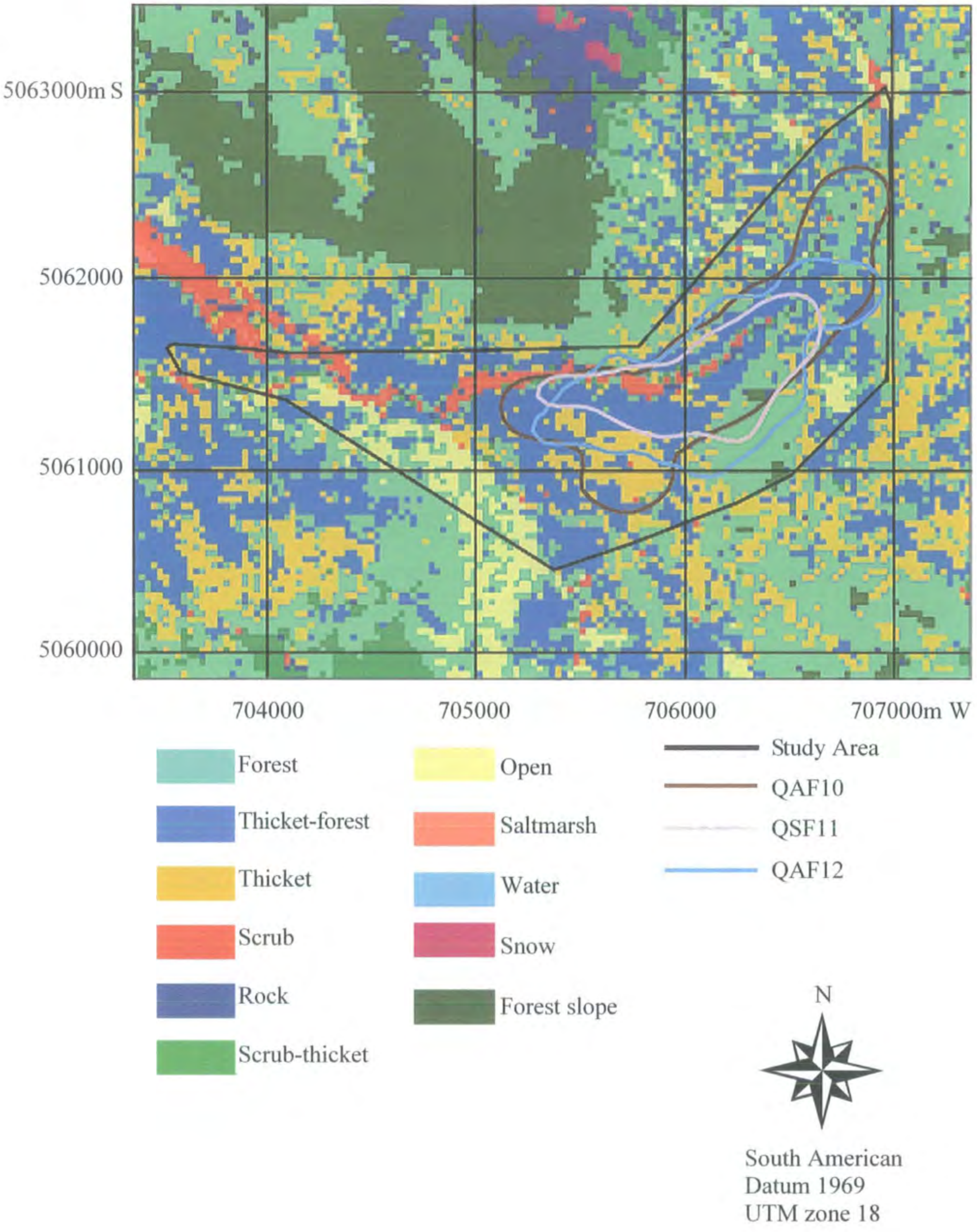


Figure 6.3.5. Selection of home range and fix location by güiña in a) PNLSR and b) PNQ. Comparison of the habitat composition inside the study areas (defined as the MCP constructed using all location data) with that inside individual home ranges (defined as the area encompassed by 95% fixed kernel isolines), and composition of buffered fix locations in comparison to that inside home ranges. Mean values and standard errors are shown.

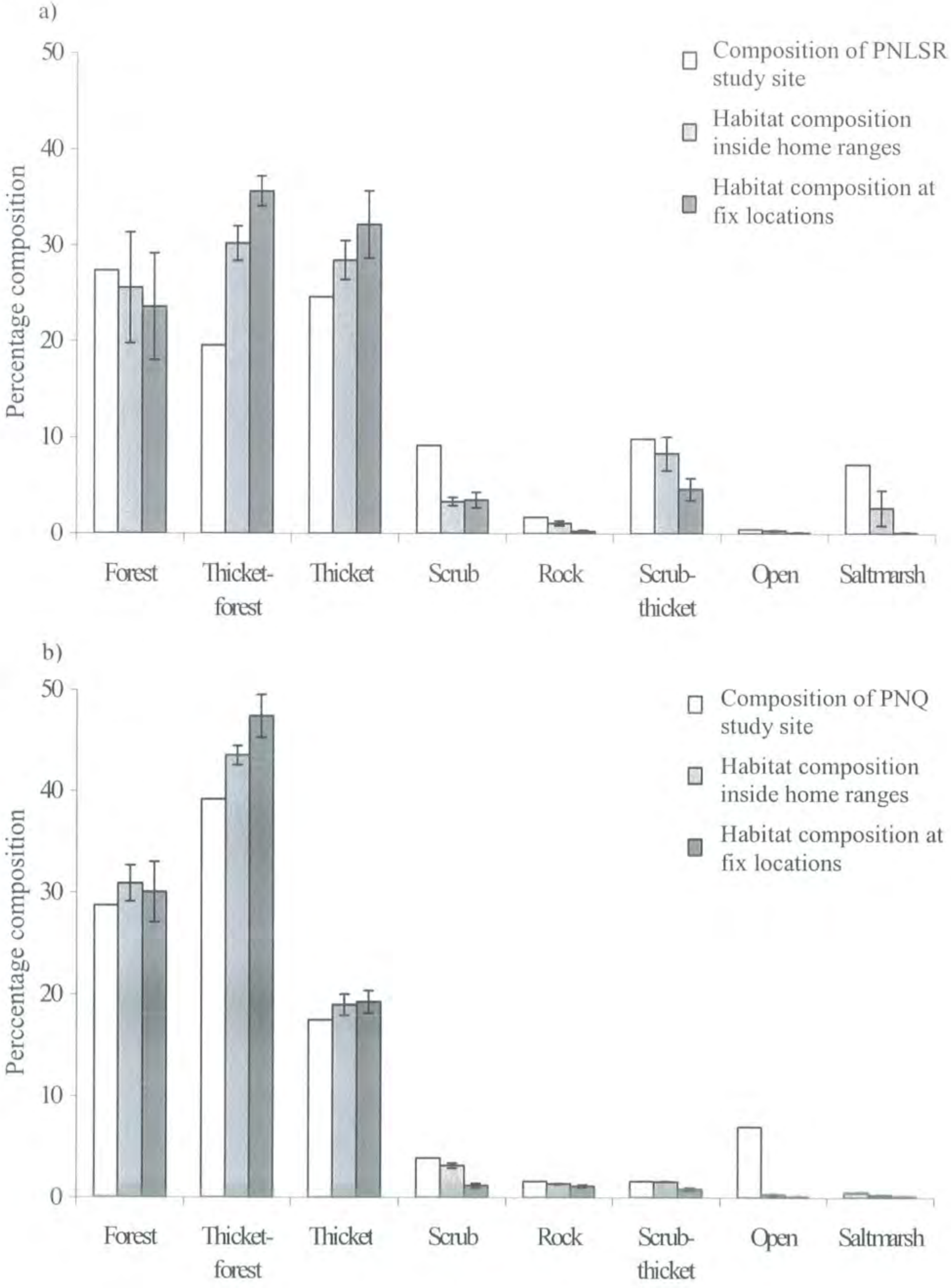


Table 6.3.2 *t*-values and relative ranking of habitat categories derived from pair-wise log-ratio differences between utilised and available habitat compositions (second-order resolution) in PNLSR. Significance is based upon departure from a two-sided *t*-distribution.

a) *t*-values

	Thicket-forest	Thicket	Forest	Scrub-thicket	Open	Rock	Scrub	Saltmarsh
Thicket-forest		4.751	2.281	2.882	4.066	3.237	9.226	4.411
Thicket	-4.751		1.240	1.929	2.910	2.257	10.358	4.004
Forest	-2.281	-1.240		0.202	0.451	2.676	2.784	2.858
Scrub-thicket	-2.882	-1.929	-0.202		0.105	0.664	2.821	2.777
Open	-4.066	-2.910	-0.451	-0.105		0.792	3.367	3.361
Rock	-3.237	-2.257	-2.676	-0.664	-0.792		1.015	1.841
Scrub	-9.226	-10.358	-2.784	-2.821	-3.367	-1.015		1.623
Saltmarsh	-4.411	-4.004	-2.858	-2.777	-3.361	-1.841	-1.623	

To simplify the above, in b) each *t*-value is replaced by its sign. A triple sign signifies where the *t*-value differs significantly from zero ($P < 0.05$, *d.f.* = 10). The rank for each habitat type according to relative preference is calculated by tallying positive and negative differences. Final ranks show relatively most selected (1) to least-selected (8) habitats.

b)

	Thicket-forest	Thicket	Forest	Scrub-thicket	Open	Rock	Scrub	Saltmarsh	Rank
Thicket-forest		+++	+++	+++	+++	+++	+++	+++	1
Thicket	---		+	+	+++	+++	+++	+++	2
Forest	---	-		+	+	+++	+++	+++	3
Scrub-thicket	---	-	-		+	+	+++	+++	4
Open	---	---	-	-		+	+++	+++	5
Rock	---	---	---	-	-		+	+	6
Scrub	---	---	---	---	---	-		+	7
Saltmarsh	---	---	---	---	---	-	-		8

Table 6.3.3 *t*-values and relative ranking of habitat categories derived from pair-wise log-ratio differences between utilised and available habitat composition (second-order resolution) in PNQ. In Table b) *t*-values are replaced by their sign and tripled where significant.

a)

	Thicket-forest	Thicket	Forest	Scrub-thicket	Open	Rock	Scrub	Saltmarsh
Thicket-forest		0.136	0.483	2.873	4.538	3.911	3.640	3.149
Thicket	-0.136		0.293	1.599	4.359	2.587	2.777	2.818
Forest	-0.483	-0.293		1.695	4.536	3.284	2.673	3.125
Scrub-thicket	-2.873	-1.599	-1.695		4.601	5.338	2.871	3.095
Open	-4.538	-4.359	-4.536	-4.601		-4.568	-4.474	-5.071
Rock	-3.911	-2.587	-3.284	-5.338	4.568		0.779	2.815
Scrub	-3.640	-2.777	-2.673	-2.871	4.474	-0.779		2.759
Saltmarsh	-3.149	-2.818	-3.125	-3.095	5.071	-2.815	-2.759	

b)

	Thicket-forest	Thicket	Forest	Scrub-thicket	Open	Rock	Scrub	Saltmarsh	Rank
Thicket-forest		+	+	+++	+++	+++	+++	+++	1
Thicket	-		+	+	+++	+++	+++	+++	2
Forest	-	-		+	+++	+++	+++	+++	3
Scrub-thicket	---	-	-		+++	+++	+++	+++	4
Open	---	---	---	---		---	---	---	8
Rock	---	---	---	---	+++		+	+++	5
Scrub	---	---	---	---	+++	-		+++	6
Saltmarsh	---	---	---	---	+++	---	---		7

Table 6.3.4 Ranked order of relative habitat preferences at the second-order of resolution derived from pairwise comparisons. Classes to the left of the symbol '>' are selected over those to the right. Non-significant differences between adjacent habitats (P > 0.05) are underlined implying their ranks are interchangeable (Aebischer and Robertson, 1992). Habitat categories are: Forest, Thicket-forest, Thicket, Scrub, Rock, Scrub-thicket, Open and Saltmarsh.

PNLSR second-order habitat preferences

TF > T > F > ST > O > R > S > SA

PNQ second-order habitat preferences

TF > T > F > ST > R > S > SA > O

6.3.1.3 Habitat diversity within home ranges

Habitat diversity was greater in each of the two study areas (available habitat) than inside the home range of any individual güiña (Table 6.3.5, mean Levin's Standardised niche breadth $B_A = 0.394$ (median, interquartile range: 0.324-0.446) PNLSR home ranges; and $B_A = 0.297$ (median, interquartile range: 0.285-0.310) PNQ home ranges. Wilcoxon Signed Ranks tests, PNLSR: $n = 6$, $P = 0.028$; PNQ: $n = 6$, $P = 0.028$).

Table 6.3.5. Levin's Standardised niche breadth B_i calculated for the PNLSR and PNQ study sites and güiña home ranges. Study sites are defined by the MCP constructed using all location fixes obtained from the appropriate site, individual ranges are delineated by 95% fixed kernel isolines.

PNLSR	B_i	PNQ	B_i
Site	0.580	Site	0.379
SSM1	0.308	QAM1	0.292
SSM2	0.513	QSM3	0.286
SAM3	0.423	QSM4	0.302
SJM4	0.382	QAF10	0.315
SAF7	0.330	QAF11	0.309
SAF8	0.407	QAF12	0.283

6.3.1.4 Habitat selection, third-order resolution

Habitat compositions recorded inside the buffered radiolocation points are detailed in Table 6.3.6; an example of habitat utilisation at the third-order scale of resolution is displayed for animal SAM3 in Figure 6.3.6.

Habitat utilisation within güiña home ranges was again non-random (PNLSR: $\Lambda < 0.001$; Aebischer's test statistic = 454.4; PNQ $\Lambda < 0.001$; Aebischer's test statistic = 467.0, Figure 6.3.5 Appendix 4), and generally mirrored that which occurred at the second-order. Thicket-forest habitat was therefore preferentially utilised within home ranges. For nine of the twelve güiña monitored, this habitat predominated over all other habitat categories within the buffered fix locations (Table 6.3.6). Thicket-forest was significantly selected over forest, scrub thicket, rock, open and saltmarsh in PNLSR, and over scrub thicket, scrub, open and saltmarsh in PNQ (Figure 6.3.5; Tables 6.3.7 to 6.3.9). Scrub-thicket, open and saltmarsh areas were consistently under-utilised, the remaining habitat categories were visited at frequencies approximately proportional to their availability (Figure 6.3.5). Habitat utilisation at the third-order of resolution was not significantly influenced by site, age-class, sex or season, or any combination of these factors (all $P < 0.05$).

Table 6.3.6 Habitat composition inside buffered (50 m radius) güiña radiolocation points recorded in the PNLSR and PNQ study sites. Zero percent utilisation vales have been replaced by 0.001% (Aebischer *et al.*, 1993).

	Habitat category (percentage composition)							
Individual	Thicket-forest	Thicket	Forest	Scrub-thicket	Open	Rock	Scrub	Saltmarsh
SSM1	**37.10**	23.40	36.38	1.14	0.001	0.54	1.13	0.31
SSM2	32.21	**41.90**	13.45	5.93	0.23	0.001	6.68	0.001
SAM3	**38.21**	34.60	18.11	5.23	0.20	0.20	3.36	0.09
SJM4	**41.42**	37.05	11.79	5.10	0.23	0.16	4.04	0.21
SAF7	32.05	19.90	**44.73**	1.66	0.001	0.001	1.57	0.09
SAF8	32.92	**36.20**	17.16	8.61	0.001	0.62	4.49	0.001
QAM1	**48.23**	17.11	30.90	1.20	0.07	1.08	1.31	0.10
QSM3	**42.65**	16.85	37.81	0.64	0.10	1.33	0.59	0.03
QSM4	**52.80**	18.54	23.07	1.67	0.13	1.44	2.03	0.32
QAF10	**49.90**	20.81	26.75	0.69	0.10	1.16	0.59	0.001
QSF11	**51.30**	23.90	22.47	0.56	0.001	0.56	1.18	0.03
QAF12	**39.58**	17.96	39.25	0.50	0.06	1.26	1.31	0.08

Table 6.3.7 *t*-values and relative ranking of habitat categories derived from pair-wise log-ratio differences between utilised and available habitat composition (third-order resolution) in PNLSR. In Table b) *t*-values are replaced by their sign and tripled where significant.

a)

	Thicket-forest	Thicket	Forest	Scrub-thicket	Open	Rock	Scrub	Saltmarsh
Thicket-forest		0.500	3.321	4.446	2.857	2.895	0.922	2.922
Thicket	-0.500		2.456	7.924	2.239	2.282	0.188	2.663
Forest	-3.321	-2.456		3.529	2.610	2.553	-0.204	2.613
Scrub-thicket	-4.446	-7.924	-3.529		1.972	2.212	-2.474	2.149
Open	-2.857	-2.239	-2.610	-1.972		-0.162	-2.696	0.404
Rock	-2.895	-2.282	-2.553	-2.212	0.162		-2.586	0.617
Scrub	-0.922	-0.188	0.204	2.474	2.696	2.586		2.367
Saltmarsh	-2.922	-2.663	-2.613	-2.149	-0.404	-0.617	-2.367	

b)

	Thicket-forest	Thicket	Forest	Scrub-thicket	Open	Rock	Scrub	Saltmarsh	Rank
Thicket-forest		+	+++	+++	+++	+++	+	+++	1
Thicket	-		+++	+++	+++	+++	+	+++	2
Forest	---	---		+++	+++	+++	-	+++	4
Scrub-thicket	---	---	---		+	+	---	+	5
Open	---	---	---	-		-	---	+	7
Rock	---	---	---	-	+		---	+	6
Scrub	-	-	+	+++	+++	+++		+++	3
Saltmarsh	---	---	---	-	-	-	---		8

Table 6.3.8 *t*-values and relative ranking of habitat categories derived from pair-wise log-ratio differences between utilised and available habitat composition (third-order resolution) in PNQ. In Table b) *t*-values are replaced by their sign and tripled where significant.

a)

	Thicket-forest	Thicket	Forest	Scrub-thicket	Open	Rock	Scrub	Saltmarsh
Thicket-forest		1.280	0.386	3.436	3.077	2.168	8.348	2.940
Thicket	-1.280		-0.353	2.757	2.808	1.024	6.666	2.491
Forest	-0.386	0.353		2.437	3.008	1.951	4.847	2.949
Scrub-thicket	-3.436	-2.757	-2.437		1.818	-2.129	1.397	1.321
Open	-3.077	-2.808	-3.008	-1.818		-3.051	-0.978	-0.215
Rock	-2.168	-1.024	-1.951	2.129	3.051		4.510	2.486
Scrub	8.348	-6.666	-4.847	-1.397	0.978	-4.510		0.802
Saltmarsh	-2.940	-2.491	-2.949	-1.321	0.215	-2.486	-0.802	

b)

	Thicket-forest	Thicket	Forest	Scrub-thicket	Open	Rock	Scrub	Saltmarsh	Rank
Thicket-forest		+	+	+++	+++	+	+++	+++	1
Thicket	-		-	+++	+++	+	+++	+++	3
Forest	-	+		+++	+++	+	+++	+++	2
Scrub-thicket	---	---	---		+	-	+	+	5
Open	---	---	---	-		---	-	-	8
Rock	-	-	-	+	+++		+++	+++	4
Scrub	+++	---	---	-	+	---		+	6
Saltmarsh	---	---	---	-	+	---	-		7

Table 6.3.9 Ranked order of relative habitat preferences at the third-order of resolution derived from pairwise comparisons. Classes to the left of the symbol > are selected over those to the right. Non-significant differences between adjacent habitats (*P* > 0.05) are underlined implying their ranks are interchangeable (Aebischer and Robertson, 1992). Habitat categories are: Thicket-forest, Thicket, Forest, Scrub-thicket, Open, Rock, Scrub and Saltmarsh.

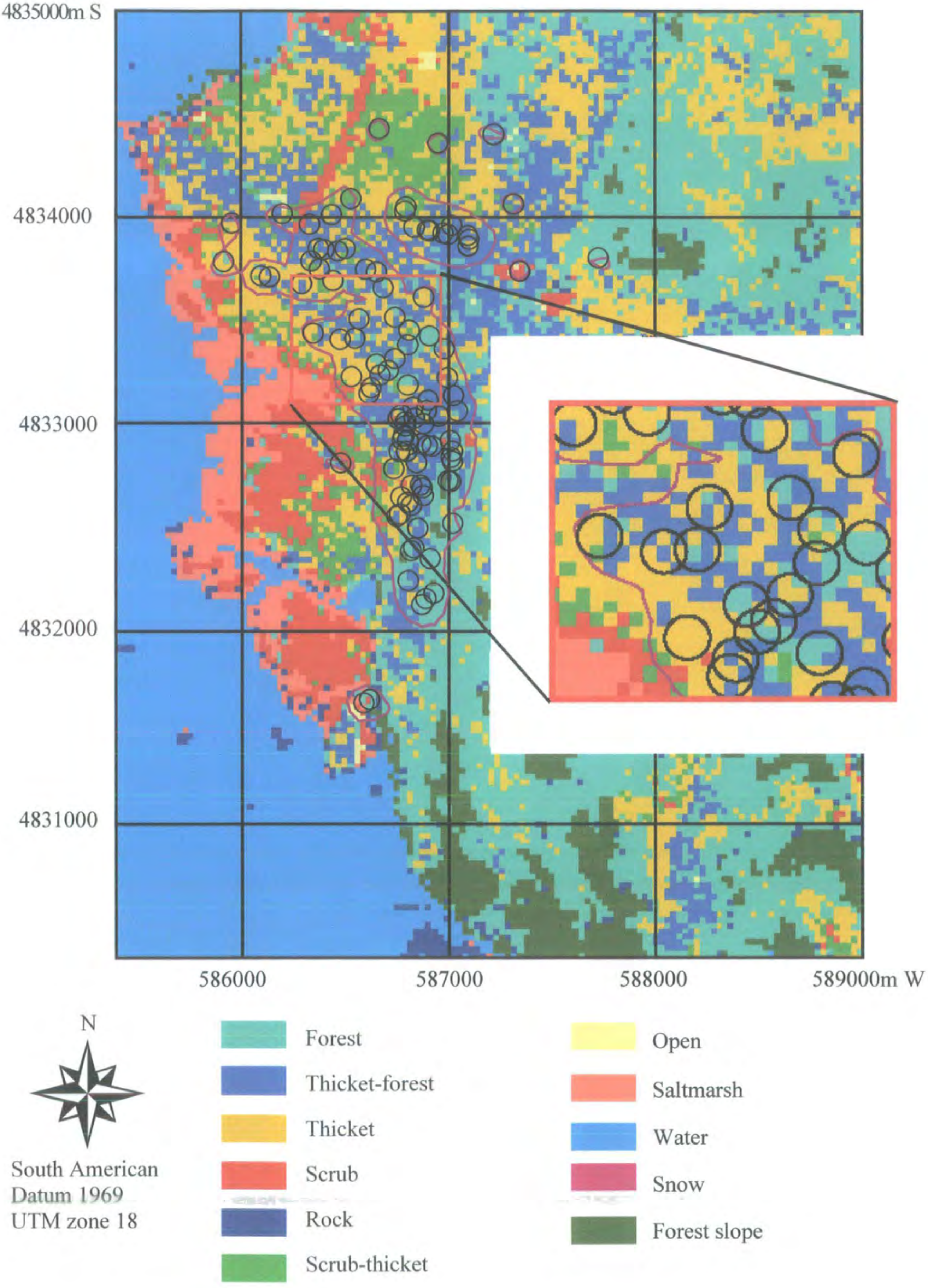
PNLSR third-order habitat preferences

TF > T > S > F > ST > R > O > SA

PNQ third-order habitat preferences

TF > F > T > R > ST > S > SA > O

Figure 6.3.6 Example of the habitat composition within 50 m radii for individual fix locations used in the evaluation of habitat selection at the third-order (animal SAM3).



6.3.2 Environmental niche factor analysis of güiña habitat associations and predictive modelling of suitable habitat

6.3.2.1 The ENFA model

Only the first two explanatory factors derived by the ENFA model were retained, from which a habitat suitability map was constructed for the entire reference area (Figure 6.3.7, site details Figures 6.3.8 and 6.3.9). The first factor described the marginality of güiña, the second the greater part of the species' niche specialisation. Together these accounted for 98.5% of the total variation observed, corresponding to 81% of the specialisation and 100% of the marginalisation (Table 6.3.10). The marginality factor *M* was very high (2.13) and accounted for 51% of the total specialisation alone. This indicates that güiña in southern Chile utilise habitat that differs greatly from the average of the wider environment, corroborating the results obtained through compositional analyses.

According to the ENFA model, güiña are primarily associated with regions of high thicket-forest (frequency = 0.86) and thicket (frequency = 0.48) coverage and display a slight tendency to avoid rock (frequency = -0.13) and scrub-thicket (frequency = -0.09) (Table 6.3.10). Scrub, open and forest were found to have the least influence on species marginality as these ecogeographical variables had scores closest to zero. The very large eigenvalue (135) attributed to the marginality factor means that randomly chosen cells within the reference area are approximately 135 times more dispersed on this axis than the cells on which güiña were recorded (Hirzel *et al.*, 2002a). Güiña are therefore extremely sensitive to shifts from optimal conditions on this axis. Specialisation as described by the second factor (the only specialisation factor retained) corresponded principally to the rock and scrub-thicket frequency variables. The thicket-forest and open categories contributed the least to this axis.

Table 6.3.10 Variance explained by the seven ecogeographical variables extracted by the ENFA model. Values in brackets indicate the amount of variance explained by each factor. Positive marginality values indicate güiña prefer locations with higher values on the corresponding ecogeographical variable (EGV) than the reference area average. The signs of the specialisation factors have no importance.

		Specialisation factor					
EGV	Marginality (51%)	1 (30%)	2 (11%)	3 (5%)	4 (2%)	5 (1%)	6 (>1%)
Forest frequency	-0.04	-0.04	-0.45	-0.30	-0.66	-0.52	-0.17
Thicket-forest frequency	0.86	-0.03	-0.09	0.04	0.10	0.00	-0.49
Thicket frequency	0.48	-0.08	-0.14	0.01	-0.26	0.04	0.85
Scrub-thicket frequency	-0.09	0.50	-0.70	0.27	0.27	0.16	-0.02
Scrub frequency	-0.01	-0.31	-0.22	-0.80	0.46	-0.24	0.01
Rock frequency	-0.13	-0.80	-0.47	0.35	-0.21	0.06	-0.05
Open frequency	-0.02	0.01	-0.06	-0.27	-0.40	0.80	0.01

Figure 6.3.7 Habitat suitability map for güiña, as computed by ecological niche factor analysis. The scale on the right displays the habitat suitability values represented by each shade in the map. The locations of the two study sites are indicated.

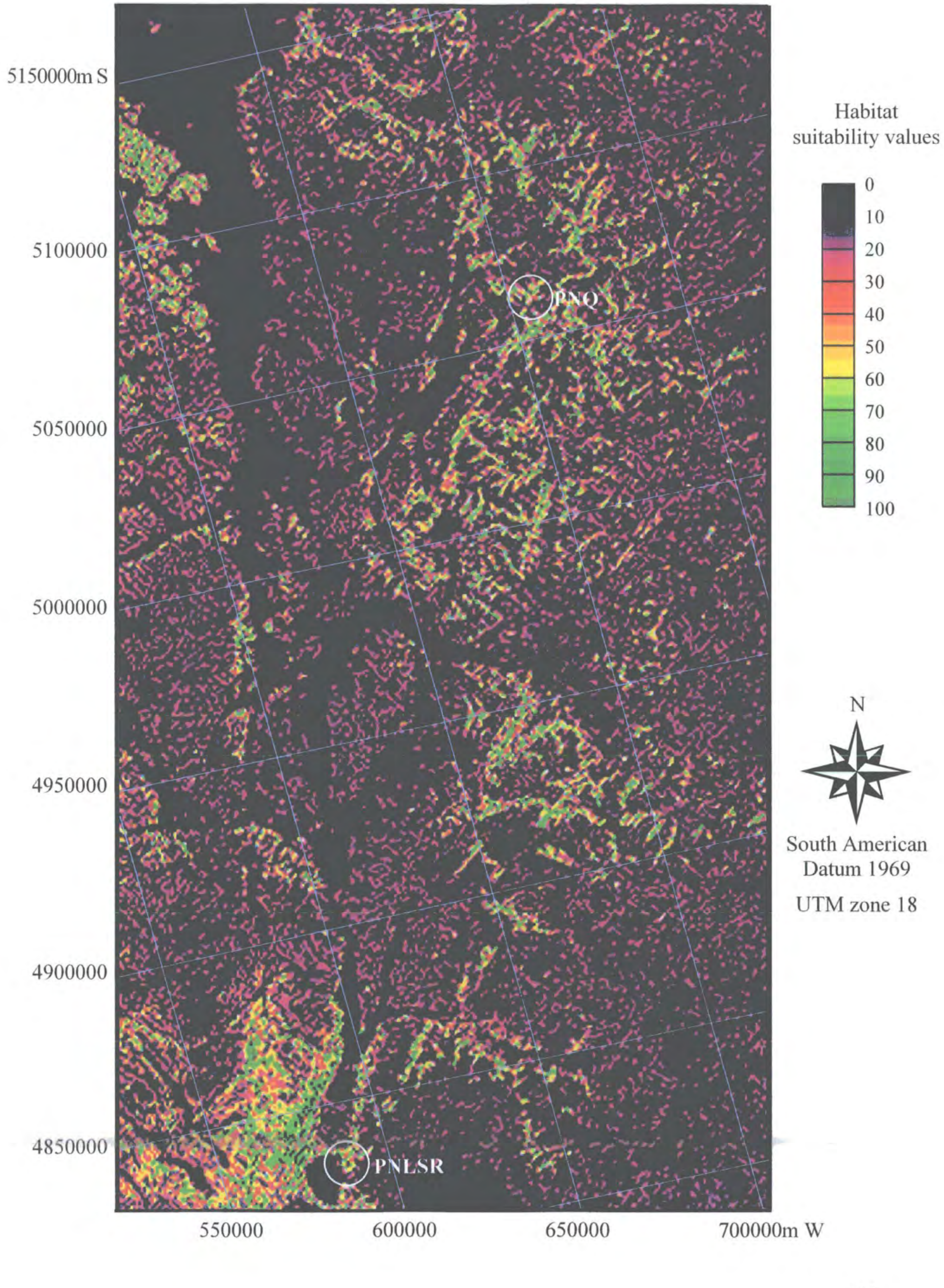


Figure 6.3.8 (a) Habitat suitability map for güiña in the PNLSR study site, as computed by ENFA. (b) Güiña presence data utilised in the ENFA and in model validation. 50 m contours are displayed in (b)

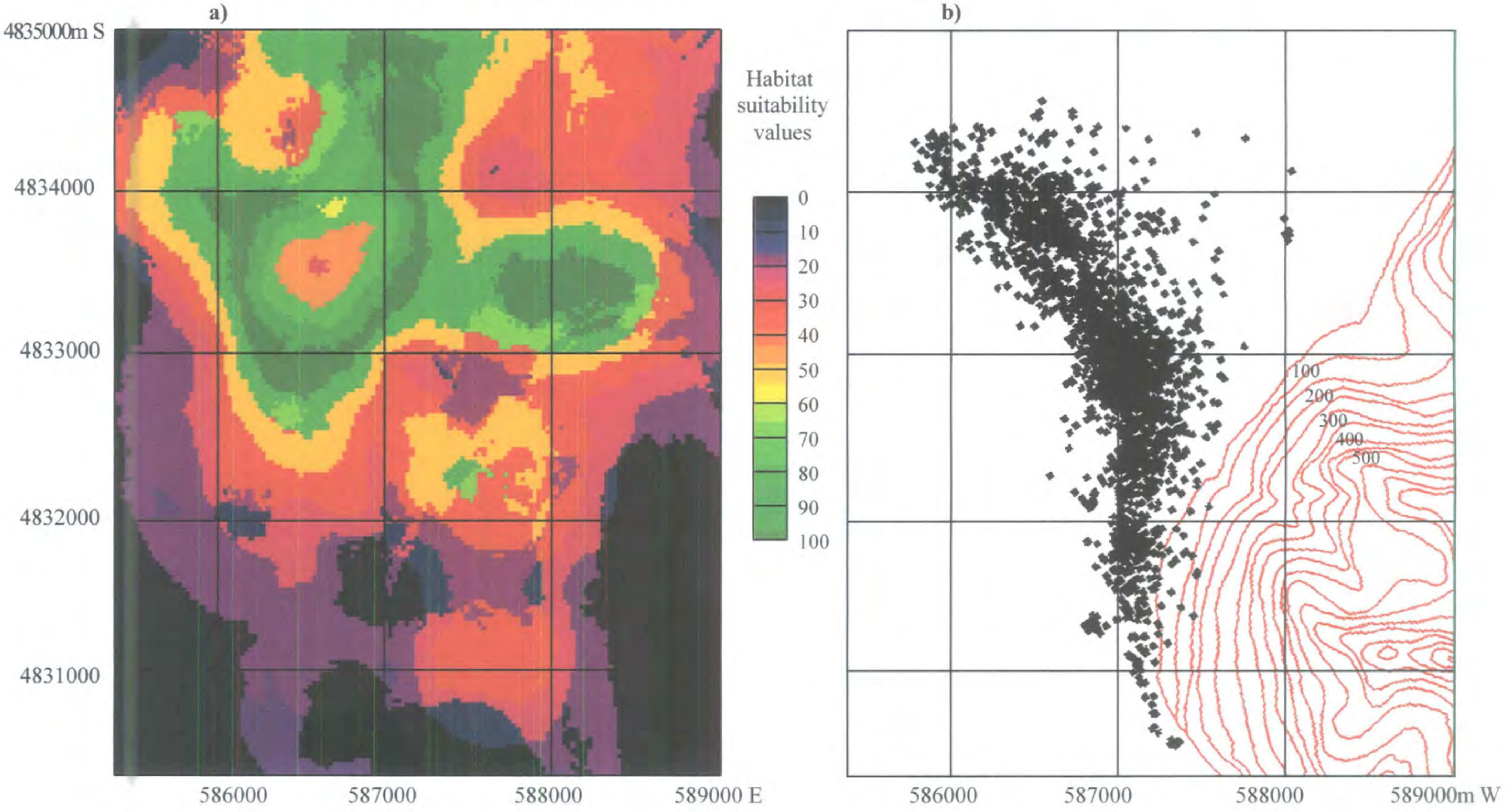
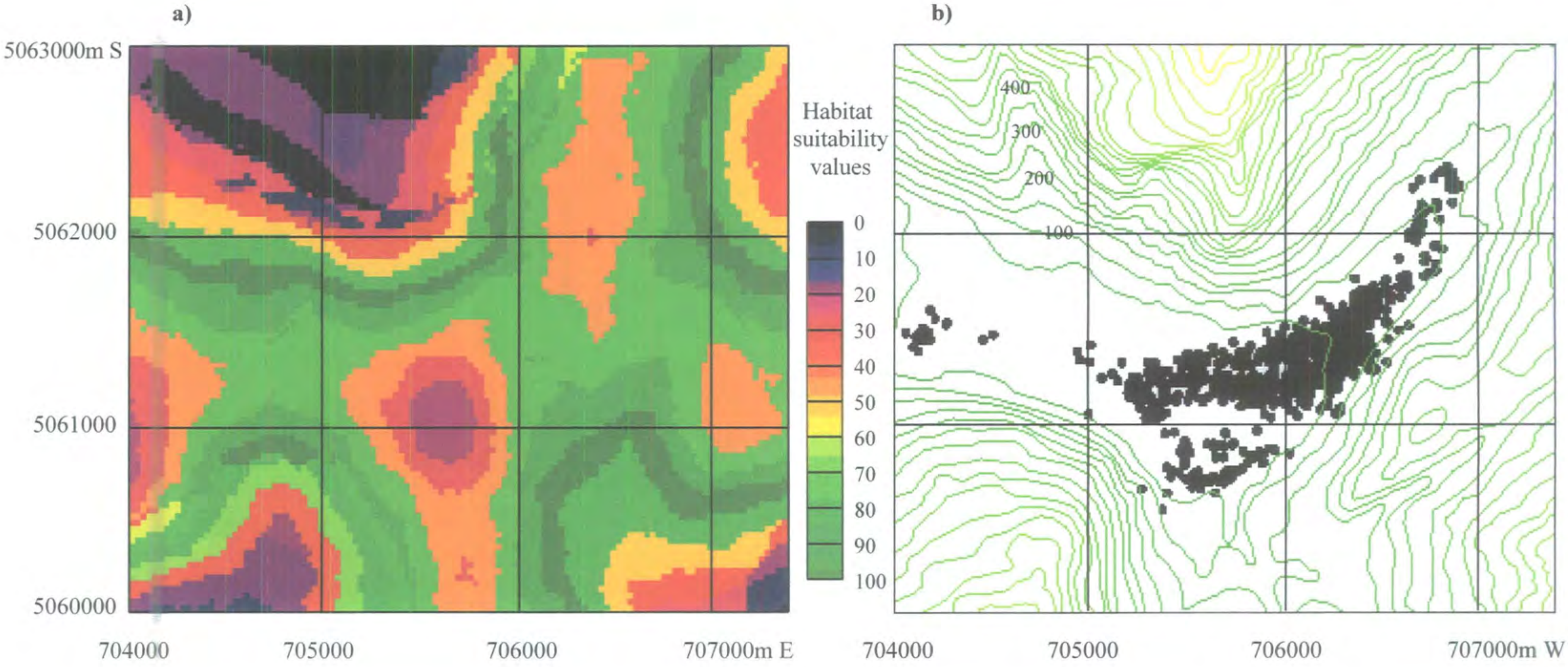


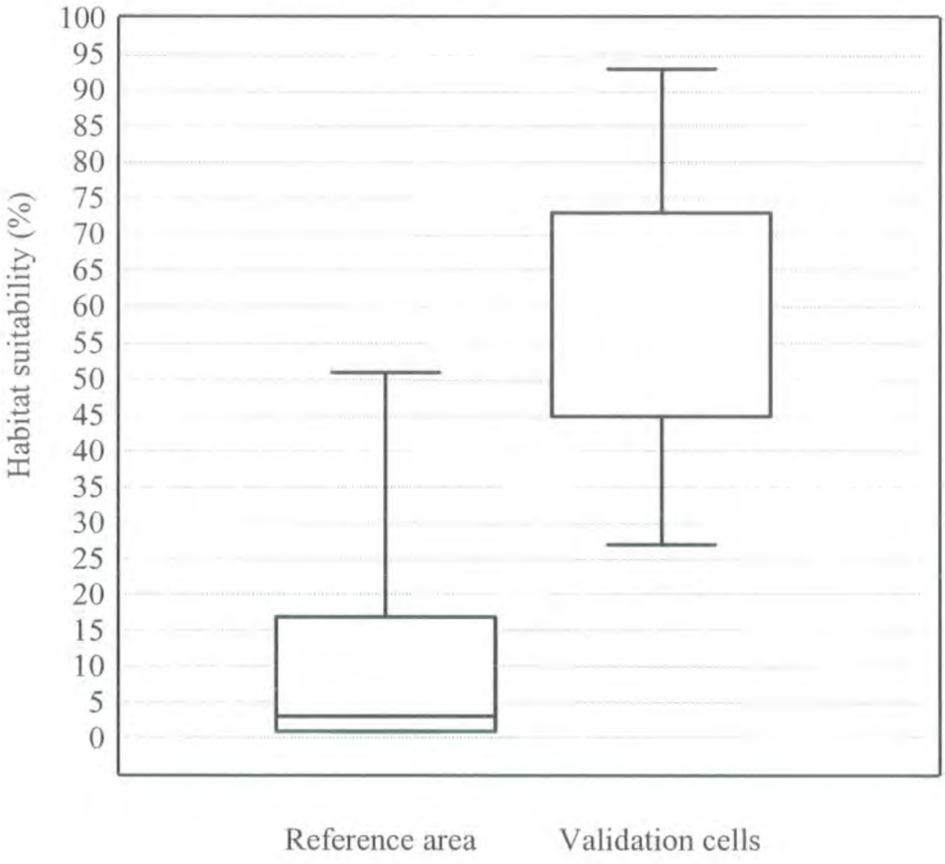
Figure 6.3.9 (a) Habitat suitability map for güiña in the PNQ study site, as computed by ENFA. b) Güiña presence data utilised in the ENFA and in model validation. 50 m contours are displayed in (b)



6.3.2.2 Validation

According to jack-knife cross-validation, predicted suitability exceeded 0.5 in 56.6% of the 977 validation cells (SD = 0.23). This differs significantly from the 5.5% (SD = 0.18) expected if these cells were randomly chosen from the global reference area (bootstrap test, $P < 0.001$). Predicted suitability values for the validation cells were greater than corresponding values calculated for the global reference area (Figure 6.3.10) i.e., the model assigned higher suitability values to cells utilised by güiña than to those where no presence data was recorded.

Figure 6.3.10 Box plots representing the distributions of habitat-suitability values for the entire reference area (left) and the ten validation subsets (right). Boxes delimit interquartile range, the middle line indicates the median and whiskers encompass the 90% confidence interval.



6.4 Discussion

6.4.1 Hierarchical habitat utilisation by güiña

At the first-order scale of habitat selection, the distribution of the güiña has long been associated with *Nothofagus* forest (Miller and Rottmann, 1976; Melquist, 1984; Nowell and Jackson, 1996), primarily on the basis of the close concordance of this species' geographic range with that of the *Nothofagus*-dominated forests of North Patagonia (Figures 1.1.1 and 1.1.2). This study found that the same association did not, however, occur at finer scales of spatial resolution. Radio-monitored güiña utilised available habitat in a non-random manner at both the second- and third-order scales of spatial resolution. Güiña selectively incorporated the relatively dense and complexly structured thicket-forest and thicket habitats into home range areas more than they did areas of (predominantly *Nothofagus*) forest (Figure 6.3.5 and Tables 6.3.1-6.3.4). Only the scrub-thicket habitat category was incorporated into home range areas in proportion to its relative availability within the study sites (neutral selection). The remaining categories (scrub, saltmarsh, rock and open) were all comparatively under-utilised.

The habitat composition of buffered radiolocation points included proportionately more thicket-forest habitat than the respective home ranges, indicating that selection for this habitat also occurred at the third-order scale of spatial resolution. The representation of forest, thicket, scrub and rock habitats at these locations however occurred in proportion to the relative availability of these habitats. Interestingly, although scrub-thicket was neutrally selected at the second-order, it appeared to be actively selected against at the third-order. Open and saltmarsh habitats were again under-utilised at this scale (Figure 6.3.5 and Tables 6.3.6-6.3.9).

Güiña within the PNQ study area incorporated comparatively more thicket-forest and forest habitat, and less thicket within their home ranges than PNLSR individuals. This corresponds to differences in the availability of these habitats in each site; PNQ has twice the percentage coverage of thicket-forest as PNLSR, but only 71% that of thicket. When the available habitat categories were ranked according to preference, the rankings were closely similar within each of the two sites, particularly at the scale of individual home ranges (second-order selection). Thicket-forest, thicket, forest, and scrub-thicket were ranked first to fourth in each site. The general patterns of habitat utilisation and selection by resident güiña were therefore relatively consistent, despite the very different successional histories of the vegetation of the two sites.

6.4.2 Ecological niche factor analysis of güiña habitat utilisation data

Figure 6.3.7 describes the output from the ENFA model in terms of the spatial location of areas considered by the model to be suitable for güiña occupation, based on the available input variables. From the model output it is again clear that the habitat category güiña radiolocation data are most closely associated with (third order resolution) is not the *Nothofagus*-dominated forest that typifies much of this region of southern Chile (Figure 2.2.1). Interpretation of the marginality factor in terms of the original ecogeographical variables describes a very similar order of habitat categories ranked by preference to those identified via compositional analysis. The variable that correlated most closely with the marginality factor, and hence identified as the most relevant for güiña ecology was thicket-forest habitat, second most important was thicket habitat, associations not evident using the coarser-grained (first-order scale) species distribution data.

Figure 6.3.7 indicates the distribution, the amount and extent of favourable güiña habitat in southern Chile. The mean suitability value for all cells within this region is just 10.3%, and only 5.5% of cells are considered by the model to have suitability values of more than 50%. Cells with high suitability scores therefore represent a very small proportion of the area mapped. The patches of suitable habitat are located predominantly between 5000000-5100000 m S and 4900000-4950000 m S on the Chilean mainland, and to the west of Laguna San Rafael between 4800000-4870000 m S (Figure 6.3.7). The distribution of suitable areas is discontinuous however, and many high quality habitat patches appear relatively isolated from other high quality areas. Güiña therefore preferentially utilise a naturally fragmented, and relatively uncommon component of the landscape, situated within a *Nothofagus* dominated matrix.

Southern Chile is a very mountainous region, and several neighbouring patches of high quality güiña habitat are separated by mountains (depicted by 'snow' and 'rock' in Figure 2.1.1). Although no conclusions can be drawn from the data presented here with respect to elevation, altitude potentially represents an additional barrier to the dispersal of animals. Temperature extremes increase with elevation, snow cover persists longer and vegetation becomes progressively reduced in stature because of the greater exposure to wind, cold, and snow. Elevation acts indirectly on the availability of small mammal prey by reducing the incidence of vegetation and therefore available food (Pizimetiti and De Salle, 1980). Observations made in the field strongly suggest that the distribution of cells with the highest suitability values is closely correlated with low elevation (see also Figures 6.3.8 and 6.3.9).

6.4.3 Causal factors of observed habitat preferences

Resource availability, specifically food availability is frequently the most influential determining factor in habitat selection studies, and has been widely documented among carnivore populations (Boyce and McDonald, 1999). Bobcats in eastern Maine for example were found to be most abundant in areas with dense understory vegetation, with which snowshoe hares, their principal prey, were also associated (Litvaitis *et al.*, 1985). Similarly, red foxes in coastal south-eastern Australia frequently used dry sclerophyll forest habitats, where small and medium-sized mammals were most abundant, and utilised less productive heathland and beach habitats only rarely (Phillips and Catling, 1991). The relative availability of potential avian prey was not investigated during this study, however live-trap indices indicated that small mammal prey was no more abundant in thicket-forest habitat than in areas of pure thicket or forest (Table 3.3.1). The observed preference of güiña for thicket-forest habitat therefore appears unrelated to survey estimates of small mammal prey availability.

The relative preferences of güiña for different habitat categories described in this chapter closely resemble those of güiña radio-tracked within the largely agricultural landscape of Isla Grande de Chiloé (Sanderson *et al.*, 2002). This more northerly site could not be incorporated within the ENFA model as it lies outside of the reference area detailed in Figure 6.3.7. Both studies however found resident animals to avoid short vegetation that afforded little cover, such as open areas, rock and scrub, and preferentially utilised dense, structured habitats. A preference for densely structured habitat appears to be a characteristic common to many of the Felidae (for example, ocelot: Ludlow and Sunquist, 1987; Konecny, 1989; clouded leopard: Austin and Tewes, 1999; jaguar: Crawshaw and Quigley, 1991, and Eurasian wildcat: Liberek, 1996). As the typical felid predatory sequence consists of concealment, stalking behaviour and sudden attack, cats possess many specialisations of predatory behaviour specially adapted to hunting amongst cover, (Kruuk and Turner, 1967; Kleiman and Eisenberg, 1973; Eisenberg, 1986; Henry, 1986; Koehler and Hornocker, 1991). The observed preference of PNLSR and PNQ güiña for thicket-forest may therefore arise because this habitat facilitates concealment from prey, and hence makes prey animals more susceptible to attack.

6.4.4 Consequences of habitat fragmentation and spatial heterogeneity

Small and/or effectively isolated populations are typically more vulnerable to unpredictable demographic events such as environmental stochasticity than are large, contiguous ones (Soulé, 1980; Harrison, 1991; Foley, 1994; Fahrig, 1997). The probability of local extinction is further increased by associated reductions in migration frequency and genetic interchange among unrelated individuals, resulting in the accumulation of deleterious mutations and loss of genetic variability through inbreeding depression.

Within a fragmented landscape, life-history characteristics that aid survival include a small body size, a high degree of mobility, low philopatry, and generalist habitat and dietary requirements (Laurance, 1991). As top predators, carnivores tend towards relatively large body sizes and large and specific habitat requirements, hence are of special concern for conservation (Myers, 1994; Noss and Csuti, 1994). The Felidae can be particularly vulnerable to the effects of habitat loss due to their relatively narrow dietary spectrum, limited fecundity and characteristically low population densities when compared, for example, with the canids (Gittleman, 1986).

Although the güiña's moderately low mobility reduces its ecological resilience within a naturally fragmented habitat, in many other respects this species' natural history appears encouraging for long-term population persistence. Despite a close association with a relatively scarce habitat resource, the güiña is able to exist within even substantially modified habitats providing sufficient dense vegetation remains for hunting and cover (Greer, 1965; Udvardy, 1975; Melquist, 1984; Sanderson *et al.*, 2002). Small mammals and birds, the güiña's staple prey, are almost ubiquitous in distribution, and finally, in high quality habitat this predator has very modest area requirements and can achieve high population densities.

6.4.5 Current limitations of the ENFA model and future developments

Some caution is required in interpreting the results presented in this chapter due to the small number of study populations and individuals monitored. Güiña are distributed over a broader range of habitats than were included within this analysis, and can occur outside of the predicted habitat areas. Individuals radiotracked as part of this study are hence unlikely to be representative of all güiña. In addition, many factors besides habitat quality, including patch size and isolation, the presence of competitors, the availability of prey, and any history of disturbance, will influence whether güiña are resident within areas of 'suitable' habitat. The output of the ENFA model should therefore only be interpreted as a representation of habitat quality, and one that can provide no guarantee of patch occupancy.

In the future it would be informative to seek out and monitor güiña populations at higher elevations (the majority of the PNLSR and PNQ and Isla Grande home ranges occurred at elevations less than 100 m above sea level), should this be possible, and also include elevation data within any subsequent predictive models for this species. At present this is not possible because of the limited resolution of available topological data. However, the Shuttle Radar Topography Mission, an international project spearheaded by the National Geospatial-Intelligence Agency (NGA) and NASA recently obtained satellite data on a near-global scale for the purpose of generating a high-resolution digital topographic database of the Earth's land surface (see http://srtm.usgs.gov/mission.html). This data is currently being processed and will soon be made freely available as 30 m resolution elevation data of vertical accuracy 16 m (at 90% confidence). Topographic data is required at this resolution to integrate with habitat maps derived from habitat imagery.

Summary

Two very different analytical approaches, compositional analysis and ecological niche factor analysis (ENFA) described very similar rankings of habitat association when applied to güiña distribution data. The output from the ENFA was applied across a large-scale reference area to provide insight into the distribution, the amount and the fragmentation of favourable güiña habitat in southern Chile. The predictive map generated using the ENFA model shows that within this region, areas with high habitat suitability for güiña represent a relatively minor part of the wider landscape. Previously güiña habitat associations have been considered only at the first-order spatial scale, i.e. at the scale of the species' geographic distribution (Nowell and Jackson, 1996), and failed to detect these finer scale associations.

Chapter 7

General Discussion

7.1 Güiña spatial ecology and habitat use

This study describes the non-random utilisation of available habitat resources by güiña from two populations separated by a distance of approximately 250 km. These cats exhibited no consistent preference for *Nothofagus* forest, the dominant category within this species' geographic range and the habitat with which the güiña is frequently cited as being closely associated (Miller and Rottmann, 1976; Melquist, 1984; Nowell and Jackson, 1996). Instead individuals within both the PNLSR and PNQ study sites consistently selected the relatively dense thicket-forest habitat that is itself often associated with *Nothofagus* forest. Thicket-forest was utilised in preference to all other available habitat categories at both the scale of individual home ranges (second-order selection) and radiolocations (third-order selection). A preference was also displayed for the densely structured thicket habitat, although güiña selection for this category was not as strong or as consistent as it was for thicket-forest (Figure 6.3.5; Tables 6.3.2-6.3.4 and 6.3.7-6.3.9).

Several factors are expected to contribute to habitat selection, but the most influential is likely to be the relative availability of small mammals and birds, the güiña's principal prey. Although broadly similar densities of small mammals were recorded within forest and thicket vegetation as in areas of thicket-forest, these two habitats probably differed in their accessibility and the degree of concealment that they provided to foraging güiña. Forest typically has very sparse ground-level vegetation (see Plate 3a), hence provides little in the way of cover for a stalking predator. Pure thicket, in contrast grows as very dense stands (Plate 3b). Movement throughout this habitat is unlikely to be easy, and visibility is expected to be low. As most cats locate their prey primarily by sight (Kitchener, 1991), the density of thicket stands may limit güiña foraging success within this habitat.

In this study, contiguous güiña home ranges within two apparently high-density populations were found to display considerable spatial overlap, both within and between the sexes. Areas of core use also overlapped extensively, and no evidence was found to indicate the temporal avoidance of conspecifics, even within these areas of intense utilisation. This apparent social tolerance is unusual for a solitary predator (Bekoff *et al.*, 1984; Cluttonbrock, 1989; Sandell, 1989) and is in contrast to the behaviour of güiña recorded during the only other radiotracking study of this kind (Sanderson *et al.*, 2002), indicating that territoriality may be facultative for this species.

A possible explanation for the pattern of güiña spatial organisation observed during this study is that individuals are encountering difficulties in establishing home ranges, resulting in 'frustrated dispersal' (Lidicker, 1973). Approximately one third of the güiña trapped during this study were of subadult or juvenile status. If these animals cannot leave their natal range at the age of independence, for example due to barriers to dispersal or a lack of suitable available areas, they may remain in their natal range. Animal SJM4 for example was captured as a juvenile towards the beginning of this study, and still remained in the vicinity of his mother's range two years later, by which time this male had reached adult status.

The hypothesis of frustrated dispersal fits well with the geography of the PNLSR study area as this site represents a habitat island almost entirely isolated from other areas of suitable habitat by the San Rafael Laguna to the west, the San Rafael glacier to the south, and by mountains to the east (see Figure 1.4.2). The PNQ study area however is situated within an extensive region of contiguous forest and associated native habitat; hence it seems less probable that PNQ güiña lacked dispersal options. This area is very mountainous however. If güiña are limited to valley floors and other areas of low elevation then the availability of suitable areas for permanent occupancy or for use as dispersal corridors is far more restricted than that predicted from landcover alone, and may severely limit opportunities for the establishment of home ranges in vacant areas.

7.2 The current status of the güiña in Chile

Although the güiña has been extirpated from parts of its former range, baseline information is lacking and there are no data on which to base accurate estimates of current population size. Environmental niche factor analysis (ENFA) identified 3,380 km^2 within the 61,400 km^2 reference area (i.e. 5.5%) where habitat 'suitability' for güiña was anticipated to be greater than 50% (Figure 6.3.7). Taking 50% suitability as a minimum quality threshold for the prediction of güiña distribution (Hirzel *et al.*, 2002a), in conjunction with the more conservative population density estimate of 0.77 individuals km^{-2} (PNLSR site estimate, Chapter 4), indicates there may be in the region of 2600 güiña living within the reference area.

The general consensus among population biologists is that for many vertebrate species the minimum number of animals required for a population to remain viable over a period of 100 years or more is between 50 and 100 breeding individuals (Seidensticker, 1986;

Shaffer, 1987; Allen *et al.*, 2001). If these populations are also relatively isolated from potential sources of immigration, then several hundred breeding animals may be needed to conserve genetic diversity (Lande and Barrowclough, 1987). Populations need to be larger still if they are to have a high probability of surviving environmental and catastrophic stochasticity (for example an epidemic or natural disaster) (Shaffer 1987, Lande, 1988). Thus minimum viable populations are often of the order of several thousand individuals (Belovsky 1987, Soulé 1987b, Thomas, 1990).

If the observed ratio of adult to non-adult animals detailed in Chapter 2 is assumed to be typical for this species, a minimum population size of 150 is therefore required to ensure the presence of approximately 100 breeding individuals. Using the PNLSR güiña population density estimate of 0.77 individuals km^{-2} as an approximation for güiña densities within good quality habitat, only those patches larger than 200 km^{2} are expected to support güiña populations of 150 or more animals. This is likely to be an underestimate of minimum patch size for two reasons: firstly no radio tracking was undertaken during the winter months, when range sizes might be expected to be larger, and secondly because it is possible that not all adult güiña are reproductively active.

Only two areas of contiguous high quality güiña habitat, as determined by the ENFA model meet the 200 km^{2} area threshold: Isla Leucayec (610000 E, 5175000 S) in the north-western corner of Figure 6.3.7, and a very flat region of low elevation to the immediate west and northwest of Laguna San Rafael. Elsewhere, high quality habitat is more fragmented and linear in shape due to the close association of thicket-forest communities with areas of low elevation, such as valley floors.

These estimates of population density and minimum viable population size must be viewed with caution however, and are intended as a guide only. Arguably this study was conducted within some of the most productive güiña habitat in Chile. Indeed, the two sites were chosen partially because of the considerable abundance of güiña spoor found in each. For this reason, the density estimate of 0.77 individuals km^{-2} may not be realistic for many güiña populations elsewhere, although some of this potential error was accounted for by the ENFA model, which identified areas of non-suitable habitat. Because the population estimate was derived by extrapolation to preferred habitat, lower quality habitat did not appreciably influence the population estimate. Furthermore, no index of landscape connectivity was incorporated into this estimate; güiña may therefore be absent from much of the area identified as suitable for occupation if barriers such as forest clearings impede dispersal.

These considerations potentially serve to reduce the probable güiña population size present within the reference area, however it should be noted that there is evidence that güiña will incorporate habitat into their home ranges for which the ENFA model assigned suitability scores of less than 50% (for example animals SSM1 and SAF7, see Figures 4.3.3a, 4.3.4a and 6.3.8a). Thus, although güiña show a consistent preference for thicket-forest, they are sufficiently adaptable to utilise alternative habitats. That neither study site is located within a large (> 200 km^2) block of contiguous, high quality habitat is a further indication of the güiña's ability to utilise more marginal habitat than that highlighted by the ENFA model (note that the PNLSR study site is geographically separated from the expanse of suitable habitat to the west by the Río Témpano, see Figure 1.5.2).

Although güiña displayed no strong or consistent preference for forest (the dominant habitat throughout the reference area; Figure 2.2.1), areas of forest were not generally avoided (frequency values -0.04, i.e. close to neutral marginality on this variable; see also Figure 6.3.5; Tables 6.3.2-6.3.4 and 6.3.7-6.3.9). Forest habitat is therefore unlikely to represent a significant barrier to güiña movements between high quality areas, and may indeed be important for foraging activities.

A similar behaviour has been recorded among dispersing Iberian lynx, which frequently use lower quality habitats than those incorporated into the long-term home range areas of resident animals (Palomares, 2001). This behavioural flexibility promotes the persistence of metapopulation dynamics between small neighbouring subpopulations (Gotelli, 1991) and serves to reduce the effective population size necessary to maintain genetic viability within a fragmented landscape (Soulé, 1987b; Boyce, 1992; Hanski and Simberloff, 1997; Reed *et al.*, 2003; Rodriguez and Delibes, 2003). At the landscape level, high-density güiña populations such as those in PNLSR and PNQ are likely to be widely and irregularly spaced and to correspond with areas of high quality habitat such as those highlighted by the ENFA model. The surrounding matrix is comprised of less optimal habitat where güiña home ranges are potentially larger, and individuals may be more territorial towards conspecifics, leading to lower population densities.

7.3 Implications for the conservation and management of güiña

Discontinuous habitat, whether naturally fragmented or resulting from anthropogenic influence can restrict an individual or species to a limited subset of its environment. Where the spatial arrangement of suitable patches is such that patch connectivity is low and many suitable areas are isolated, the potential for movement between these patches is determined by the inter-patch distance, the dispersal capabilities of the species, and the level of aversion it has for the intervening habitats. For all but the most vagile or generalist species the process of habitat fragmentation thus simultaneously reduces the potential for migration and genetic interchange between remaining populations, and increases the probability of extinction of such populations due to demographic and stochastic effects (Gilpin and Hanski, 1991; Harrison, 1991).

The continuing deforestation and modification of native habitat within central and southern Chile is producing ever smaller and more isolated habitat remnants within matrices of transformed landscape (Ancient Forest International, 1990; Donoso and Lara, 1996; Lara *et al.*, 1996; San Martín and Donoso, 1996; Bustamante and Castor, 1998). Furthermore, in this region as in other mountainous areas, low-lying land such as valley floors is relatively accessible and thus often the first to be disturbed by human intrusion, for example agro-forestry or tourism. Throughout this study, radio-collared güiña displayed a consistent preference for thicket-forest habitat at both the second- and third-order spatial scales. Whilst this naturally fragmented resource represents only a small proportion of available habitat, its importance to güiña conservation is nevertheless high since it provides cover both during foraging and for movement across more exposed landscapes. Because high elevations are suspected to act as a barrier to güiña movement, disturbance of thicket-forest corridors at low elevations therefore threatens to further reduce and fragment this important habitat.

A preliminary examination of güiña nuclear (microsatellite) DNA and mitochondrial DNA from samples obtained during this study suggested low levels of genetic variability within each of the PNLSR and PNQ populations. Twenty polymorphic mtDNA nucleotide sites (out of 500 bp) revealed only two haplotypes among ten güiña from PNLSR, and three haplotypes among eight individuals from PNQ. No mtDNA haplotype occurred in both samples, and microsatellite DNA alleles unique to just a single study population were determined at three out of four loci (n = 23 for the microsatellite data; 11 individuals from PNLSR and 12 from PNQ), suggesting some level of isolation of these populations. The single individual captured on the western shore of Laguna San Rafael had a unique mtDNA haplotype that was highly dissimilar from those identified from the neighbouring PNLSR population, differing by 3%.

Although these sample sizes are small and results may be biased by sampling kin, these preliminary analyses indicate that there is a high degree of genetic dissimilarity between the PNLSR and PNQ güiña populations, yet within each population individuals exhibit very little genetic variation.

Due to the restricted nature of its geographical distribution the güiña is considered particularly vulnerable to habitat loss (Nowell and Jackson, 1996). However, a more thorough understanding of the mechanisms responsible for its decline from the northern regions of its historical range is needed if the success of long-term conservation measures for this species is to be achieved. The current study helps to explain the retraction of the güiña's range, and indicates that the preferred habitat of this species was never likely to have been common. Assuming dense vegetation such as thicket-forest is key habitat for the güiña, the widespread reduction and replacement of native vegetation with, for example, conifer plantations and pasture, particularly in the relatively accessible, low elevation regions of central Chile, would have dramatically reduced the availability of prime güiña habitat and further fragmented its already patchy distribution.

7.4 Management recommendations

Environmental niche factor analysis described, by way of a simple visual output, the predicted amount, distribution, and current level of fragmentation of favourable güiña habitat in southern Chile. Both the ENFA output and the results obtained from compositional analysis highlight the güiña's close association with thicket-forest habitat. The most obvious targets for conservation planning and management that emerge from these analyses are therefore to preserve contiguous areas of dense vegetation, as characterised by the thicket-forest category used in these analyses, and any intervening patches of suitable habitat that link these areas. Since güiña will also utilise more marginal habitat, including stands of pure forest and thicket, these habitat 'corridors' need not necessarily be comprised of thicket-forest.

Both this study and that of Sanderson *et al.* (2002) found güiña to consistently avoid open areas and short vegetation where this provided little or no overhead cover. Thus open areas are expected to represent barriers to güiña movement unless they are very small. In sites where the movement of güiña is already restricted, for example valley systems, the clearance of native habitat therefore need not be extensive to effectively block güiña dispersal routes. This risk needs to be taken into consideration during the planning stages of valley system developments, for example the clearance of native vegetation for agriculture, and efforts should be made to encourage the preservation of intact habitat corridors.

Despite the creation of several national parks, much of what was once public forest has been converted to private ownership. Within Chile only 1.4 million hectares of the original 30 million hectares of native forest are currently contained within protected areas (Armesto *et al.,* 1994). Figure 1.2.2 shows the existing network of national parks and other protected areas. There are many such areas in the south of the country, however the majority of these lie further south than the güiña's predicted distribution range (Nowell and Jackson, 1996; Figure 1.2.1). In general, the forested part of the güiña's southern range is sparsely populated by man, and a substantial proportion of the remaining forest in southern Chile is protected (World Conservation Monitoring Centre, 1992), as are several large areas within the güiña's Argentinean range (Melquist, 1984).

In central Chile, at the northern limit of the güiña's range, there are fewer protected sites and most of these are very small (Armesto *et al.*, 1998; Simonetti, 1999). A preliminary modelling exercise based on the central Chilean coastal forests between 35° 30′ to 38° S highlights the need for the preservation of native forest fragments outside of protected areas, and indicates that only 10% of güiña populations within this area numbered more than 70 individuals (Acosta-Jamett *et al.* in press). Consequently, management planning for güiña should seek to establish more protected areas throughout the species' range, particularly at more northerly latitudes, and target sites where güiña presence has been confirmed or is suspected, in addition to neighbouring areas of suitable güiña habitat.

Parque Nacional Laguna San Rafael and the region of land highlighted by the ENFA output to the west and northwest of this park are both protected areas; however Isla Leucayec is not, and Parque Nacional Queulat is surrounded to the north, east and south by private land. The majority of the North Patagonian forests are privately owned (CONAF *et al.,* 1997), and so many güiña populations are likely to reside within areas lacking formal protection. The maintenance of existing suitable habitat and of corridors that enable the dispersal of güiña between these patches therefore requires integrative ecosystem management involving the cooperation of all interested parties wherever possible.

Maintaining, or re-establishing corridors between fragmented populations will reduce the loss of genetic variation and be a step towards ensuring the long-term survival of existing populations. Although thicket-forest habitat may represent optimal habitat for güiña, this species is able to use secondary vegetation, hence plantations, logging and agricultural practices do not necessarily pose a serious threat to güiña dispersal if they are located sensitively and maintain travel corridors of dense vegetation. Through compromise and careful exploitation of privately owned land in a way that is sensitive to güiña requirements, the detrimental impacts of future developments may be minimised.

Considerable local interest in the güiña was evident among the local villagers living close to the two study areas, and even people within the larger towns where very few had had direct contact with this species were able to instantly identify güiña from photographs. From a conservation perspective, therefore, the güiña has the potential to act as a 'flagship species', by which to motivate and providing a focus for public support for the conservation and management of remaining temperate rainforests. As the largest resident predator (with the occasional exception of puma) within each of the two study areas the güiña may also fulfil the role of 'keystone species' (Mills *et al.*, 1993). Furthermore, where other species have similar associations for thicket-forest habitat, including the plant species themselves, management strategies that conserve this habitat for the güiña will also indirectly benefit these species.

7.5 Future work

The use of models to predict the distribution of target species is an important preliminary step in the conservation planning and management process (Pearson *et al.*, 1999; Manel *et al.*, 2001). This current study has identified both the location and size of 'islands' of highly suitable güiña habitat within a comparatively less suitable matrix that can be used to predict the distribution of güiña populations. There is much latitude for refinement of the current ENFA model however, for example by incorporating güiña presence data collected from additional sites within this species' distribution range, particularly from locations within more marginal habitat and from sites at higher elevations wherever possible.

Long-term conservation efforts also require a better understanding of güiña dispersal patterns. There is a particular need to investigate güiña movement capabilities within landscapes interrupted by, for example, non-native vegetation or other unfavourable terrain. Land use data, such as the distribution of private lands may also be incorporated into the model to aid the mapping of potential barriers to dispersal, and to enable management schemes to address the threat of inbreeding depression under alternative management schemes. The subsequent step should be to apply population viability analyses (Boyce, 1992; Lindenmayer *et al.*, 2001) to existing habitat patches in southern Chile to assess whether these are large enough to support viable güiña populations in the long term.

Because the spatial layout of the landscape is explicitly incorporated within the ENFA model this predictive approach can also be applied to assess how güiña populations might be affected by changes in habitat composition, fragmentation, and location within the landscape over time (Dunning *et al.*, 1992). Simulation models require very detailed data as input; however if it is possible in the future to incorporate data on dispersal, terrain and prey biomass, such an approach can prove useful in areas where these factors are limiting, and may contribute to land-use planning by representing habitats from a species perspective (Knick and Dyer, 1997). Dynamic modelling can also be used to assess to what extent population viability is influenced by factors acting at both broad and local scales, such as road construction and reforestation or plantation schemes.

While the techniques employed in this study may aid in locating potential güiña habitat, they are no substitute however for ground-based verification of güiña presence or absence. Unfortunately, field surveys are very expensive and time-consuming, require trained and motivated personnel and also standardisation of methodologies. The ENFA model applied in this study, and other, equivalent predictive models are able to identify areas of habitat potentially suitable for güiña. Such models therefore represent a valuable tool by which sites could be prioritised for visitation and status validation. These status surveys should then contribute towards regionally based conservation plans for key güiña areas, and intervening habitat that permits movement between these important areas.

The primary constraints of this study are the small number of individuals that were successfully monitored, the relatively short duration of this study (two years in each site) and the lack of winter data. However, the findings presented here represent the first detailed study of the güiña, and provide a good starting point from which to direct population surveys and more informed management programs in the future. Despite the inherent uncertainty in extrapolating population distributions and size estimates from survey data, I provide here the first estimate of the current güiña population size based on detailed landcover and habitat preference data, although it is recognised this should be further verified by winter work.

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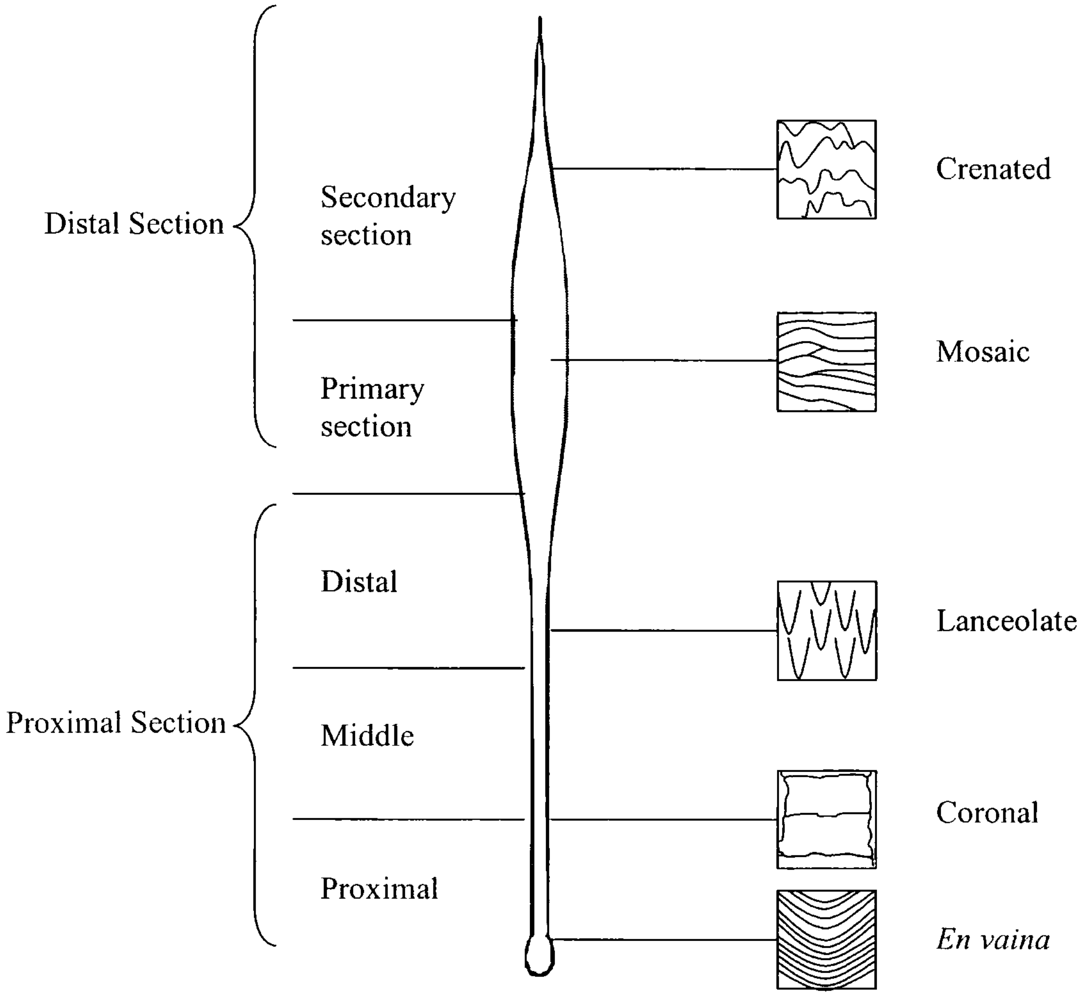
Appendix 1 Major land cover categories within PNLSR and PNQ, as identified from field surveys.

Land cover type	Description
Forest	Forest habitat is dominated by *Nothofagus nitida* and *N. betuloides*, with *Weinmannia trichosperma*, *Podocarpus nubigena*, *Drimys winteri* and *Laureliopsis philippiana* interspersed. The sparse understory is mostly comprised of moss and hymenophyllaceous fern cover.
Thicket	Thicket species *Berberis buxifolia, B. chilensis, Fuschia magellanica* and *Desfontainia spinosa* form a dense understory, to a height of approximately 1.5 m.
Thicket-forest	Tree species *N. nitida, N. betuloides, D. winteri, W. trichosperma, L. philippiana* and *P. nubigen* are interspersed within a dense understory of *B. buxifolia, B. chilensis, F. magellanica, D. spinosa, Chusquea quila* and *Gunnera chilensis*
Scrub	Scrub habitat is characterised by relatively open areas of low (< 1 m) vegetation, dominated by *Gaultheria phillyreifolia, Escallonia alpina, Empetrum rubrum* and *Acaena megallanica.*
Scrub-thicket	Scrub-thicket grows more densely than scrub, and to a height of approximately 1m. This habitat includes many short, scrubby species, including *G. phillyreifolia, E. alpina, E. rubrum* and *A. megallanica*, in addition to thicket species *B. buxifolia* and *B. chilensis.*
Open	'Open' areas are often the result of landslides. Vegetation that colonises these open spaces is typically very short (< 10 cm), often stunted due to minimal soil cover.
Saltmarsh	Saltmarsh communities are comprised of short (< 50 cm) salt-tolerant species, including *Arenaria serpans, Senecio candidans, Colobanthus quitensis* and *Puccinellia glaucescens.*

Appendix 2 Identification of small mammal species from guard hair morphological characteristics.

Mammals typically possess two distinct types of pelage: guard hair and undercoat. Guard hairs have highly variable, species-specific cuticular scale patterns and are of considerable value for species identification. The fine undercoat hairs display less distinct variation between related species and are less suitable for use in reference keys (Day, 1966). Guard hair can be divided longitudinally into discreet sections (see Figure A1 below). The distal section (the hair tip) is comprised of broad scales that create lateral 'line' patterns across the hair width, and can be further subdivided into primary and secondary parts. 'Mosaic' and 'crenated' scale patterns are both common within this section. The edges of mosaic scales align to form smooth lines, though in some species these are interrupted by tooth-like projections. Crenated scales in contrast are rough or corrugated. Mosaic and crenated scale patterns occur in a variety of combinations between the primary and secondary parts of the distal section. Their alignment can be straight across the hair width, chevronated or form a wave pattern.

Figure A1. Structure and cuticular scale pattern of a typical guard hair (adapted from Chehébar and Martín, 1989).



The proximal sections of different species display variable combinations of scale patterns and are further subdivided into distal, middle and proximal parts. The principal scale pattern is *lanceolate*, where the overlapping spear-tip shaped scales are arranged in one of several alternative arrangements:

Even - scales are approximately in equal size and are arranged evenly across the breadth of the hair. Scales may be long or obtuse and have rounded or pointed tips. Exaggerated styles include the semi-obtuse *rhomboid* or *diamond lanceolate* arrangement (see Plate 7h).

Uneven - scales are uneven or unequal in appearance.

Fused - scales appear fused, often generating a twin tipped scale with a faint join running from the tip to the base of the scale. In extreme cases the scales are fused into plate-like structures with uneven tips.

En vaina – Adjacent scales meet and overlap across or near the centre of the hair. This pattern is common in the most proximal section, the hair base.

Appendix 3 Dichotomous key for the identification of small mammal species from the forests of the Valdivian and Magellanic bioregions using guard hair morphological characteristics.

1. Secondary part of distal section mosaic	2
Secondary part of distal section crenated	6
2. Mosaic in secondary part toothed	*Auliscomys micropus*
Mosaic in secondary part simple	3
3. Mosaic in secondary part fine	*Dromiciops gliroides*
Mosaic in secondary part broad	4
4. Distal part of proximal section uneven lanceolate, proximal part of proximal section diamond shaped	*Irenomys tarsalis*
Distal part of proximal section not lanceolate	5
5. Distal part of proximal section with large v-shaped plates	*Oryzomys longicaudatus*
Distil part of proximal section *en vaina*	*Phyllotis darwini*
6. Primary part of distil section crenated, distil part of distil section broad, rounded lanceolate	*Geoxus valdivianus*
Primary part of distil section mosaic, distil part of proximal section fused	7
7. Proximal part of proximal section *en vaina* preceded by lanceolate scales	*Akodon olivaceus*
Proximal part of proximal section *en vaina* preceded by fused scales	*Akodon longipilis*

Appendix 4 Matrices of mean-corrected sums of squares (R_1) and raw sums of squares (R_2) calculated from log-transformed ratios of available and utilised habitat.

PNLSR Second-order selection

R_1

334.15	56.88	24.15	345.04	-214.18	52.73	-10.99
56.88	100.07	68.33	57.48	39.57	53.31	-43.46
24.15	68.33	51.14	3.30	34.99	44.58	-26.34
345.04	57.48	3.30	470.82	-202.28	-0.98	-46.94
-214.18	39.57	34.99	-202.28	248.39	-58.25	-8.41
52.73	53.31	44.58	-0.98	-58.25	156.01	129.13
-10.99	-43.46	-26.34	-46.94	-8.41	129.13	774.29

R_2

851.08	988.25	769.57	605.28	237.04	479.72	-469.87
988.25	1778.14	1411.37	526.36	822.63	822.63	-870.23
769.57	1411.37	1126.03	378.57	685.65	660.30	-688.04
605.28	526.36	378.57	601.83	24.88	213.98	-277.95
237.04	822.63	685.65	24.88	642.24	314.46	-408.95
479.72	822.63	660.30	213.98	314.46	508.71	-249.91
-469.87	-870.23	-688.04	-277.95	-408.95	-249.91	1181.63

$\Lambda < 0.001$; Aebischer's test statistic = 431.07.

PNLSR Third-order selection

R_1

133.54	161.73	89.70	73.59	122.08	-22.89	955.52
161.73	212.61	116.54	244.02	144.87	43.76	1295.70
89.70	116.54	70.85	233.67	103.47	-65.74	662.91
73.59	244.02	233.67	4105.90	386.55	-635.14	1904.50
122.08	144.87	103.47	386.55	192.68	-425.00	678.93
-22.89	43.76	-65.74	-635.14	-425.00	4548.11	1034.21
955.52	1295.70	662.91	1904.50	678.93	1034.21	9062.87

R_2

134.68	155.32	84.98	152.80	138.50	64.12	1063.27
155.32	248.53	142.98	-199.53	-443.44	-443.44	692.34
84.98	142.98	90.31	-92.81	35.78	-424.35	218.80
152.80	-199.53	-92.81	9583.02	1522.06	5380.96	9355.07
138.50	-443.44	35.78	1522.06	428.09	822.26	2223.58
64.12	-443.44	-424.35	5380.96	822.26	11156.25	9217.98
1063.27	692.34	218.80	9355.07	2223.58	9217.98	19197.96

$\Lambda < 0.001$; Aebischer's test statistic = 454.37

Appendix 4 continued.

PNQ Second-order selection

R_1

31.06	19.02	20.20	13.11	16.80	-86.48	-29.25
19.02	21.08	24.81	8.66	13.45	-106.17	-41.14
20.20	24.81	34.75	7.62	14.72	-157.20	-60.91
13.11	8.66	7.62	9.60	9.66	11.48	-2.53
16.80	13.45	14.72	9.66	11.63	-35.49	-17.93
-86.48	-106.17	-157.20	11.48	-35.49	1221.03	368.47
-29.25	-41.14	-60.91	-2.53	-17.93	368.47	126.57

R_2

75.45	68.81	68.99	20.30	45.97	-552.35	-121.74
68.81	76.93	79.54	16.73	-628.72	-628.72	-144.88
68.99	79.54	88.37	15.53	46.78	-669.18	-162.56
20.30	16.73	15.53	10.77	14.39	-64.02	-17.52
45.97	-628.72	46.78	14.39	30.80	-341.63	-78.71
-552.35	-628.72	-669.18	-64.02	-341.63	6109.96	1339.11
-121.74	-144.88	-162.56	-17.52	-78.71	1339.11	319.28

$\Lambda < 0.001$; Aebischer's test statistic = 486.51.

PNLSR Third-order selection

R_1

107.02	90.91	121.59	121.68	60.04	253.25	-84.17
90.91	111.15	143.53	101.74	67.47	80.43	-157.12
121.59	143.53	193.63	128.00	68.82	75.62	-267.03
121.68	101.74	128.00	175.34	91.92	465.36	-69.96
60.04	67.47	68.82	91.92	100.55	262.01	7.28
253.25	80.43	75.62	465.36	262.01	2095.64	167.24
-84.17	-157.12	-267.03	-69.96	7.28	167.24	1387.03

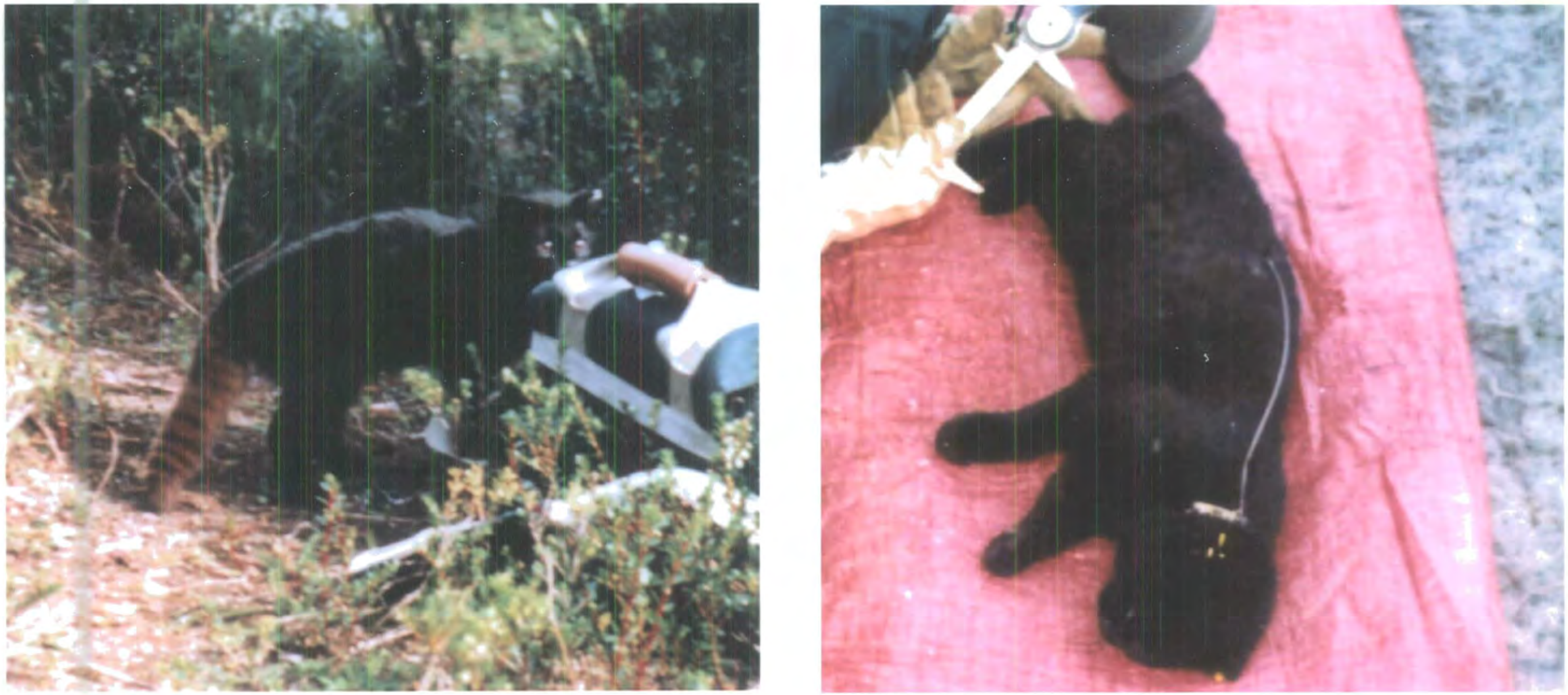
R_2

891.66	974.86	950.62	792.86	338.72	-271.33	-537.31
974.86	1106.96	1077.47	857.86	-510.54	-510.54	-667.60
950.62	1077.47	1069.54	837.13	363.26	-478.63	-745.79
792.86	857.86	837.13	749.47	330.31	16.64	-457.56
338.72	-510.54	363.26	330.31	199.54	75.69	-153.66
-271.33	-510.54	-478.63	16.64	75.69	2446.36	470.19
-537.31	-667.60	-745.79	-457.56	-153.66	470.19	1648.72

$\Lambda < 0.001$; Aebischer's test statistic = 466.97.

Plate 1 Sedated adult male güiña (animal QAM2) with whip-antennae of radio collar visible.

Plate 2 Melanistic güiña displaying the spots and stripes characteristic of this species a) juvenile male SJM4 and b) adult male SAM3.



a)

b)

Plate 3 Predominant habitat categories within the PNLSR and PNQ study sites.

Plate 3a Forest

Dominant species are *Nothofagus nitida and N. betuloides*.
Note the sparsity of ground-level vegetation relative to thicket-forest (see Plate 3b).

Plate 3b Predominant habitat categories within the PNLSR and PNQ study sites continued.

Thicket-forest

Thicket

Thicket-forest. Dominant species are: *Nothofagus nitida*, *N. betuloides*, *Drimys winteri*, *Weinmaninia trichosperma*, *Laurelia semperirens*, *Podocarpus nubigen*, *Chusquea quila* and *Gunnera chilensis*.

Thicket. Dominant species are: *Embothrium coccineum*, *Fuschia magellanica*, *Berberis buxifolia*, *B. chilensis*, and *Desfontainia spinosa*.

Plate 3c Predominant habitat categories within the PNLSR and PNQ study sites continued.

Scrub-thicket

Scrub

Scrub-thicket. Dominant species are: *Berberis buxifolia, B. chilensis* and *Empetrum rubrum*

Scrub. Dominant species are: *Escallonia alpina, Empetrum rubrum, Gaultheria phillyreifolia* and *Acaena megallanica.*

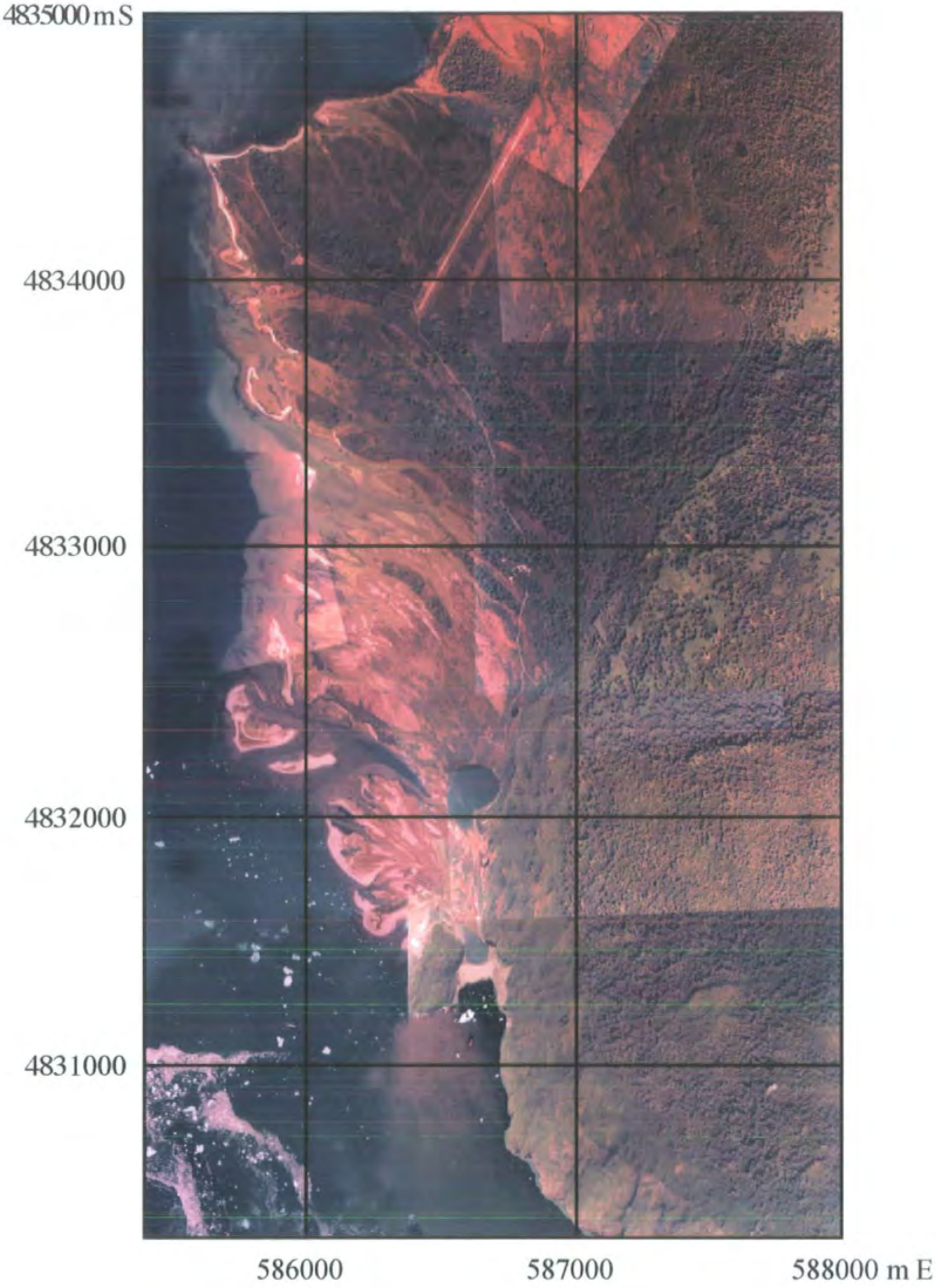


Plate 4 Photomontage of true colour planometric aerial photography of the Parque Nacional Laguna San Rafael (PNLSR) study area, taken during March 1999.

Plate 5 Photomontage of true colour planometric aerial photography of the Parque Nacional Queulat (PNQ) study area, taken during March 2000.

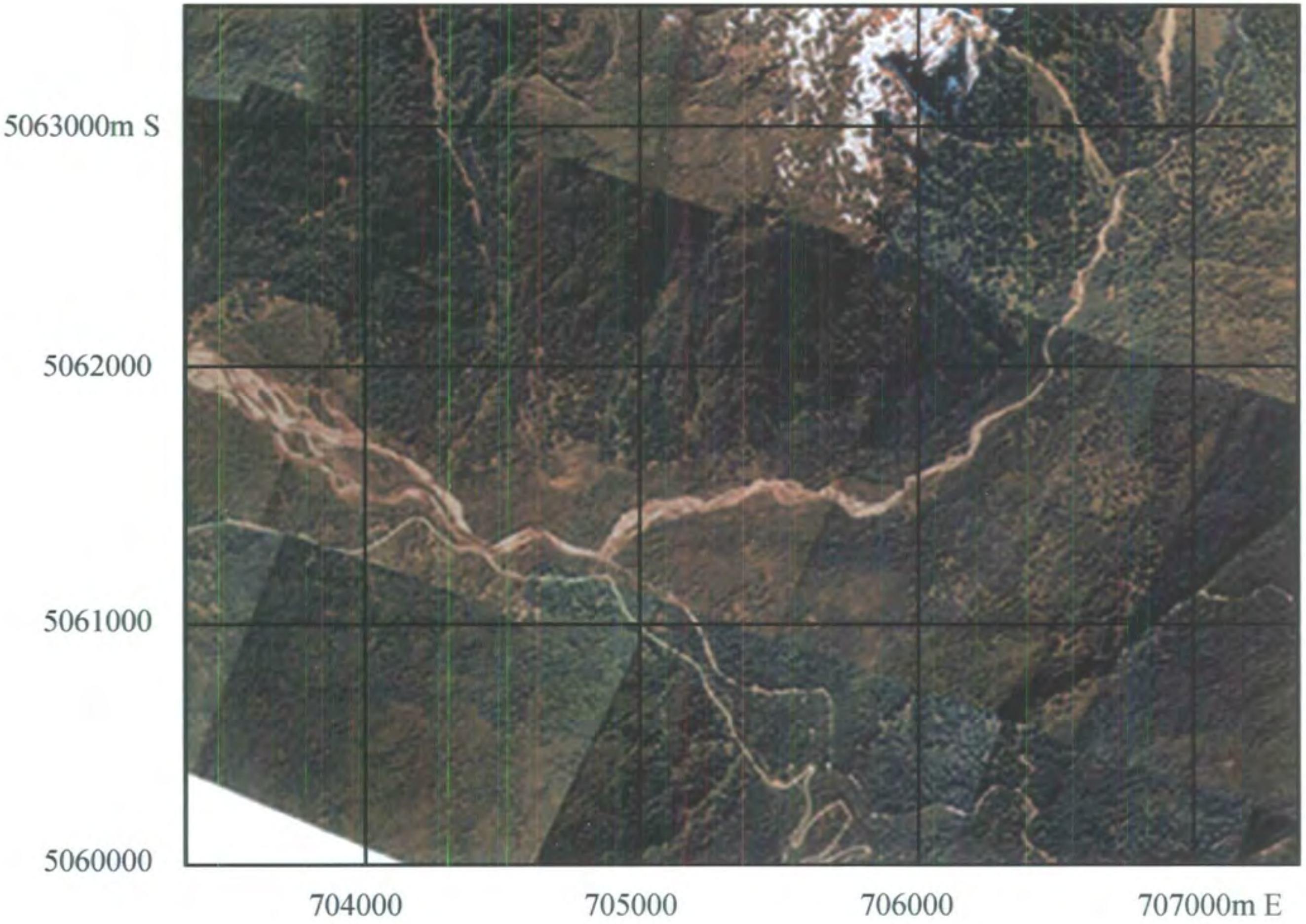
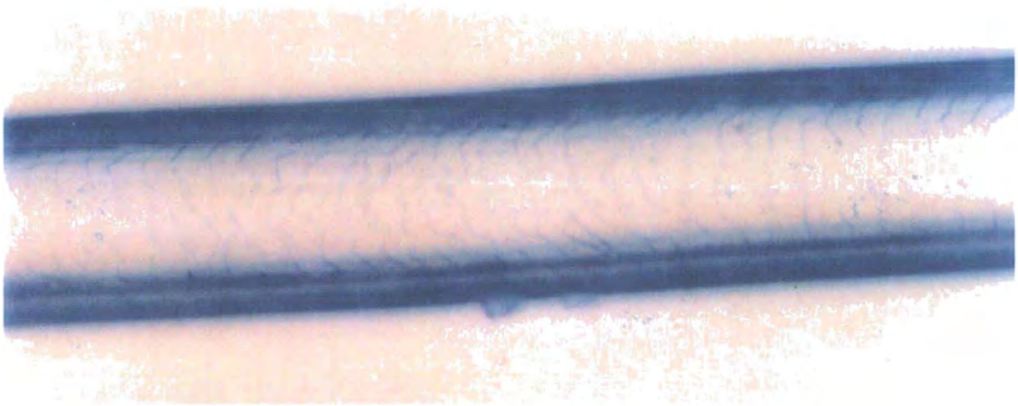


Plate 6 Güiña scat *in situ*

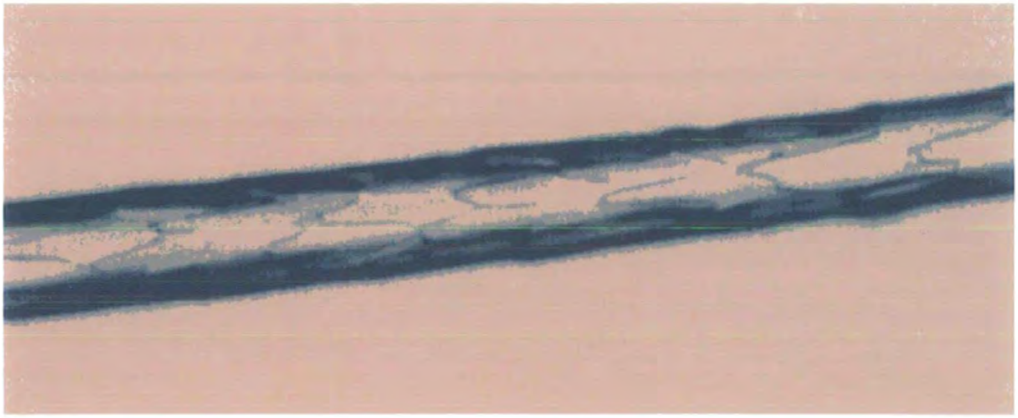
Plate 7 Guard hair scale pattern imprints used in the identification of small mammal species.

Plate 7a *Akodon longipilis*



(a) Hair tip

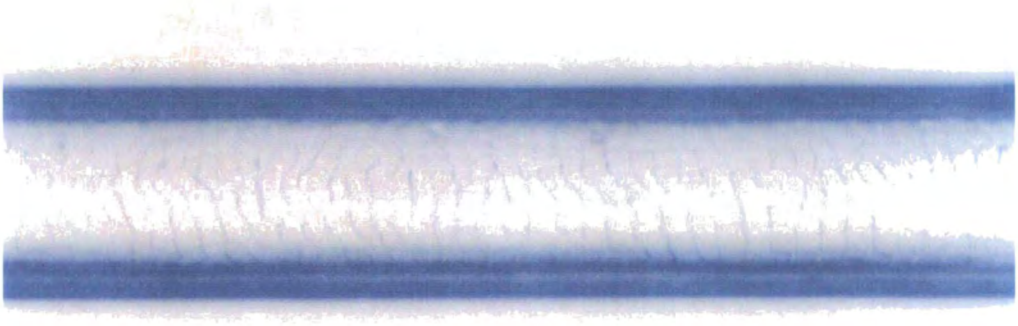
(b) Hair centre



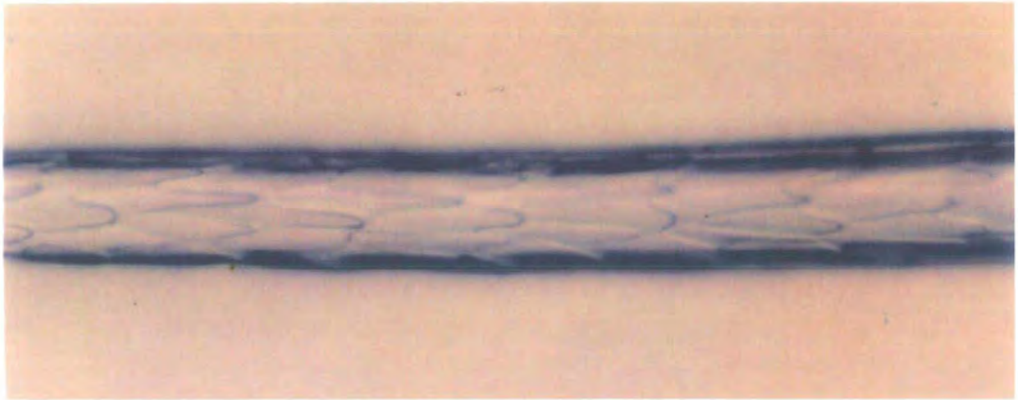
(c) Hair base

Plate 7 continued.

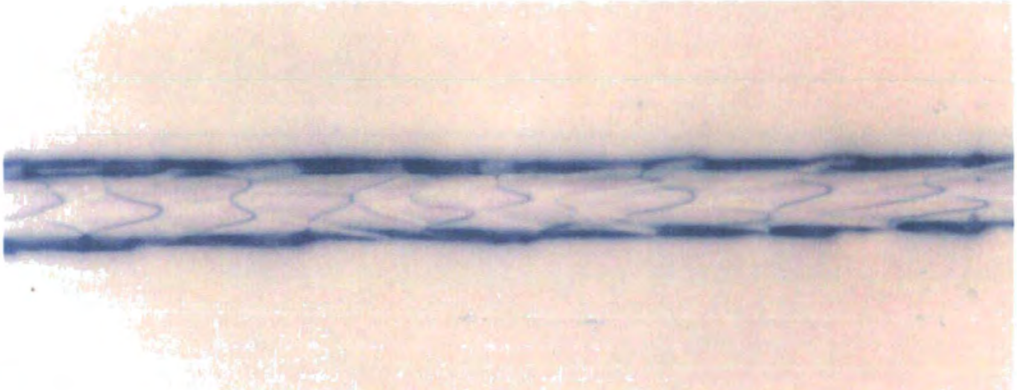
Plate 7b ***Akodon olivaceus***



(a) Hair tip



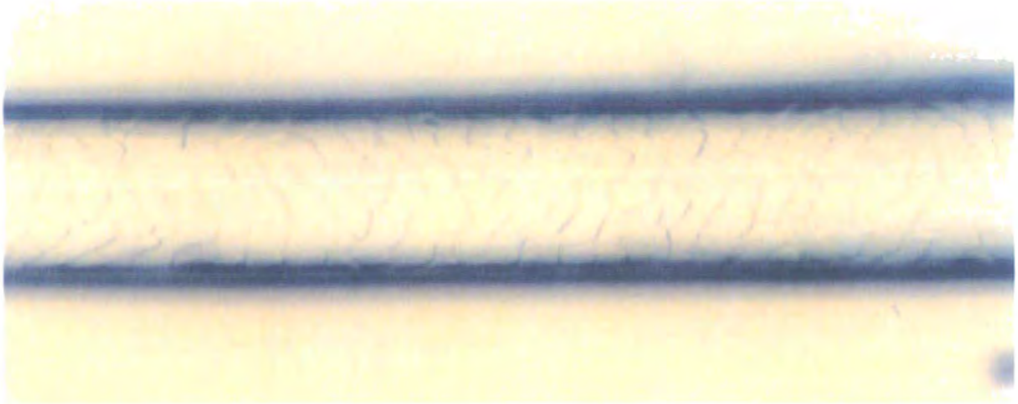
(b) Hair centre



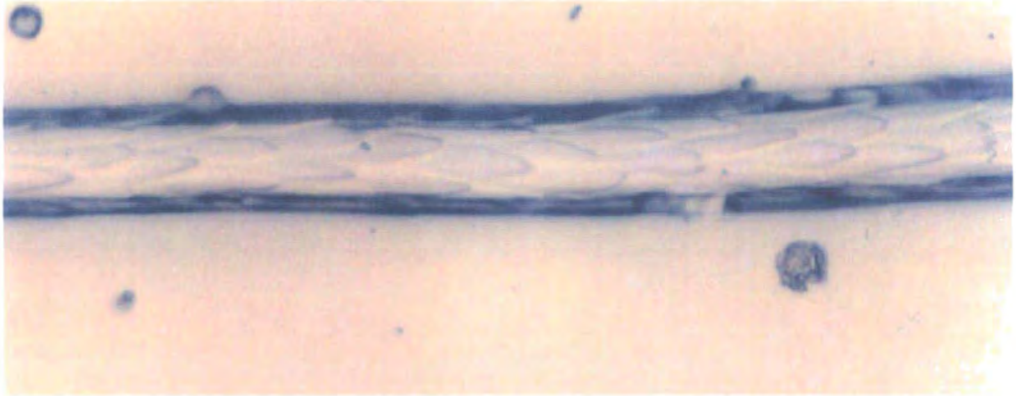
(c) Hair base

Plate 7 continued.

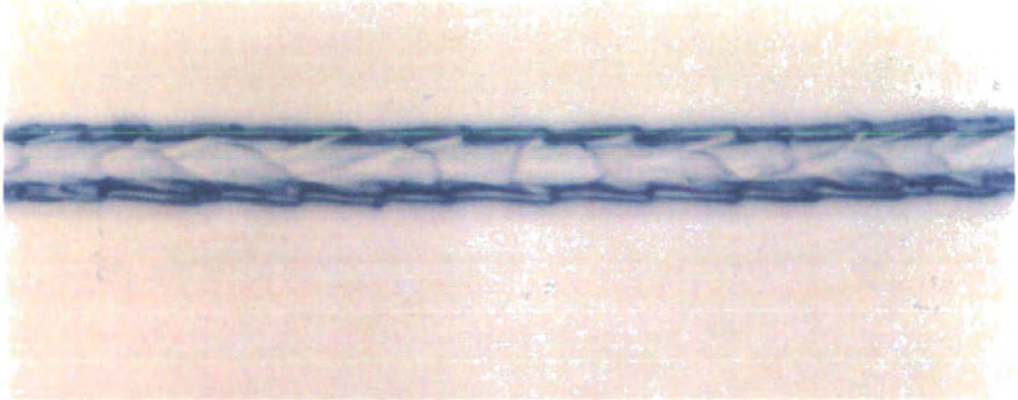
Plate 7c *Auliscomys micropus*



(a) Hair tip



(b) Hair centre

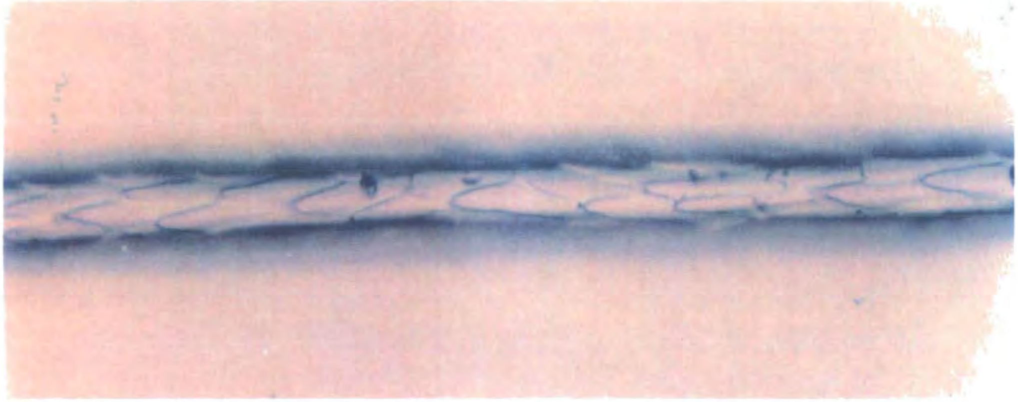


(c) Hair base

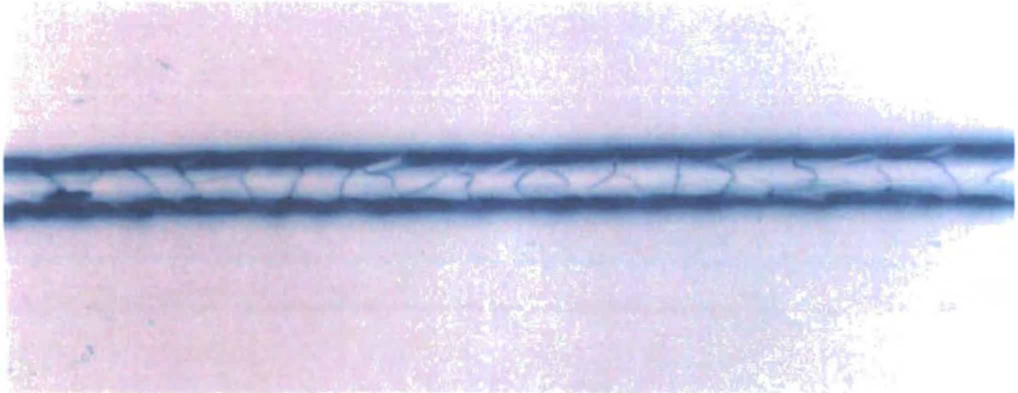
Plate 7 continued.

Plate 7d *Geoxus valdivianus*

*No photograph was obtained for this section. The hair tip was crenated in pattern.



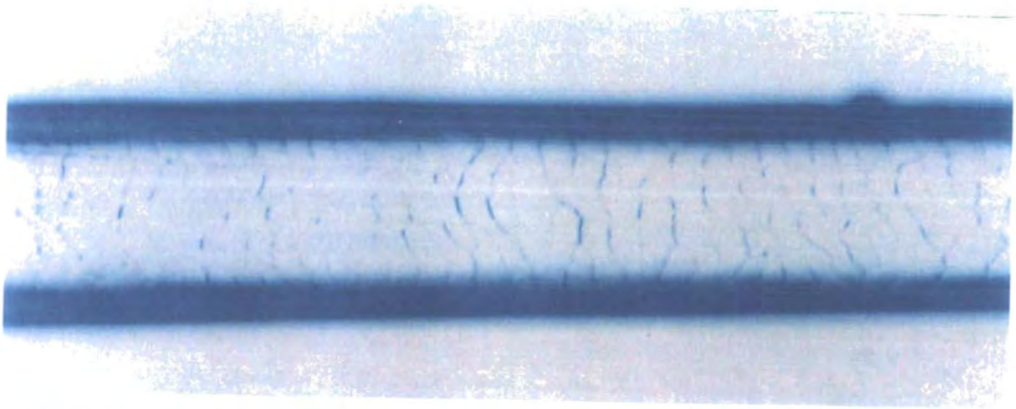
(b) Hair centre



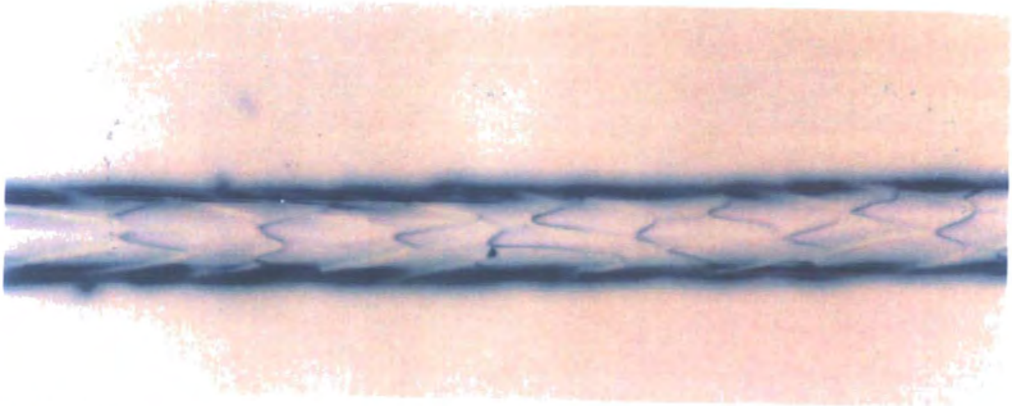
(c) Hair base

Plate 7 continued.

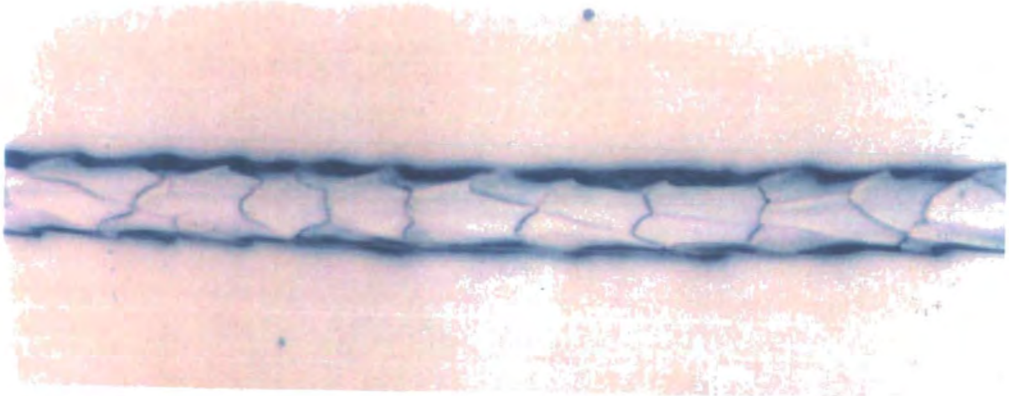
Plate 7e *Irenomys tarsalis*



(a) Hair tip



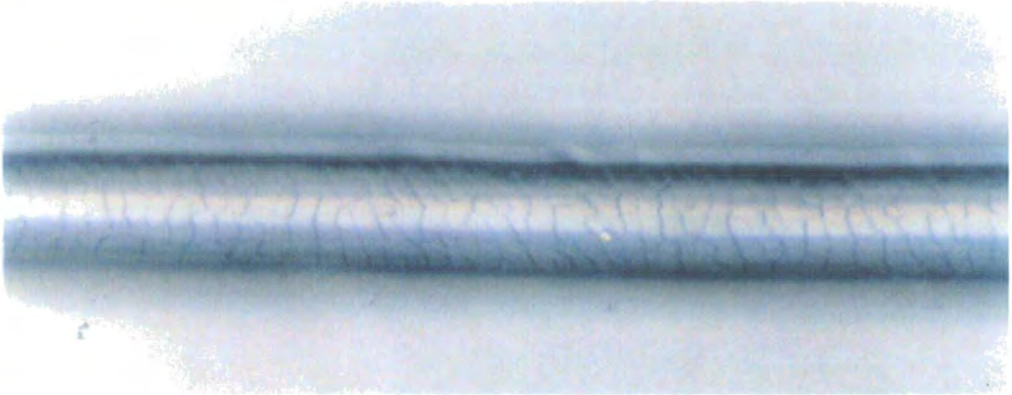
(b) Hair centre



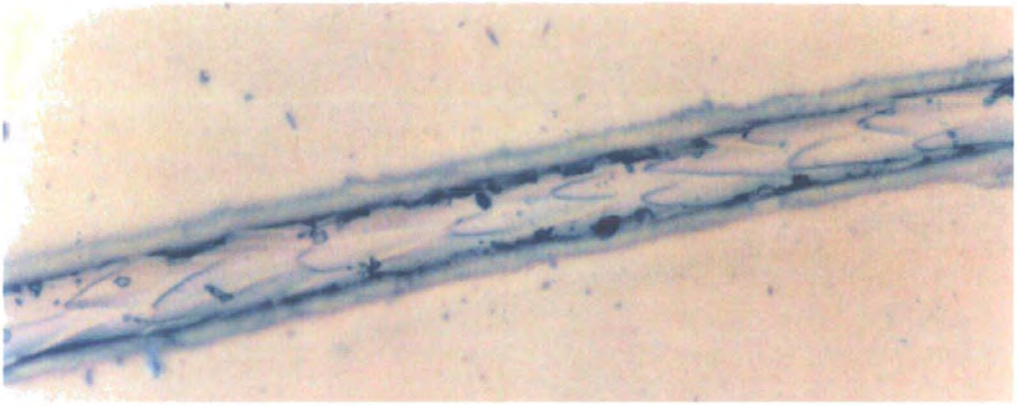
(c) Hair base

Plate 7 continued.

Plate 7f ***Oryzomys longicaudatus***



(a) Hair tip

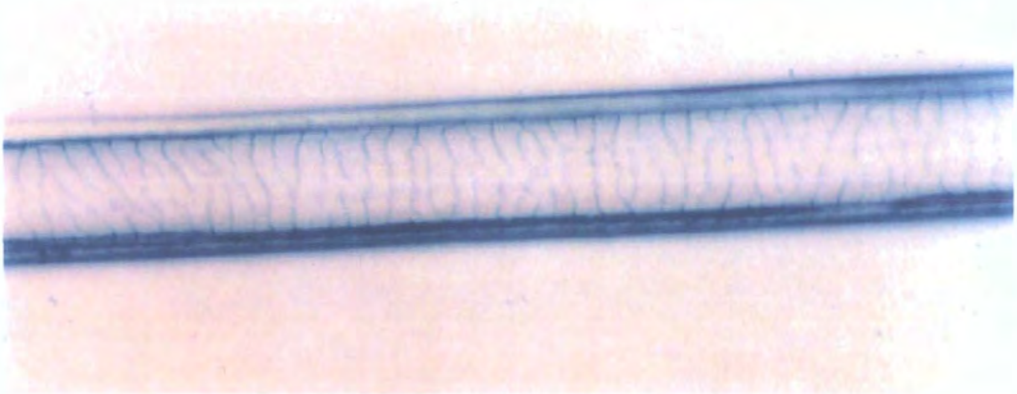


(b) Hair centre

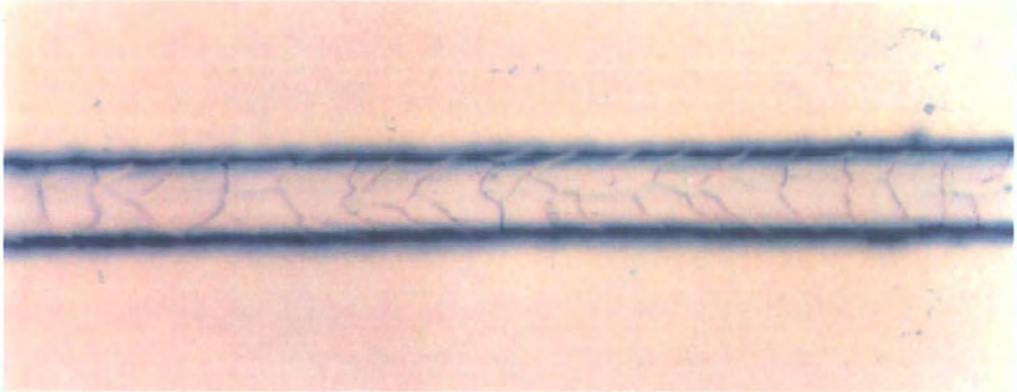
(c) Hair base

Plate 7 continued.

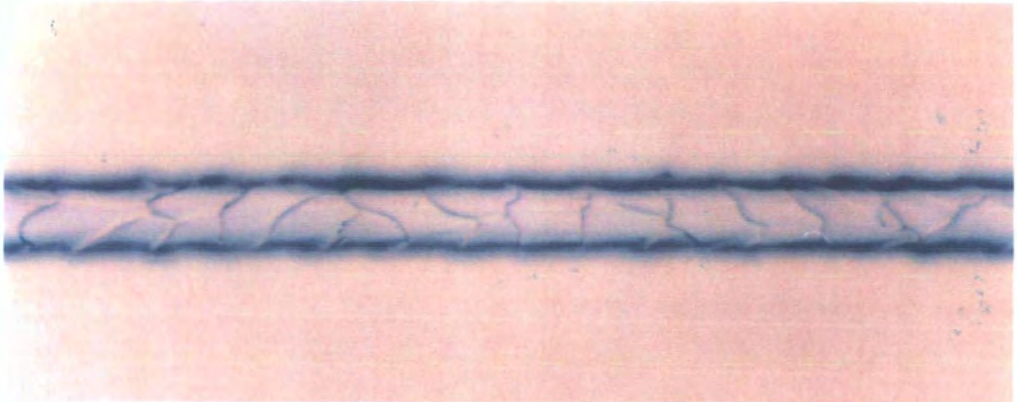
Plate 7g *Phyllotis darwini*



(a) Hair tip



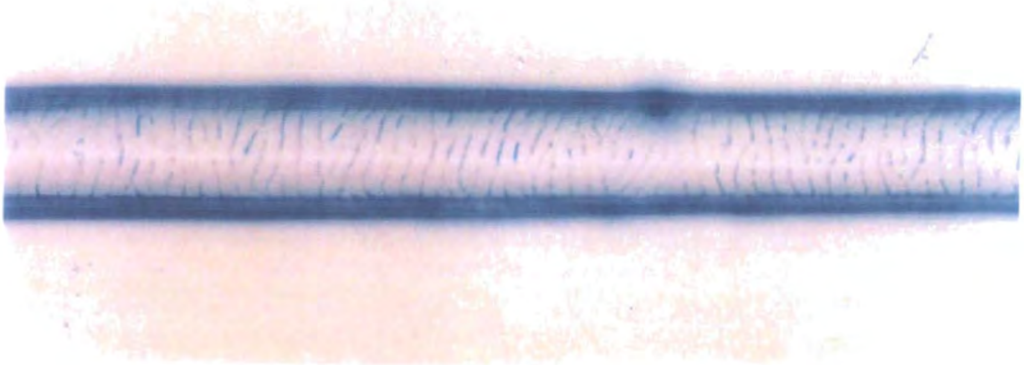
(b) Hair centre



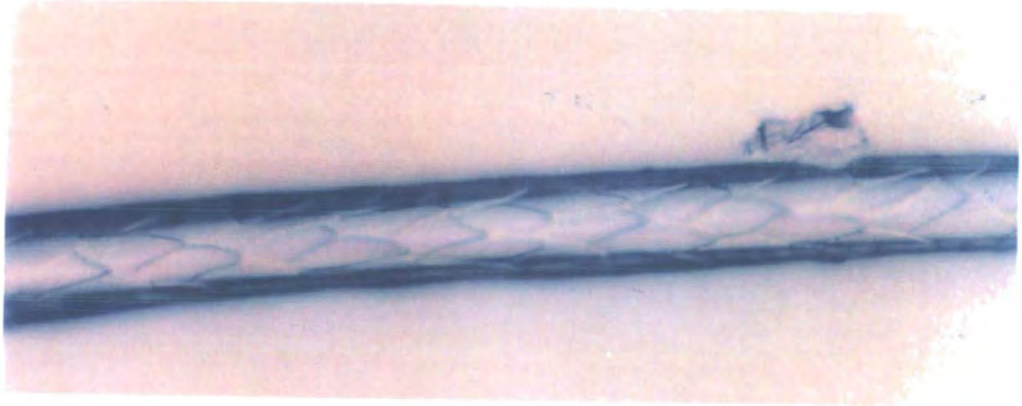
(c) Hair base

Plate 7 continued.

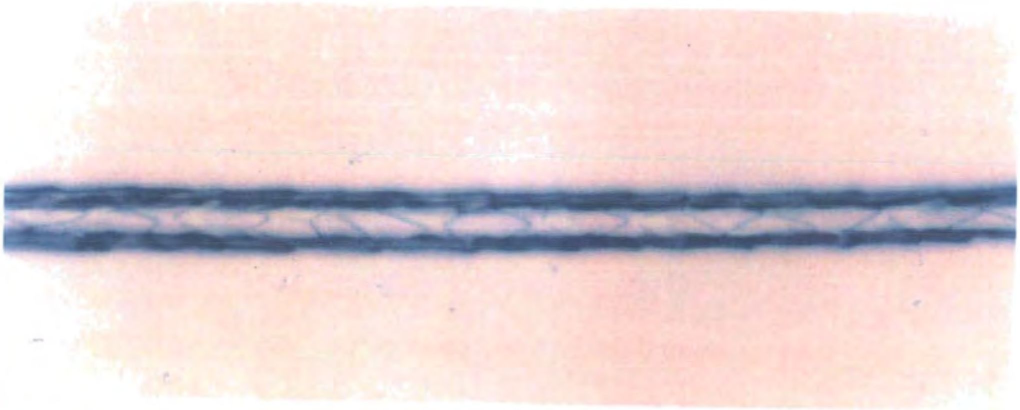
Plate 7h *Dromiciops gliroides*



(a) Hair tip



(b) Hair centre



(c) Hair base