Non-breeding ecology of New Zealand falcon (*Falco novaeseelandiae*) in a pine plantation forest

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Chifuyu Horikoshi

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ABSTRACT

Deforestation and conversion to intensive agriculture historically caused a large reduction in numbers of the New Zealand falcon or Kārearea (*Falco novaeseelandiae*), resulting in its current classification as Nationally Vulnerable. Several studies in plantation forests have documented the ecological benefits of limited timber harvesting on diversities of avian species through providing habitat heterogeneity. New Zealand falcons occur in managed plantation forests. To date, however, detailed information regarding falcon prey abundance, habitat use, home-range size, and breeding behaviour has been limited to their breeding season. Little is known about their winter use of managed forests and how forest operations affect their survival and reproductive ability by restricting their mating system.

I investigated a falcon population living in a large plantation forest, Kaingaroa forest through addressing the following questions: (1) how changes in forest structures influence falcons' habitat use and home-range size in relation to winter prey abundance and availability, (2) how the reduction in habitat heterogeneity by large-scale harvesting affects falcon's home-range size and overlap, (3) the risk of secondary poisoning from 1080 operations and falcon annual survival, and (4) how constraints by changes in the forest structure and compositions shape the mating system of the Kaingaroa falcon population. I used radio-tracking data to establish the extent and habitat composition of winter home-ranges, and monitoring survival of falcons before and after 1080 poisoning operations. I used transect surveys to assess the availability of potential prey birds, and behavioural observation to measure pair breeding activities.

I found that falcons used the ecotone between mature-pine stands and young-pine stands (the edge-habitat) most frequently followed by their hunting ground (young-pine stands – 0–3-year-old pine trees). Total prey abundance was similar across all habitats and sizes of open fields. The dynamic changes to forest structure created by clear-cutting and its effect on prey accessibility are the most profound factor influencing falcon space use. Winter home-range sizes of forest falcons (used Kaingaroa exclusively) were smaller than those of farmland falcons, which used farmland > 10 % of total tracking duration. I found that falcons used smaller home ranges when the forest provided the edge-habitats that were concentrated among mature-pine stands through creating open-patches less than 3 km^2 that are distributed closely (< 3 km apart). Results indicate that timber forests could hold a greater number of falcons with these forest compositions. Thirty-seven adult New Zealand falcons were exposed to carrot bait 1080 poison during the three winter months (May–August), and 17 adult falcons were exposed to cereal bait 1080 poison by aerial droppings in 2013 and 2014, and all these falcons except one survived. One radio-tagged male died and although a toxicology test found not 1080 residues, however, the possibility of 1080 secondary poisoning was not entirely cleared. The survival rate of adult Kaingaroa falcons was 80% and that of juveniles was 29%. All divorces (40%) were initiated by females leaving their territories regardless of reproductive outcomes, while males exhibited greater mate and site fidelity. A high rate of extra-pair interaction occurred by females (71%) but was absent in males. Female's extra-pair interaction implemented as their strategy for securing breeding opportunities. In

contrast, the mate-guarding strategy may be the most effective male's mating strategy in the Kaingaroa falcon population. Male's vigilant personality likely enhanced mate-guarding performance. Home-range overlap was greater in pairs that retained partners than pairs that divorced. Winter courtship displays were used for pair formation (the process of establishing a social bond) rather than pair bonding (the process of maintaining a social bond), and also used for intra-sexual competition over females. A rapid rotation of habitat quality and sufficient prey availability in the area may shape falcons' various mating systems.

A further long-term continual monitoring that includes the juvenile falcons is required to measure the effects of 1080 poison on the Kaingaroa falcon population. A well-designed harvesting regime could enable the timber industry to contribute importantly to the conservation of this threatened New Zealand raptor.

This dissertation is dedicated to
my parents and my second mother
who taught me to follow my dreams

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CHAPTER 1

Introduction

A male chick of Juvjuv and Balbal 2014/2015

Study species

The New Zealand falcon or kārearea (*Falco novaeseelandiae*) is the only extant endemic-diurnal raptor in New Zealand. It is widely distributed in various habitats throughout New Zealand, from native podocarp forests in the North Island (Barea 1995; Barea et al. 1997) to farmland and dry tussock land in the South Island (Fox 1977; Heather & Robertson 2005; Bell & Lawrence 2009). The New Zealand falcon is non-migratory, yet the species appears to be tolerant of breeding in modified habitats as shown by the recent successful introduction to vineyards (Kross et al. 2012) and by breeding populations in the exotic pine plantation forests in the central North Island of New Zealand (Addison et al., 2006; Seaton, 2009; Thomas, 2008; Thomas et al., 2010) and throughout New Zealand (Pawson et al., 2006).

The population was estimated in 1978 at approximately 3700 to 4000 pairs: North island (c. 1300 pairs), South Island (c 3150 pairs) and Fiordland, Stewart Island and the Auckland Island (c. 400 pairs) and is expected to be declining due to ongoing deforestation and degradation of habitat quality (Fox 1977), depredation by introduced species (Lawrence and Gay 1991, Barea 1995, Gaze and Hutzler 2004, Seaton et al. 2009, Kross et al. 2013a) and human persecution and electrocution (Fox and Wynn 2010, Kross 2014). The New Zealand falcon is categorised as a near-threatened species under IUCN criteria (IUCN 2012) and threatened and 'At Risk' by the New Zealand Department of Conservation (Robertson et al. 2016).

Landscape modifications

Landscape modifications are believed to have negative effects on almost all taxonomic groups (Cain et al. 2003; Oli 1994; Didham et al. 1996; Gibbons et al. 2000; Hobbs & Yates, 2003; Stuart et al., 2004). Human settlements and agriculture lead to human-wildlife conflicts (Gehring and Potter 2005), loss of habitat and biodiversity (Kerr & Deguise 2004; Luck et al. 2004) and habitat fragmentation (Fahrig 2003). These changes can result in extended travel distances (Norris & Stutchbury 2001), enlarged home-range sizes (Pope et al 2005), interruption to dispersal of animals (Brooker & Brooker 2002), and a reduction of native avifauna (Recher 1999). Consequently, changes can affect breeding patterns (Hinsley et al. 1999; Zanette et al. 2000), and mating systems (Ims et al 1993), and potentially lead to population declines (Felton et al. 2003; Temple & Cary 1988).

Nevertheless, gradual or small-scale landscape modifications can have positive effects on native ecosystems via habitat edges (Tubelis et al. 2004). Habitat edges provide shelter, foraging sites, and singing substrates to breeding birds and these can promote increased biodiversity (Roth 1976; Yahner 1988). Furthermore, landscape modifications can unintentionally contribute benefits to wildlife. Pine plantations encompass a diverse range of understory plant species (Gibb, 1961; Clout and Gaze, 1984; Ogden et al., 1997; Maunder et al., 2005), and are therefore not considered to be biological deserts (Allen et al. 1995; Ogden et al., 1997). Environmental benefits of pine plantations include improving water quality by providing filtration, reducing erosion rates (Dyck 1997), offering shelter and food for wildlife, acting as ecological buffers from adjacent non-forest land use, and enhancing connectivity between indigenous forest remnants (Brockerhoff et al. 2001; Denyer et al. 2006; Norton 1998).

In the last decade, studies of a breeding population of New Zealand falcons (hereafter simply ‘falcons’) in a large exotic pine plantation, Kaingaroa forest in central North Island of New Zealand, revealed that the plantation forest offers various ecological benefits to falcons, in part through habitat heterogeneity (Ogden et al. 1997; Seaton 2007). A rotation of timber harvesting of mature trees (i.e. trees 20 years or older) and replanting with seedlings creates a mosaic-like landscape consisting of different-aged tree stands ranging from cutover (stands cleared without planting trees) to mature stands (Pawson et al. 2010). This structural complexity can support plant communities (Brockerhoff et al. 2001) and a diverse group of bird species (Drapeau et al. 2000; Maunder et al. 2005; Seaton et al. 2010), which are primary food sources for falcons (Fox 1977; Kross et al. 2013b; Seaton et al. 2008).

New Zealand falcons in a pine plantation forest

To date, the studies of this falcon population have mostly been restricted to the breeding season and have documented prey bird species and abundance, home-range size, habitat selection, juvenile dispersal, and nesting behaviour (Seaton 2007; Thomas 2008). Falcons primarily preyed on exotic passerines such as chaffinch (*Fringilla coelebs*), yellowhammer (*Emberiza citronella*), and blackbird (*Turdus merula*; Seaton et al. 2008). The most used habitat was the edge habitat (the ecotone between mature-pine stands and young-pine stands), and use of this habitat was correlated with prey abundance (Seaton et al. 2013). During the nesting period, males had a larger home-range size (9 km^2 minimum convex polygon [MCP]) than females (6 km^2; 95% MCP). Yet, overall the non-breeding season home-range size of a single female obtained by satellite tracking methods for two years was much larger (33 and 78 km^2, 95% kernel density estimate[KDE]) than of a single male (6 and 10 km^2, 95% KDE; Thomas et al. 2010). Winter home-range size of these individuals was similar to those of the breeding season, 41 and 52 km^2 (95% KDE) for the female and 6 and 13 km^2 (95% KDE) for the male. Falcons nest in epiphytes of large trees in indigenous podocarp and beech forests (Barea et al., 1997), but Seaton (2007) found that nests of Kaingaroa falcons were mostly on the open ground, typically in forest stands aged 0–4 years old. Eighty percent of pairs at Kaingaroa re-nested together in successive breeding seasons. Thomas (2008) documented that breeding behaviour and nest development of two wild falcon pairs in Kaingaroa forest were consistent with incubation observations reported on captive falcons and wild falcons in South Island. Nest disturbance by logging operation and land preparation operation (windrowing operation – see the detailed forestry operation cycle below in Forest Rotation) could be prevented when these machinery operations had a 200 m set-back from a nest until breeding attempts were completed (Seaton 2007).

Previous studies of falcon prey abundance, habitat use, and home-range size are limited to the falcons' breeding season. Raptors may undergo a crucial period during the winter season by means of cold stress, resulting in high dietary demands for thermoregulation (Newton 1979) while having limited daylight for foraging (Wikar et al. 2008), and shortage of prey (Fairhurst & Bechard 2005; Kostrzewa and Kostrzewa 1991; Moser and Garton 2009; Wikar et al. 2008). Therefore, during the winter period falcons are expected to experience the greatest mortality, which may influence population dynamics (Newton 1979, Fairhurst & Bechard 2005). In addition, falcons residing in managed landscapes undergo various forestry regimes. New Zealand softwood forestry regimes typically include *Sodium fluoroacetate*, 1080, poison operations for pest control, which may directly impact on falcons' survival. Furthermore, forestry operation regime, such as timber harvesting and herbicide applications, create constant habitat modifications that falcons need to adapt to. These operations may indirectly influence habitat use and the home-range size of falcons. For instance, large-scale timber harvesting causes the reduction of habitat heterogeneity, resulting in the habitat ecologically resembling the monoculture forest. Too much clearing could alter local microclimate and change plant communities (Karanth & Sunquist 1995). This may interfere with the abundance and spatial organization of prey species (Ryall & Fahrig 2006), potentially resulting in the interruption of (healthy) predator-prey relationships (Karanth & Sunquist 1995). Moreover, constant changes in the forest structure may influence the mating system of falcons (e.g. pair formation, pair bonding, mating strategies and nest site selection). Nevertheless, these concerns have not been addressed for this species. All-year-round and detailed knowledge on the species-habitat relationship, in particular, which aspects of forestry regimes affect New Zealand falcon populations and to what extent, are of crucial importance for developing effective conservation strategies for the sustainability of falcon populations in pine plantations.

Study site – Kaingaroa Forest

Kaingaroa forest lies on the volcanic plateau of the central North Island of New Zealand. The forest was once called the Kaingaroa State Forest, owned as a state asset by the New Zealand government generated in the late 1920s (Roche 2012). When the government sought to sell the forest to private interests in the 1980s, several Māori iwi claimed that the ownership of the land was traditionally theirs. After two decades of court deliberation, a settlement of the claim reached on 1 July 2009, and the ownership of the land was changed from the New Zealand government to several Māori iwi (New Zealand Herald, 2008). Currently trees are owned by four shareholders: New Zealand Superannuation Fund (38.8%), Canada’s Public Sector

Pension Fund (30.0%), Harvard University Management Company (28.8%), and six Central North Island iwi that are formed as Kakano Investment Limited Partnership (2.5%; Rotorua Daily Post 2014). Kaingaroa Timberlands holds a forestry license over the land and is the major supplier to the New Zealand wood processing industry in the Central North Island. An independent forest management company, Timberlands Limited, manages the Kaingaroa forest. Products include pruned logs, structural logs, industrial and utility logs, pulp logs and paper products. Products are also exported to markets in Japan, China, Korea, India and other Pacific Rim countries (Timberlands, 2016).

The Forest Steward Council (FSC) is an international non-profit organisation established in 1993 to manage the world’s forests as environmentally sustainable, socially beneficial, and economically viable (Timberlands, 2016). FSC certifies an independent and credible guarantee to the international market that wood products come from sustainable or ‘eco-friendly’ forests. This study will enhance the efforts of New Zealand’s softwood industry to demonstrate good environmental stewardship by identifying management regimes that most impact the survival and prosperity of falcons.

Forest rotation

The forestry cycle consists of land preparation, timber harvesting, windrowing for planting, herbicide release, fertilizing, pruning and thinning (FITEC, 2011). Land preparation begins with road preparation within and surrounding the planned harvested stands. Windrowing operation involves piling logging debris by lining them up in a clear-cut stand and making space to plant seedlings. The trees are harvested throughout the year by clear-cutting trees 26–32 years of age in a unit of 1–2 km^2. Clear-cut stands are windrowed by excavators and then subjected to weed control by several herbicides and pest control by 1080 poison operations, targeting brushtail possums (*Trichosurus vulpecula*) and European rabbits (*Oryctolagus cuniculus*). The stands harvested before the end of March in each year are scheduled for planting nursery trees within the same year during the colder months, usually July and August. Pruning and thinning on intermediate-aged trees are completed based on the types of products that the trees will be used for. These forest operations are conducted by numerous local contractors.

Thesis aims and layout

The goal of this study is to promote sustainability of the Kaingaroa New Zealand falcon population by providing new information to forestry management. The aims of this project are twofold: (1) to investigate the non-breeding season ecology of New Zealand falcons in the Kaingaroa forest, and (2) to understand how landscape modifications shape the mating system of Kaingaroa falcons.

This dissertation describes the winter ecology of the New Zealand falcon population in a pine plantation forest. The main chapters of this dissertation (Chapter 2 to 5) are structured as a series of manuscripts anticipating publication in peer-reviewed journals. Each paper stands alone as a piece of work, hence, there are unavoidable repetitions in the study site description and methodology.

Chapter 2: Winter habitat use of New Zealand falcons (*Falco novaeseelandiae*) in an intensively managed pine plantation. (NZJE in press)

This chapter describes winter habitat use and the home-range size of adult New Zealand falcons in relation to prey abundance and availability, and winter weather. I survey falcon prey bird species and their numbers in various classified forest stands using belt transect technique. I use radio telemetry to track adult New Zealand falcons to understand their habitat use in relation to prey availability and various weather conditions.

Chapter 3: Logging influences winter home-range size and home-range overlap of New Zealand falcons (*Falco novaeseelandiae*) in a mosaic landscape: a test of the Resource Dispersion Hypothesis

Using the Resource Dispersion Hypothesis as a tool, I assessed factors determining home-range size and overlap of falcons in Kaingaroa forest. Results will identify a suitable size and layout of clear-cutting stands that can promote sustainable falcon habitats, which could lead to an increased carrying capacity of the Kaingaroa falcon population.

Chapter 4: Annual survival estimates and risk of 1080 secondary poisoning for New Zealand falcons in a managed exotic forest

I investigate the risk of secondary poisoning of 1080 on adult New Zealand falcons using radio-telemetry and identifying causes of mortality by post mortem examination and histopathology analysis. Annual survival of adult falcons and the first year survival/emigration of juvenile falcons are estimated from a long-term banding record (2003–2015) of the population.

Chapter 5: Effects of logging-induced changes in habitat shaping the mating system of New Zealand falcons: causes and consequences of divorce

This chapter demonstrates how changes in forest structure by timber harvesting shape mating systems of New Zealand falcons and tests recognized hypotheses to explain pair formations and interactions. This is achieved by monitoring marked pairs using radio telemetry over winter seasons and behavioural observations during the pre-breeding season. Findings of Chapter 2, 3, and 4 support the underlying effect of divorce, pair-bonding, and pair formation. Mate and site fidelities of falcons are determined by analysing the long-term banding records.

Chapter 6: Synthesis

The final chapter identified the major themes of this dissertation, main findings, and provides recommendations to forestry management sectors for conservation management of New Zealand falcons, as well as direction for future research.

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CHAPTER 2

Winter habitat use of New Zealand falcons (*Falco novaeseelandiae*) in an intensively managed pine plantation

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Co-authors: Phil F. Battley, Richard Seaton, and Edward O. Minot

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Abstract

Deforestation and conversion to intensive agriculture historically caused a large reduction in abundance of the New Zealand falcon, resulting in its current classification as 'At Risk'. Many New Zealand falcons occur in managed plantation forests, although little is known about their winter use of the mosaic of different aged stands present in these forests. We radio tracked adult falcons (*n* = 36) during three winters (2012–2014) in Kaingaroa Forest, an intensively managed pine plantation located in the Central Plateau of the North Island of New Zealand. We used tracking data to establish the extent and habitat composition of winter home ranges, and transect surveys to assess the availability of potential prey (passerine birds). We also investigated whether falcon habitat use was related to weather. Open fields created by clearcutting were the primary hunting ground of falcons. Falcons occupied young pine stands (30.4%) and the ecotone between young and mature pine stands (31.2%) most frequently despite its limited availability (20.1% and 3.7%, respectively). Total prey abundance was similar across all habitats and sizes of open fields, but the species composition of potential prey differed significantly between habitats. Thus, the dynamic changes to forest structure created by clearcutting and its effects on prey accessibility are the most profound factors influencing falcon space use. We observed that falcons used the mature portion of the forest edge area as a vantage point for hunting or for territorial defence and as a shelter from heavy rain, and interiors of mature tree stands as a shelter from strong winds. Females had larger home range size (95% KDE, 32 km^2) than males (15 km^2). The availability of mature/young edge within a home range may be the key factor determining home range size during winter. Maintaining the availability of ecotones of young stands adjacent to mature trees in plantation forests can assist in supporting falcon populations in this novel habitat and hence the conservation of this threatened endemic raptor.

Keywords: clearcutting; forest management; habitat selection; home range size; plantation; prey; raptor

Introduction

Prior to human arrival, 78% of New Zealand's landscape was covered by native podocarp forest, but over the past seven centuries, more than 60% of the forest has been destroyed and converted largely into pasture for grazing livestock (Ewers et al. 2006). This forest clearance has drastically reduced the range of forest dependent species. The New Zealand falcon or kārearea (*Falco novaeseelandiae*; hereafter referred to simply as 'falcon') is the last extant endemic diurnal raptor in New Zealand. Historically, falcons found in the North Island of New Zealand (*Falco novaeseelandiae ferox*) inhabited indigenous podocarp and beech forests and nested in the epiphytes growing in large trees (Fox 1977; Barea 1995). Deforestation and degradation of habitat quality through conversion to intensive agriculture appear to be the largest contributors to the reduction in abundance, particularly of bush falcons (Fox 1977). The falcon is currently listed as near threatened by the IUCN (IUCN 2012) and At Risk by the New Zealand Department of Conservation (Robertson et al. 2016). Ensuring access to suitable habitat is a priority for conserving this species.

Over the past decade, several studies have confirmed breeding populations of falcons occupying a novel habitat, exotic pine plantation forest (Stewart & Hyde 2004; Maunder et al. 2005; Seaton 2007; Thomas 2008). Pine plantations cover approximately 7% of New Zealand's landmass (MAF 2013) and comprise roughly 20% of the forest area in New Zealand (Hartley 2002).

Large-extent plantation operations can provide falcons with various ecological benefits, in part through providing habitat heterogeneity (Ogden et al. 1997; Seaton 2007). In typical New Zealand soft wood forestry schemes, stands of mature trees are clearcut (i.e. harvested) and then replanted with seedlings. This practice creates a mosaic-like landscape consisting of different aged tree stands ranging from cutover (stands cleared without planting trees) to mature stands (i.e. trees 20 years or older; Pawson et al. 2010). Such structural complexity usually supports a diverse group of bird species (Drapeau et al. 2000; Maunder et al. 2005; Seaton et al. 2010) and plant communities (Ogden et al. 1997; Brockerhoff et al. 2001). For instance, clearcutting causes a sudden exposure of deep forest insect fauna to open environments and results in the attraction of insectivorous and generalist bird species (Clout & Gaze 1984; Moorman & Guynn 2001; Pawson et al. 2006). The newly created open fields (clearcut, stands <3 years old or farmland pasture) are colonised by forbs and grasses (Pawson et al. 2006), whose seeds are an attraction to introduced small passerine birds (Moorman & Guynn 2001), the preferred prey of falcons (Fox 1977; Seaton et al. 2008, 2010; Kross et al. 2013). An additional benefit of the harvest practices in these plantations is that logging debris left in stands after a harvesting event (e.g. branches, underbrush and upturned root clumps) creates pockets of suitable nesting habitat for New Zealand falcon pairs (Seaton 2007).

Detailed knowledge of falcons' habitat use in plantation forests is limited to the summer breeding season (September to March; Thomas 2008; Seaton et al. 2013). Winter weather can affect raptor survival and influence population dynamics (Newton 1979; Fairhurst & Bechard 2005). During winter, raptors must increase their energy intake for thermoregulation in order to maintain their body temperature and can experience decreased survival rates as energy requirements rise (Newton 1979) at the same time that shorter days constrain foraging opportunities (Wikar et al. 2008).

Survival strategies of resident raptor species include using shelter to minimise heat loss, broadening habitats used (Newton 1979; Wikar et al. 2008), and hunting less desirable, but more available, prey (Steenhof & Kochert 1988). Given the role of plantation forests in supporting resident falcon populations (Seaton 2007), a detailed investigation of the species-habitat relationship throughout the entire year is critical to developing effective conservation strategies (Barea 1995) that promote the long-term survival of falcons.

We studied a falcon population living in Kaingaroa Forest, situated on the Central Plateau of the North Island, New Zealand (Fig. 1; hereafter Kaingaroa) during the non-breeding season (April to August). Due to forestry operations, the landscape is subject to constant localised alterations, created by clearcutting and herbicide applications. These activities have sudden impacts on the environment and are likely to have direct and indirect influences on the way falcons use the habitat. For instance, the size of clearcutting is typically in a unit (stand) of 0.7–1 km^2. The area of clearcutting increases when a stand is harvested adjacent to an existing open field or two or more stands are harvested at the same time, which may influence the distribution of prey (Moorman & Guynn 2001). Moreover, stands that include <2 year-old trees are subject to herbicide treatments. Application of herbicides to kill weeds and forbs may indirectly affect falcons through altering the distribution or reducing abundance of potential prey species that feed on plant seeds. Falcons may need to adjust home range sizes to match prey abundance and distribution across the local landscape. During the non-breeding season, falcons are not constrained by the position of a nest. Thus, information from falcons in the non-breeding season (April–August) may provide a more in-depth insight into how forest management influences habitat use.

Here we study the temporal and spatial variation of habitat use of adult falcons in Kaingaroa during the non-breeding season. Specifically, we examine whether the winter habitat use of falcons is explained by spatial and temporal variations in the availability of prey and ongoing habitat modification patterns created by clearcutting. We also explore whether changes in habitat use can be explained by weather conditions, whether the pattern of habitat use varies between the sexes, and what other factors influence the home range size of falcons during the winter.

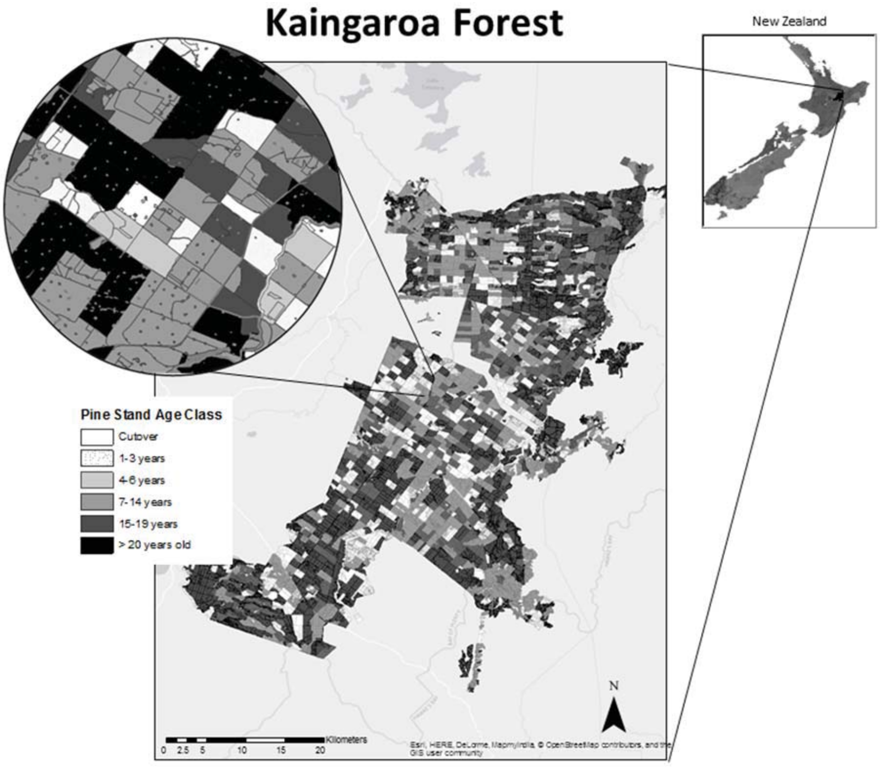

Figure 1. Study site map – Kaingaroa situated in the Central Plateau of the North Island, New Zealand. The mosaic landscape consists of different aged pine stands from clearcut to mature (>20 years).

Methods

Study site

The Kaingaroa pine plantation covers 1800 km^2 from southeast of Rotorua (Bay of Plenty Region) to the northeast of Taupo (Waikato Region) in the North Island of New Zealand (Fig. 1). The forest sits on an elevated volcanic plateau with an elevation range of 490–900 m (Washbourn 1978). Winter occurs between June and August, but frosts can occur in any month due to the relatively high elevation of the plateau. Broadly, Kaingaroa is bordered by dairy farms to the west and south, small forest plantations to the south and southwest, indigenous podocarp forest to the east, and dairy farms and lakes to the north.

Kaingaroa comprises 1342 harvestable stands. The focal harvest species is *Pinus radiata* (Seaton 2007; Pawson et al. 2010). A typical pine harvest consists of clearcutting a mature stand 26–32 years after planting (Pawson et al. 2010). The annual harvest rate depends on market demands, and averaged 5.2 km^2 monthly from 2012–2014 (Timberlands Ltd., pers. comm.). A standard annual forestry operation generally runs from April to the following March. Stands harvested by March are prepared for planting seedlings through land windrowing (piling logging debris by lining up in a clearcut stand and making space for planting seedlings), followed by aerial application of herbicides, usually between March and May. The stands are then replanted using nursery grown seedlings between June and August of the same year. Stands harvested after March are left fallow for the year and replanted in June–August the following cycle year (C. Hindle, Timberlands Ltd., pers. comm.).

Weather information

Hourly meteorological information consisting of temperature (°C), wind speed (km h^{-1}), and rainfall (mm) was obtained from three weather stations: Goudies (elevation 500 m), Tahorakuri (440 m) and Matea (700 m; B. Goodall, Communication Networks Management Ltd., pers. comm.). These weather stations were located within 14 km (range 4–14 km) of the study falcons' home ranges.

The mean 24 hour temperature during the study (April–August, 2012–2014) was 6.4°C, and the lowest and the highest temperatures were –6.7°C (July 2012) and 23.7°C (April 2014,Fig. 2). Mean wind speed was 12.7 km h^{-1}, with highest recorded wind speeds of 55.2 km h^{-1} in May 2014 and 51.5 km h^{-1} in June 2012. Mean monthly precipitation was 83.9 mm, with the highest levels of rainfall 128 mm and 120 mm recorded in May and June 2012, respectively.

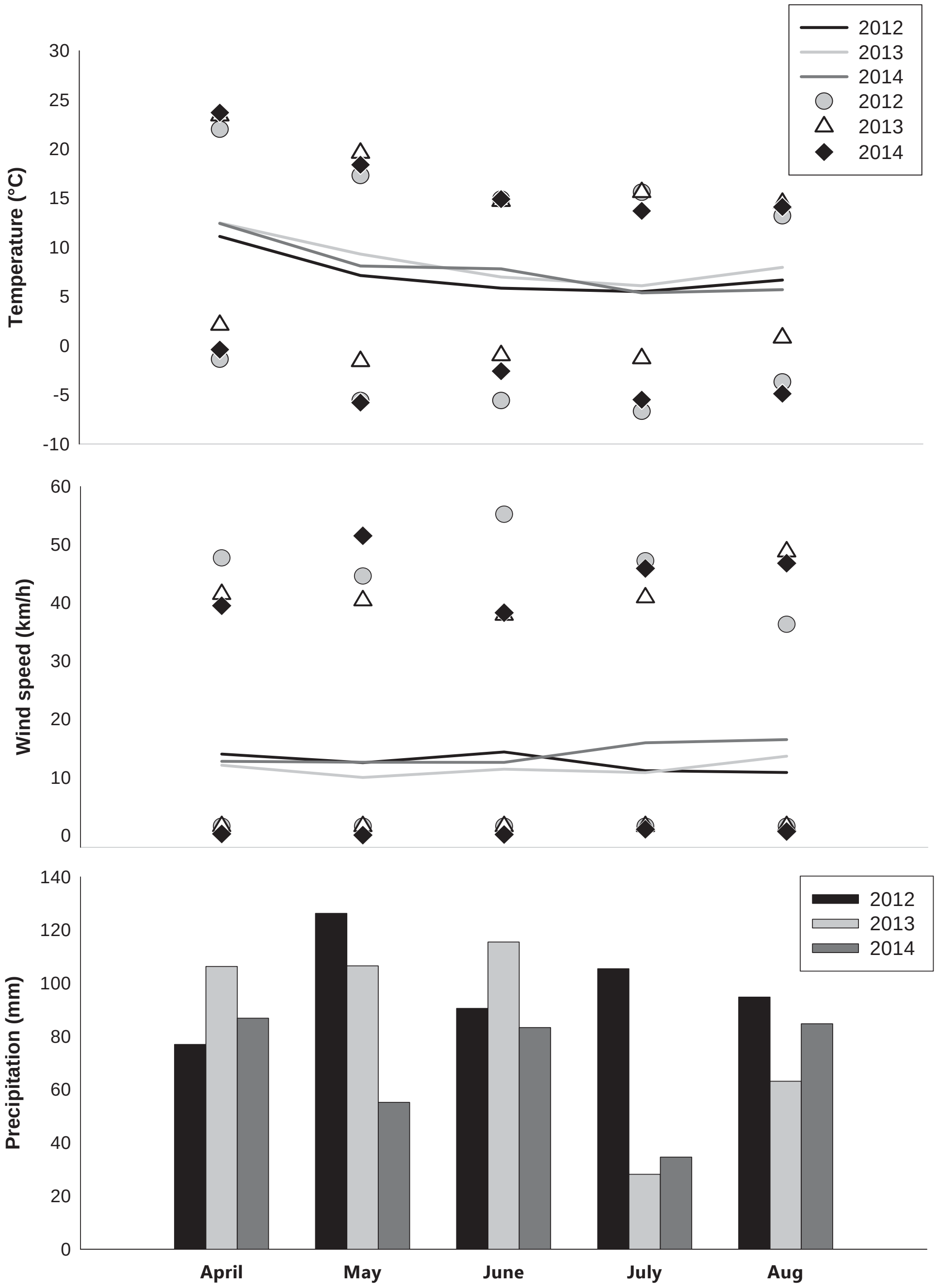

Figure 2. Mean (line), maximum (upper symbols) and minimum (lower symbols) hourly temperature (°C) and wind speed (km h^{-1}) and precipitation (mm) from April to August in 2012, 2013 and 2014 in Kaingaroa. The meteorological data were collected from three weather stations located within 14 km (range 4–14 km) of the study falcons' home ranges.

Prey census

Prey census in classified habitats

We surveyed bird species and abundance using a belt transect census method (Bibby et al. 2000). To begin, we established 11 habitat classes based on pine tree age (<3, 7–14, >20 years old) and position in a stand (interior and edge; see Table 1 for all habitat classes). The edges between different aged pine stands are important for falcons because they create an ecotone that maximises prey abundance alongside conditions that favour their hunting style (Seaton 2007). Edges were defined as the area 50 m from the border between two stand classes with an age difference >4 years. Interiors were defined as being over 50 m from the boundary. We studied three interior categories and seven edge categories. Finally, we denoted farm barns or trees located near a silage pit as shelter. We established 400 m belt transects in each habitat class. In 2013, we established three replicates for young, young/intermediate, and young/mature habitat classes and two replicates for each of the remaining classes, and surveyed each transect twice a month from June–August.

Prey census in young and young/mature

In 2014, we investigated the effects of harvest size and season, and the presence or absence of seedling plantings, on bird abundance in young and young/mature (Table 2). We first categorised ten open habitat classes by dividing the young stands into three classes: fresh, cutover and planted. We then divided young stands by area into standard (≤2 km^2) or large (2–4 km^2). Cutover and planted were additionally split by season of harvest into winter and summer. Winter stands were left alone in spring and summer without receiving herbicides. Thus, the forestry regimes for winter stands allow grass weed plants (e.g. *Agrostis capillaris*, *Holcus lanatus*) to produce seeds, which are the primary food for exotic finches. In contrast, summer stands receive the first herbicides within 1–6 months. This short interval may not allow weeds to produce seeds. For each stand categorised as young, we then established 400 m belt transects in the interior as well as the mature forest edge of the stand. We established two replicates for each young and young/mature transect, and surveyed each twice a month from June–August.

Table 1. Habitat classes used for general prey census and falcon habitat use in Kaingaroa. Pine ages 3–6 years and 15–19 years were excluded from the prey census so that each category of habitat would be different enough from the others, therefore, when contiguous, they would establish an ecological edge.

	Habitat class	**Prey census descriptions (tree years)**	**Falcon habitat descriptions (tree years)**	**Interior or edge**	**Replicates**
1	Young	0–2	0–2	Interior	3
2	Intermediate	7–14	3–14	Interior	2
3	Mature	≥20	≥15	Interior	2
4	Young/intermediate	(0–2)/(7–14)	(0–2)/(3–14)	Edge	3
5	Young/mature	(0–2)/(≥20)	(0–2)/(≥15)	Edge	3
6	Intermediate/mature	(7–14)/(≥20)	(3–14)/(≥15)	Edge	2
7	Young/pasture	(0–2)/pasture	(0–2)/pasture	Edge	2
8	Intermediate /pasture	(7–14)/pasture	(3–14)/pasture	Edge	2
9	Mature/pasture	(≥20)/pasture	(≥15)/pasture	Edge	2
10	Pasture		Farmland pasture	Interior	
11	Trees/pasture	Trees in pasture, windbreaks		Edge	2
12	Shelter	Farm barn and trees near silage pit in farmland		Edge	2

We walked slowly along each transect and recorded bird species and numbers seen or heard within 30 m of the transect line. We used the 30 m belt exclusively as opposed to use of multiple belts for distance sampling to calculate detection probability (Thomas et al. 2010b), as our ability to detect birds at distances greater than 30 m differed greatly between open and closed habitats. Therefore, it was not feasible to accurately measure distances to each bird. All censuses were conducted in the morning on days without rain and with a wind speed generally <15 km h^{-1}.

Table 2. Habitat classes for bird censuses in open stands conducted between June and August 2014 in Kaingaroa. Young stands are pooled into three categories: fresh (unplanted), cutover (unplanted), and planted, and then divided by area into standard (>1 km^2 and <2 km^2) and large (≥2 km^2 and <4 km^2). Cutover and planted were additionally split by season of harvest into winter (where clearcutting occurred between June and October within the same cycle) and summer (clearcut between November and May within the same cycle). A total of twenty 400 m belt transects were then established in the interior of each classified young stand and the border with mature pine stand (young/mature).

Category of young stand	Descriptions	Size	Harvested season	Interior or edge
Fresh	Clearcut in March, April or May	Standard	Summer	Interior
				Edge
		Large	Summer	Interior
				Edge
Cutover	Clearcut occurred >3 m after June	Standard	Summer	Interior
				Edge
			Winter	Interior
				Edge
		Large	Summer	Interior
				Edge
			Winter	Interior
				Edge
Planted	Pine age >1 and <2 y	Standard	Summer	Interior
				Edge
			Winter	Interior
				Edge
		Large	Summer	Interior
				Edge
			Winter	Interior
				Edge

Trapping and radio tracking

We caught adult falcons during the breeding season (November–January) with a Bal-Chatri trap or a Dho-gaza net using an exotic passerine as a lure (Bloom et al. 2007). Birds were caught near nests when chicks were at least 14 d old (Seaton 2007) to prevent the interruption of critical incubation periods and to avoid inciting nest abandonment. Falcons were fitted with either a Kiwi Track (Havelock North, New Zealand) Brown Teal radio-transmitter (15 g; used for three females in 2012) or a Holohil (Carp, Ontario, Canada) RI-2CM (7.5–12.8 g; all other falcons) using a backpack harness with a weak-link. Transmitters weighed 2.8% ± 0.3% (mean ± 1 SD) of the body mass of the tagged females and 3.6% ± 1% of the body mass of the tagged males. We used triangulation methods (White & Garrott 1990) and visual verification when possible (Seaton et al. 2010) to track falcons from April–June in 2012 and from June–August in 2013 and 2014. Triangulation was conducted mostly by a single person who obtained a fix by quickly moving around a focal falcon and measuring up to three different bearings.

In 2012, we continuously tracked each falcon for 8 h daily between dawn and dusk. In 2013 and 2014, we continuously tracked for 6 h daily and alternated shifts weekly, from dawn to early afternoon one week and early afternoon to dusk the next. We calculated duration per location from two sequential locations within a consecutive tracking period. We used a point sampling method two times per week for four falcons we were unable to track continuously due to lack of trackers. We obtained at least one fix per falcon in every hour during a 6-hour or 8-hour tracking session. When recording habitats used by falcons we used the same categories as in the bird censuses with three modifications, classifying intermediate as interiors of stands 3–14 years and mature as interiors of stands ≥15 years (Table 1). Additionally, we included farmland pasture (pasture) as a falcon habitat category. We obtained a mean of 159 ± 63 (SD) fixes per falcon. The mean total tracking time per falcon was 60 ± 20 h, ranging between 8 and 91 h.

Data analysis

Home range size and habitat selection

We assessed home range size and habitat selection of tagged falcons using a geographic information system (GIS; ArcGIS 9.3, ERSI, Redlands, California, USA). Shapefiles of Kaingaroa, containing information on stand age and boundaries, were obtained and used with permission from the Kaingaroa forest management company (C. Maunder, Timberlands Ltd., Rotorua, NZ).

We entered tracking data for each winter into a GIS map that included tree age classes during a single season: young, intermediate and mature. We calculated home ranges by kernel density estimates (KDE) using Hawth's Analysis Tools 3.27 for ArcGIS (Beyer 2004). The KDE was used because the method can provide more accurate home range estimates than MCP models (Worton 1989; Seaman & Powell 1996). The 50% (core home range size; Samuel et al. 1985) and 95% KDE (the entire home range size; Seaman & Powell 1996) were chosen for compatibility to other home range studies. We used a reference smoothing parameter (Gitzen et al. 2006) to estimate core home range size and the entire home range size. Smoothing parameter *h* values were obtained using the 'rhr' function in the reproducible home ranges (rhr) package in R (version 2.15.1; Signer & Balkenhol 2015). Temporal autocorrelation associated with sequential observations from radio telemetry may bias home range estimates (Swihart & Slade 1985) and a common perception is that autocorrelated data should be subsampled (Swihart & Slade 1985) or adjusted by variance inflation (Nielsen et al. 2002). However, some studies argue that autocorrelated observations will reveal biologically significant and more relevant behavioural information than would independent observations (Reynolds & Laundre 1990; Otis & White 1999), or biased variance would be of little concern in home range estimates (McNay et al. 1994). Other studies stated that serial independence of observation is not required for home range estimates when using kernel density (De Solla et al. 1999) with large sample sizes (a minimum of 30 and preferably ≥50; Seaman et al. 1999). Moreover, unlike territorial mammals, falcons can travel a large distance in a short time. For these reasons, we use all data points collected from our study birds to estimate their home range sizes.

For each falcon, we determined the habitat availability within a single tracking year by calculating the proportion of each habitat class available within an individual's entire home range (White & Garrott 1990). For this purpose, we standardised home range estimates by using a single smoothing parameter (h = 1000) to calculate habitat composition availability within home range of each falcon. This was in order to reduce potential bias in home range estimation as a result of individual variations in sample size (Seaman et al. 1999) or space use (Worton 1995). The area of a habitat edge was calculated by measuring the length of each habitat edge multiplied by 100 m (50 m either side of the border between two stand classes; Seaton 2007). The remaining area was categorised as stand interior.

Proportional habitat use of each falcon per tracking year was determined by calculating the duration (minutes per location) spent in each habitat class. Some habitat classes associated with farmland pasture were not available for some falcons. Hence, we categorised falcons as forest falcons (those found in neighbouring farmland for less than 10% of the total sampling locations; $n = 25$), and farmland falcons (those found in farmland for over 10% of the total sampling locations; $n = 11$), and conducted analyses separately.

We determined the habitat selection of falcons by using compositional analysis (Aebischer et al. 1993) in the 'adehabitat' package (version 1.8.18; Calenge 2006) in R to determine the degree of selection. Analyses were conducted separately for forest and farmland falcons and for males and females. Some habitat classes were not available to some individuals (e.g. farmland was often not available to forest falcons), so for the habitat preference analysis, we pooled some habitat classes by combining unused habitats with used habitats based on ecological similarities for the habitat preference analysis (e.g. intermediate/pasture and mature/pasture pooled into young/mature; Bingham et al. 2007).

Habitat use in response to weather

Falcons' responses to weather were assessed in two ways: descriptive local weather and hourly meteorological information. Descriptive local weather (i.e. sunny, cloudy, shower, rainy, drizzling, foggy or hail) was recorded while radio tracking each falcon. Hourly precipitation data obtained from the weather stations were classified based on intensity: no rain (0 mm), very light rain (0.01–0.25 mm), light rain (0.26–1.00 mm), moderate rain (1.10–4.00 mm) and heavy rain (4.10–16.00 mm; precipitation scale modified from Met Office 2007). Recorded temperatures were pooled into five standard meteorological categories: one (<0°C), two (0.1–4.9°C), three (5.0–10.9°C), four (11.0–16.9°C) and five (>17.0°C). Wind speed was classified into six rates: calm (<1 km h^{-1}), light air (1.0–5.5 km h^{-1}), light breeze (5.6–11.9 km h^{-1}), gentle breeze (12.0–19.9 km h^{-1}), moderate breeze (20.0–29.9 km h^{-1}) and strong breeze (>30.0 km h^{-1}; modified Beaufort scale; Met Office 2010).

Statistical analysis

Generalised linear mixed models (GLMM) were constructed to identify factors associated with spatiotemporal variations of prey bird abundance and the habitat use of falcons using the 'nlme' package (Pinheiro & Bates 2000) in R (version 3.1; R development Core Team 2015). We used transect as a random effect accounting for repeated use of the same transects for the analysis of prey bird abundance and Falcon ID as a random effect for repeated observations of each falcon. We used the same Falcon ID for each of the seven falcons radio tracked in multiple years.

We constructed a suite of plausible candidate models for each analysis of bird numbers or falcon activity (duration spent per location) in relation to multiple independent variables (climatic, habitat, sex and time; see Tables S1–S10 in Supplementary Material). In essence, these are manual stepwise simplifications of the complex models. Following analysis of coefficients and standard errors, no evidence of high collinearity or spatial autocorrelation were apparent in the data. We calculated AIC values for each model using 'sem.model.fits' function in the 'piecewiseSEM' package (version 1.2.0; Letcheck 2016) in R (in which alternative models are compared) and ranked models by their AIC. The piecewise structural equation modelling (SEM) is a goodness-of-fit test that allows for fitting of models to different distributions and incorporates nested random structures (Letcheck 2016). For the falcon activity models in relation to meteorological weather information, we calculated AIC values for each model using the 'AIC' function in R as the SEM function was not possible. This was because we had imbalances in the dataset between habitat classes and weather components, so we manually built models with specific interactions of interest. However, the SEM function could not perform when a model included a custom interaction. Where alternative models were within two AIC units of each other, we evaluated the relevance of the models by whether there was statistical support for the independent variables in the models, and whether any significant variables differed between the models (*P* value for individual variables of <0.05). For the models of bird counts and falcon activity in relation to the descriptive weather conditions, we additionally compared conditional R^2 values (which incorporate both fixed and random effects) as a measure of overall model fit. This comparison was not possible for the falcon activity models in relation to meteorological weather information due to the methodological incompatibility. We assessed the normality of residuals of each variable in the final regression models by constructing diagnostic plots.

For the two prey bird censuses (classified habitats and in young and young/mature), data were pooled into three groups (total bird abundance, native bird abundance and exotic bird abundance). To illustrate the differences in prey abundance, we generated contrasts between levels of the main factors, with August as a reference to contrast prey abundance between late-winter (August) and mid-winter months (June and July) and young forest (the primary hunting ground of falcons).

For falcon activity, we constructed models for general weather and also for temperature, wind speed and precipitation separately, as due to imbalances in the data we could not analyse these factors simultaneously. For contrasts between habitats, we used young forest (the primary hunting ground habitat) as the reference. For contrasts between weather conditions we selected mature and young/mature forests as reference habitats, and an extreme weather condition as a reference for each. We give beta coefficients based on the best supported models in text but figures and tables are based on raw summaries. Note that the nlme package does not compute 'conventional' degrees of freedom (see Pinheiro & Bates 2000) and so here we report coefficients ± SE for model-generated results (where beta [⍰] values are expressed relative to the intercept, which is the reference category or state) and means ± SE for summaries of raw numbers.

Results

Prey abundance and availability

Prey census in classified habitats

Bird abundance did not differ significantly among the available habitats for falcons except at shelter where there were clusters of small passerines such as house sparrow (*Passer domesticus*), yellowhammer (*Emberiza citronella*) and chaffinch (*Fringilla coelebs*; β = 1333 ± 88, $P < 0.0001$).

For all birds counted at Kaingaroa, the abundance of introduced and native birds was similar, constituting 57% and 43% of the total bird count, respectively. The abundance of introduced species was greatest in interior of young (β = 43 ± 15 per transect) but differences were not statistically significant among the available habitats for falcons (*P* = 0.1279). In contrast, more native birds were found in mature (β = 24 ± 5, *P* = 0.0004), mature/pasture (β = 26 ± 6, *P* = 0.0008), and young/mature (β = 27 ± 4, *P* = 0.0022) than young (intercept = 11 ± 3; see summary in Table 3). There were no statistically significant monthly variations of bird abundance among introduced birds in the forest habitat classes (*P* = 0.4998), or locations (interior or edge) within each habitat class (*P* = 0.1224). Among native birds, August had significantly higher counts (intercept = 11 ± 3) compared to June (β = -8 ± 3, *P* = 0.0006) or July (β = -10 ± 3, *P* = 0.0039). The house sparrow was the most abundant bird species ($\bar{x}$ = 454 ± 189, 39.7% of the total counts) found in farmlands. The most abundant species within Kaingaroa was the endemic whitehead (*Mohoua albicilla*; $\bar{x}$ = 8 ± 1, 24.0%), a species found exclusively in forest, followed by the introduced redpoll (*Acanthis flammea*; $\bar{x}$ = 6 ± 2, 18.9%) and chaffinch ($\bar{x}$ = 6 ± 1, 17.9%). Whiteheads and redpolls were often observed in large flocks (>10 birds), while chaffinches were distributed individually or found in flocks.

Prey census in young and young/mature

Overall bird abundance did not differ statistically by sizes of open field, harvested seasons or categories (*P* = 0.940). When we separated native species from introduced species, we found young/mature had significantly higher abundance of native birds in August (β = 23 ± 3, *P* = 0.0001) compared with July (β = -11 ± 4, *P* = 0.0064), but not compared with June (β = -5 ± 4, *P* = 0.2355).

Table 3. The mean number of birds ± SE (native and exotic passerines) per 400 m belt transect and per (selected) habitat class in Kaingaroa and adjoining farmland. An asterisk denotes a statistically significant ($P < 0.05$) difference in bird abundance between each habitat class (young/mature, mature, mature /pasture) and the reference class, young, within Kaingaroa, and all the categorised habitat classes including shelter.

Habitat	Birds	Mean ± SE/ all transects	Young	Young/ mature	Mature	Mature / pasture	Farmland shelter
Kaingaroa	Native	15 ± 1	6 ± 1	22 ± 2*	30 ± 1*	33 ± 2*	
	Exotic	19 ± 3	39 ± 6	9 ± 1	12 ± 1	25 ± 1	
Farmland	Exotic	616 ± 78					1466 ± 258*

Home range size and habitat selection

Home range sizes of forest falcons (those that used Kaingaroa exclusively) were smaller in both entire ($\bar{x}$ ± SE = 19 ± 4.9 km^2) and core (4 ± 0.8 km^2) than those of farmland falcons (which used farmland >10% of total tracking duration; 38 ± 5.9 km^2 and 7 ± 1.0 km^2, respectively) though the differences were not significant ($P = 0.0611$ and $P = 0.0706$, respectively). Females had larger home range sizes (32 ± 6.4 km^2, range 2–124 km^2) than those of males (15 ± 2.6 km^2, range 7–38 km^2, $P = 0.041$). Core home range sizes for females were also larger (6 ± 10 km^2, range 0.5–20 km^2) than those of males (3 ± 1 km^2, range 1–7 km^2, $P = 0.0315$).

Young/mature was the most selected habitat class by both forest and farmland falcons (36 ± 4%, $P < 0.0001$ and 22 ± 5%, $P = 0.002$, respectively; Fig. 3A and Table 4) despite the low availability of this habitat within their home ranges (4 ± 1% and 3 ± 1%, respectively). Tree/pasture (24 ± 6%) was the second most selected habitat used by farmland falcons and used at a comparable rate to young/mature. Habitat selection did not differ between the sexes except that the selection of intermediate and mature was in the reverse order (Fig. 3B).

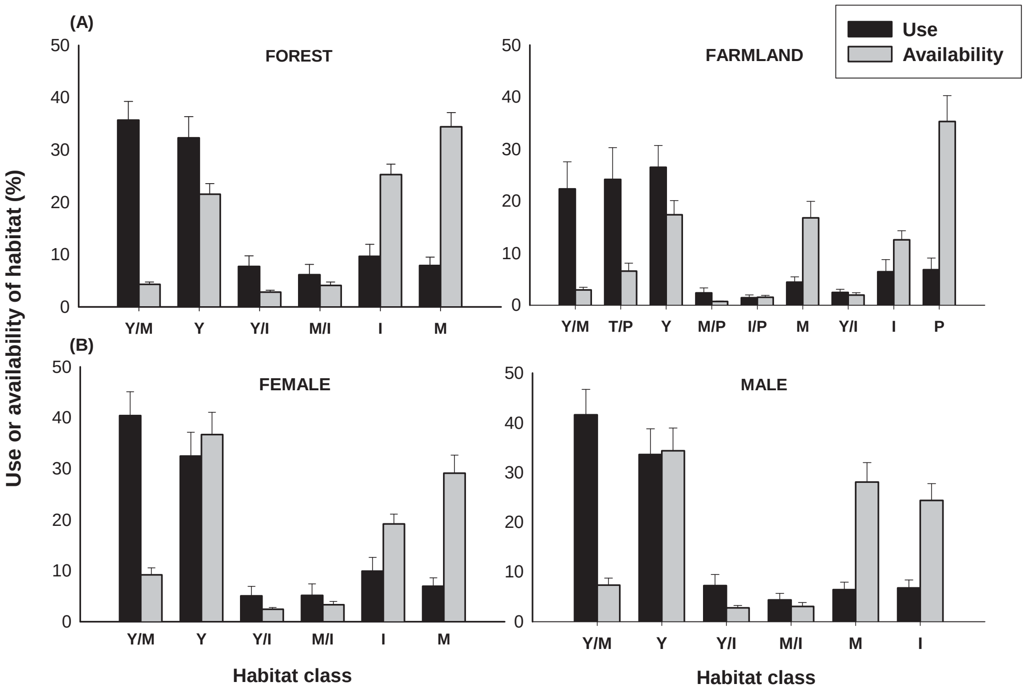

Figure 3. Habitat use and habitat availability of falcons: (A) forest falcons (*n* = 25) and farmland falcons (*n* = 11) and (B) sexes (female = 21 and male = 15) in Kaingaroa. Habitat classes are arranged from most to least preferred based on results of compositional analysis. Habitat classes: Y/M (young/mature), Y (young), Y/I (young/intermediate), M/I (mature/intermediate), I (intermediate), M (mature), T/P (trees/pasture), M/P (mature/pasture), I/P (intermediate/pasture), and P (pasture). Bars are one SEM of the proportion of the duration falcons spent in each habitat class.

Table 4. Log-ratio of habitat use/availability of falcons: males (*n* = 15), females (*n* = 21), forest falcons (*n* = 25), and farmland falcons (*n* = 11) in Kaingaroa during the non-breeding seasons, 2012–2014. The columns are ordered from the most selected (left) habitat to the least selected (right) habitat.

	Young/ mature	**Trees/ pasture**	**Young**	**Young /intermediate**	**Mature /intermediate**	**Mature /pasture**	**Intermediate /pasture**	**Intermediate**	**Mature**	**Pasture**
Male	1.86		0.07	-0.22	-1.18			-1.90	-2.12	
Female	1.56		-0.20	-0.92	-1.33			-1.89	-2.08	
Forest falcon	1.78		0.21	-0.30	-0.44			-1.72	-2.17	
Farmland falcon	2.06	1.40	0.38	-0.83		0.38	-0.39	-1.90	-1.44	-2.66

Activity in relation to season, habitat and weather

Temporal variations in activity

Activity level of falcons (the duration that each falcon remained at one place) varied with both time of day and month for all falcons but not with sex (*P* = 0.656) or falcon category (forest vs farmland, *P* = 0.965). Falcons were slightly less active (i.e. longer duration (minutes) per tracking fix) during mid-day hours (1100–1400; β ± SE = 23 ± 2 minutes per location) compared to during afternoon hours (1400–1800; β = -6 ± 1, $P < 0.0001$) but not compared to morning hours (0700–1100; β = -0.4 ± 1, *P* = 0.7941).

Monthly variations were found during sunny periods, with falcons being more active in April, July and August (range β = -6 ± 2 to β = -8 ± 1, $P < 0.05$) but not significantly different in May (β = 3 ± 2, *P* = 0.1866) compared to June (intercept = 23 ± 2; Fig. 4).

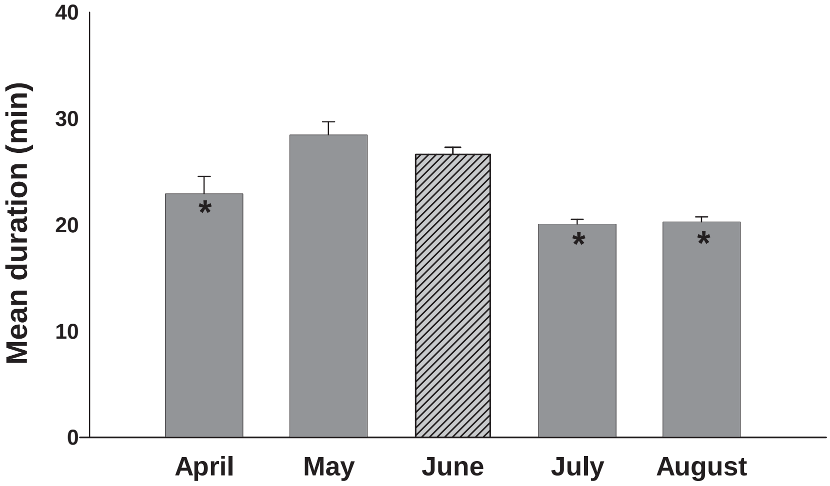

Figure 4. Relative activity level of falcons (*n* = 36) in each month from April to August 2012–2014. Mean duration (minutes ± 1 SEM) represents that falcons remained at a site in each month. When falcons remained at a site for a long duration it indicated a low activity level. June (hatched bar) was used as the reference for statistical comparisons; an asterisk indicates a statistically significant difference from the reference.

Spatial variations in activity

Seven falcons used shelter for foraging for a mean of 1.4% of the total tracking duration. Falcons were more active (lower stationary durations during tracking) in shelter (β = -6 ± 2, *P* = 0.0063) than young (intercept = 23 ± 2), but were less active in all other habitats (range β = 3 ± 1 to β = 18 ± 3, *P* <0.05) apart from pasture and young/pasture (Fig. 5)

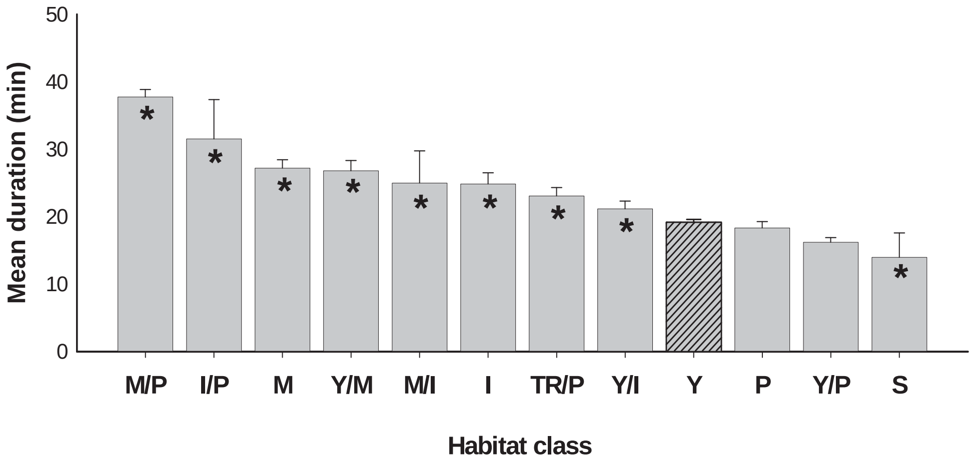

Figure 5. Relative activity level of falcons (*n* = 36) in each habitat class in Kaingaroa during the study period (2012–2014). Mean duration (minutes ± 1 SEM) represents that falcons remained at a site in each habitat class. Habitat classes: M/P (mature/pasture), I/P (intermediate/pasture), M (mature), Y/M (young/mature), M/I (mature/intermediate), I (intermediate), T/P (trees/pasture), Y/I (young/intermediate), Y (young), P (pasture), Y/P (young/pasture), and S (shelter). Habitat Y (hatched bar) was used as the reference for statistical comparisons; an asterisk indicates a statistically significant difference from the reference.

Weather and activity

Analysis of falcon habitat use in relation to descriptive weather conditions suggest that falcons were less active during drizzling (β = 15 ± 3, $P < 0.0001$) or rain (β = 5 ± 1, $P = 0.0007$) compared to during sunny (intercept = 23 ± 2; Fig. 6).

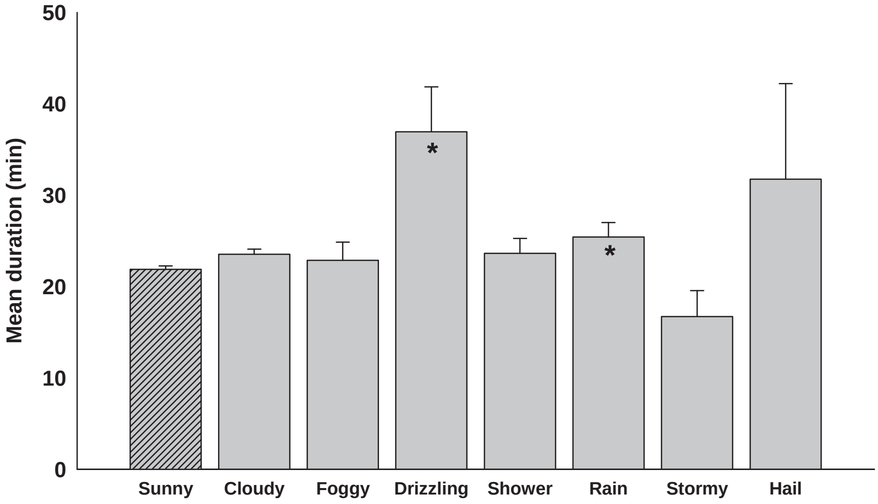

Figure 6. Relative activity level of falcons (*n* = 36) in each descriptive weather condition in Kaingaroa during the study period (2012–2014).Mean duration (minutes ± 1 SEM) represents that falcons spent per site in each descriptive weather condition. Sunny (hatched bar) was used as the reference for statistical comparisons; an asterisk indicates a statistically significant difference from the reference.

Analysis of meteorological information and activity level of falcons showed that falcons were more active in young forest during no rain (intercept = 19 ± 2) compared to during light rain to heavy rain (range β = 7 ± 3 to β = 41 ± 13, $P < 0.05$; Fig. 7A). During heavy rain, falcons remained in young/mature forest longer (intercept = 48 ± 11) compared with periods of no rain to moderate rain in the same habitat class (range β = -21 ± 11 to β = -24 ± 10, $P < 0.05$) except very light rain (β = -19 ± 10, $P = 0.0596$).

Ambient temperature did not influence falcon activity levels when they were in young forest (Fig. 7B). When the temperature exceeded 17°C (category 5), falcons remained in young/mature forest longer (intercept = 51 ± 8) compared with the lower temperature (range $\beta = -24 \pm 8$ to $\beta = -28 \pm 9$, $P < 0.05$), and they also remained in mature significantly longer (intercept = 74 ± 16) compared with the lower temperature categories (range $\beta = -46 \pm 16$ to $\beta = -51 \pm 16$, $P < 0.05$) except category one (<0°C), $\beta = -40 \pm 22$, $P = 0.0722$). Wind intensity also influenced falcons' habitat use. During strong breeze, they were less active in young forest ($\beta =27 \pm 4$) compared to the other wind categories (range $\beta = -7 \pm 3$ to $\beta = -9 \pm 2$, $P < 0.05$), and remained longer in mature forest ($\beta = 41 \pm 5$) compared to during the other wind intensities (range $\beta = -13 \pm 5$ to $\beta = -15 \pm 5$, $P < 0.05$) except during calm ($\beta = -14 \pm 9$, $P = 0.0892$; Fig. 7C). In summary, falcons were less active during wet weather and when in young forest. They were also less active in young/mature and mature forest during extreme weather such as heavy rain, warmer temperature or strong winds.

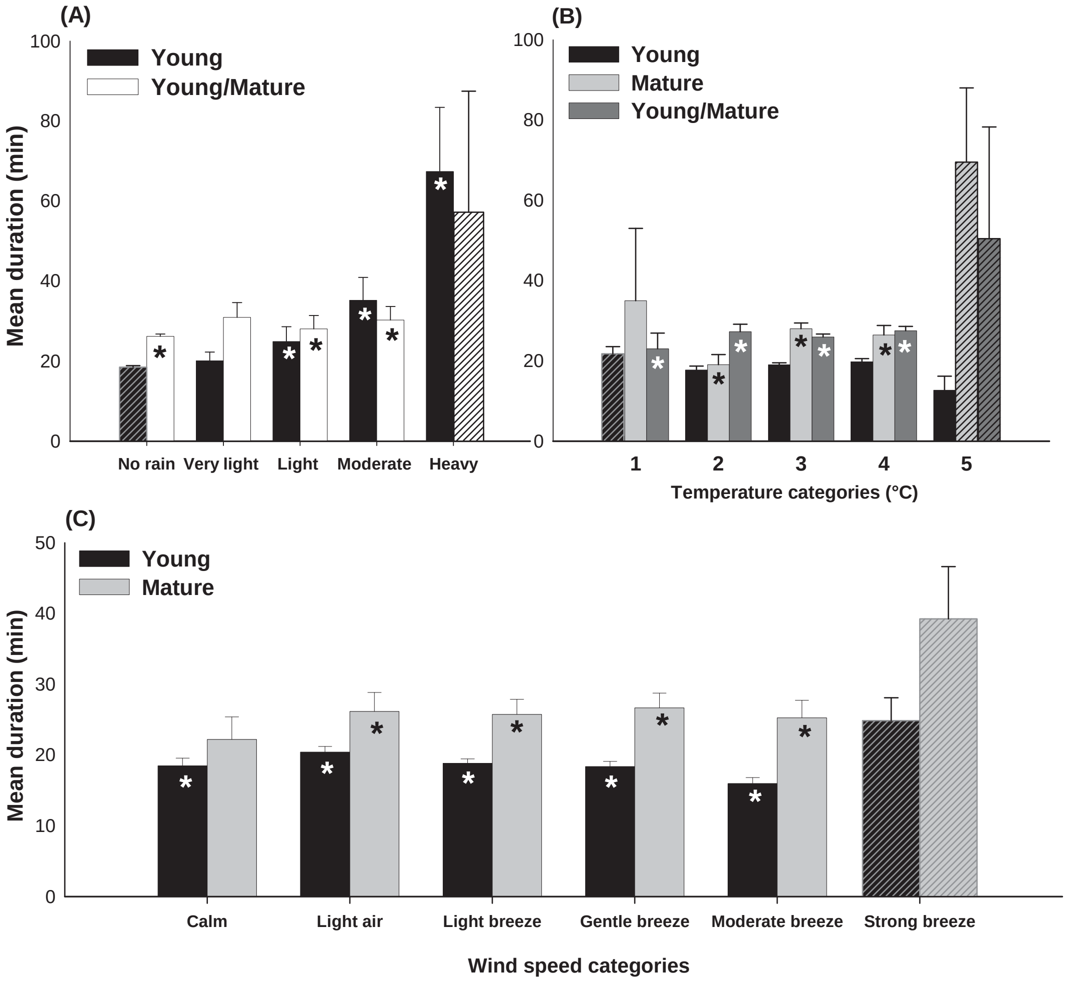

Figure 7. Relative activity level of falcons (*n* = 36) in each weather condition in Kaingaroa during the study period (2012–2014). Mean duration (minutes ± 1 SEM) duration represents that falcons spent per site in the habitat classes in relation to weather conditions: (A) precipitation (mm), (B) ambient temperature (°C), and (C) wind speed (km h^{-1}) during non-breeding season of falcons (April to August) 2012 to 2014. Weather data were categorised based on intensity: precipitation – no rain (0 mm), very light rain (0.01–0.25 mm), light rain (0.26–1.00 mm), moderate rain (1.10–4.00 mm), and heavy rain (4.10–16.00 mm); ambient temperature (°C) – 1 (<0°C), 2 (0.1–4.9°C), 3 (5.0–10.9°C), 4 (11.0–16.9°C), and 5 (>17.0°C); and wind speed (km^{-1}) – calm (<1 km h^{-1}), light air (1.0–5.5 km h^{-1}), light breeze (5.6–11.9 km h^{-1}), gentle breeze (12.0–19.9 km h^{-1}), moderate breeze (20.0–29.9 km h^{-1}), and strong breeze (>30.0 km h^{-1}). Bars are SE of mean duration (minutes). Shaded patterns on the bars indicate that these habitat classes and weather conditions were used as references in statistical analyses and asterisk marks represent statistical significance.

Discussion

Prey abundance and availability

Prey abundance did not vary throughout the classified habitats in Kaingaroa during the winter period. We found higher abundances of native birds in August compared with June and July. This difference could be explained by an increased detectability of birds during the early spring when birds become more active and vocal rather than an increased abundance of birds (Gibbs 1996). The assemblage of prey species was not uniformly distributed. Relatively high abundance of introduced species occurred in the interior of young stands while significantly greater abundance of native (forest) species occurred in young/mature forest edges. This may explain why bird abundance did not vary by size of open field as a standard-sized open stand (<2 km^2) has proportionately more young/mature forest edges than does a large-sized open stand (>2 km^2). Overall, we counted a high number of species dependent on forest edge habitat, e.g. New Zealand fantail (*Rhipidura fuliginosa*) and tomtit (*Petroica macrocephala*) as well as introduced bird species commonly occupying open interiors, e.g. redpoll and European goldfinch (*Carduelis carduelis*; Drapeau et al. 2000; Burton 2002). A large open stand (>2 km^2 and <4 km^2) in Kaingaroa encompasses a mixture of habitats at a variety of successional phases thus supporting a wide diversity of flora and fauna. For instance, freshly cutover stands can attract avian insectivores such as fantail and tomtit that feed on the old growth forest invertebrates that survive for the short term in cutover stands (Pawson et al. 2006). Exotic grasses, forbs and fruit-bearing species colonise young stands (Burton 2002), and we counted large flocks (>100 individuals) of ground foraging seedeaters (Moorman & Guynn 2001) such as redpoll, goldfinch, and chaffinch and some fruit-eaters (Burns 2009) such as blackbird (*Turdus merula*) and silvereye (*Zosterops lateralis*) in young stands. Even after exotic grasses and forbs in these stands were thinned by forestry herbicide operations, seedeaters seemed to be able to find seeds remaining on the forest floor (CH pers. obs.). Therefore, it appears that the variety of habitats and successional stages at Kaingaroa can provide enough winter food for the falcon population, a conclusion supported by the fact that all radio tagged adult falcons remained within Kaingaroa throughout the winter.

Falcons primarily selected open fields for hunting (i.e. young pine stands or pasture), probably because prey are more visible in open fields, facilitating hunting (Bechard 1982), rather than because the habitat might have higher densities of prey. This finding differs from a study of the same falcon population during the breeding season, which reported a positive correlation between falcon activity and prey density (Seaton 2007). This discrepancy may be explained because breeding adult falcons must increase hunting efforts to meet greater demands for feeding nestlings (Toland 1987; Olsen & Tucker 2003); thus, hunting efficiency is the most likely primary factor for falcons' habitat selection. Furthermore, although we do not have a direct comparison (prey density in summer versus mean prey abundance in winter), overall prey abundance might have been lower in winter compared with summer as we anticipate that the abundance of passerine birds, especially vulnerable fledglings, will decline during autumn and winter (Perrins 1965). Thus, it is likely that falcons might need to explore further to encompass the young/mature habitat in part for increasing hunting opportunities in winter.

Home range size and habitat selection

The non-breeding season home ranges of falcons were larger (29 ± 5 km^2 [MCP] for female and 17 ± 3 km^2 [MCP] for males) than breeding season home ranges of the same population observed by Seaton et al. (2013) (6 km^2 [MCP] for females and 9 km^2 [MCP] for males; note that here we report MCP home range sizes to facilitate comparison with Seaton et al. (2013)'s analyses). Similar seasonal variations of home range sizes have been observed in other raptors, including the American kestrel (*F. sparverius*; Ardia & Bildstein 1997), gyrfalcon (*F. rusticolus*; Burnham & Newton 2011), European sparrowhawk (*Accipiter nisus*; Marquiss & Newton 1982) and golden eagle (*Aquila chrysaetos*; Marzluff et al. 1997). The seasonal difference in home range size is mainly attributed to the movement of breeding adult falcons being constrained by the need to provision young frequently at the nest site (Marquiss & Newton 1982; Thirgood et al. 2003; Thomas 2008). In fact, Seaton (2007) noted that the home range size of breeding female falcons in Kaingaroa increased as their young became more self-sufficient. Thomas et al. (2010a) analysed PTT/Argos satellite tracking data for two adult falcons (a male for one non-breeding season and a female for two non-breeding seasons) in Kaingaroa. Although technical issues and limitations regarding the accuracy of the PTT/Argos satellite tracking are noted, their findings are comparable to our results. For the male, the non-breeding home range size was 13 km^2 (95% KDE) in 2006 and 6 km^2 in 2007, and the core home range was 3 km^2 (50% KDE) in 2006 and 0.5 km^2 in 2007. The female had much larger home range sizes, 52 km^2 in 2002 and 41 km^2 in 2003 (95% KDE), and her core home range was 11 km^2 in 2002 and 10 km^2 in 2003.

Winter habitat use and home range size of our study falcons appeared to be influenced principally by the distribution of the young/mature forest edge within their home ranges rather than by prey abundance alone. This may be because the taller trees of the young/mature forest edge provided a vantage point to view potential hunting areas (Bechard 1982) with introduced small passerines. Farmland falcons used arboreal windbreaks or mature pine trees established along streams situated in pastures at a rate comparable with use of the young/mature forest edge habitat within the pine forest, further suggesting that tall trees in or adjacent to open habitat afford key hunting opportunities for this species. Some of the farmland falcons (7 of 11) additionally foraged at shelter (farm barns and trees near silage) where there were many prey (>1000 individuals). They spent only 1.4% of their tracked time there, perhaps because hunting success was high (Bechard 1982; Temeles 1986; McGrady et al. 2002; Ganusevich et al. 2004). We recorded only one female falcon that selected the interior of mature stands more than the young/mature forest edge habitat. She mostly used a valley landscape (comprising <10% of the total area) where we regularly recorded her perching in emergent trees facing down to gullies (CH pers. obs.). Consequently, her spatial use of emergent trees would have been similar to falcons in native podocarp forests of New Zealand (Barea 1995; L. Barea, pers. comm.). We also observed falcons using the taller trees of the young/mature forest edge as a vantage point for territorial defence against other species such as Australasian harriers (*Circus approximans*) and Australasian magpies (*Cracticus tibicen*), and as sun basking spots for rest, preening, and interaction with mates. Falcons in the tussock-clad hill country of the eastern South Island, New Zealand, use elevated greywacke rocks as vantage points (Fox 1977). These findings suggest that use of vantage points is a characteristic typical of New Zealand falcons across various landscapes and as such trees may constitute an important habitat for falcons living in relatively flat country.

There is no evidence of sex specific habitat preferences in New Zealand falcons. However, other raptors do exhibit sex specific habitat preferences that are commonly explained by characteristics driven by reverse sexual size dimorphism. For instance, males have better manoeuvrability than females due to their smaller body size. Thus, males can forage in denser tree vegetation than females, resulting in food niche segregation (e.g. European sparrowhawks, Marquiss & Newton 1982; northern spotted owl *Strix occidentalis caurina,* Solis & Guttierrez 1990; and tawny owl *Strix aluco*, Sunde et al. 2003). In our study, females were 1.9 times heavier than males (male, mean ± SD = 243 ± 20.3 g, *n* = 19; female, mean ± SD = 463 ± 30.1 g, *n* = 31; CH unpubl. data). The size dimorphism shown by falcons at Kaingaroa was much greater than that of other raptor species including the species listed above (females 1.2–1.5 times heavier than males; Temeles 1986; Sunde et al. 2003). Female falcons are capable of hunting larger prey such as pheasant (*Phasianus colchicus*; Hyde & Seaton 2008; Kross et al. 2013), spur-winged plover (*Vanellus miles*, CH unpubl. data), and European rabbit (*Oryctolagus cuniculus*; Fox 1977; Kross et al. 2013). Nevertheless, female falcons in Kaingaroa primarily prey on small passerine birds during the summer (Seaton 2007). Compatible findings are reported in studies of goshawks in Europe. The goshawks selected heterogeneous habitat for hunting similar prey and had no sex specific habitat segregation (Kenward 1982; Widen 1989) despite exhibiting strong sexual size dimorphism.

Activity in relation to season and weather

Temporal variations in falcon activity levels are explained in part by prey activity level in winter weather. During our prey bird censuses, we often recorded that prey birds remained relatively inactive in cold and early mornings until frost on the open ground was melted by the sun. Flocks of seedeaters such as redpoll and goldfinch were more active feeding on the ground in the afternoon when the temperature was warmer than in the morning (CH pers. obs.). This pattern may explain why falcons were more active during the afternoon. The lower activity level of falcons in May and June corresponded with the higher wind velocities and precipitation recorded in these two months as opposed to July and August when birds were relatively active overall. The lower activity levels of falcons during rain or strong wind suggests these weather events may interfere with a falcon’s hunting efficiency, possibly by limiting visibility and hearing, and also by lowering the activity levels of their prey (Elkins 2004). The combination of heavy rain and strong wind could result in high energy expenditure in flight (Kennedy 1970), reducing effective hunting opportunities. The taller trees of the young/mature ecotone play a valuable role in providing falcons with cover from these extreme weather events as shown by their increased time spent there during heavy rain. The interior of mature stands also afforded falcons shelter from severe wind. Use of these habitats could mitigate the risk of hypothermia or winter weather related mortality of falcons (Newton 1979).

Conclusion

We have documented the first details of the winter ecology of New Zealand falcons in a pine plantation. With the heterogeneous landscape created by different stand ages, the Kaingaroa pine plantation can offer sufficient prey for the New Zealand falcon population throughout the non-breeding season. An open field created by clearcutting is a dynamic habitat that can support a great diversity of prey birds irrespective of its size. A few falcons used neighbouring farmland silage pits where potential prey were present in high concentrations. However, we found that falcons selected habitat based on forest structure partly associated with prey availability, not solely abundance. The young/mature forest edge was the habitat most frequently selected by falcons and served as an important winter habitat niche for them. Hence, availability of young/mature forest edges within a home range is likely to be a key factor in determining the home range size of our study population in winter. Our results suggest that providing habitat containing ecotones of young trees adjacent to mature trees throughout plantation forests can assist in the conservation of this threatened endemic raptor.

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Birds were captured and handled according to Animal Ethics guidelines approved by Massey University (Protocol No. 11/96) and Department of Conservation National Permit (National Permit Number BP-32336-RES.).

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DRC 16

MASSEY UNIVERSITY
GRADUATE RESEARCH SCHOOL

STATEMENT OF CONTRIBUTION
TO DOCTORAL THESIS CONTAINING PUBLICATIONS

(To appear at the end of each thesis chapter/section/appendix submitted as an article/paper or collected as an appendix at the end of the thesis)

We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of Candidate: Chifuyu Horikoshi

Name/Title of Principal Supervisor: Associate Professor Phil F. Battley

Name of Published Research Output and full reference:

Horikoshi, C., Battley, P.F., Seation, R., Minot, E.O. 2017. Winter habitat use of New Zealand falcons (Falco novaesslandiae ferox) in an intensively managed pine plantation, cnetral Norht Island, New Zealand. New Zealand Journal of Ecology 41(2)

In which Chapter is the Published Work: 2

Please indicate either:

- The percentage of the Published Work that was contributed by the candidate:

  and / or

- Describe the contribution that the candidate has made to the Published Work:

  Chifuyu Horikoshi contributed to the development of the research questions and experimental designs, and undertook all data collection, analysis, and writing.

Chifuyu Horikoshi Digitally signed by Chifuyu Horikoshi
DN: cn=Chifuyu Horikoshi, o=Massey University, ou=Ecology Group, email=gizmoglee7@gmail.com, c=NZ
Date: 2017.05.23 15:27:33 +12'00'
Candidate's Signature

23/05/2017
Date

Phil Battley Digitally signed by Phil Battley
Date: 2017.05.23 16:33:18 +12'00'
Principal Supervisor's signature

23/05/2017
Date

GRS Version 3– 16 September 2011

Appendices

Appendix S1. Model selection and significance for bird abundance in Kaingaroa Forest and adjacent farmland.

```
Model                         N      Marginal    Conditional     AIC        dAIC
TOTAL~category               195   0.588382214   0.5883822     2699.854   0.000
TOTAL~category+MONTH         195   0.586128041   0.5861280     2703.663   3.808
TOTAL~MONTH                  195   0.001314057   0.6913008     2768.263  68.409


TOTAL~category                             numDF  denDF  F-value   p-value
                            (Intercept)        1   169  34.10088    <.0001
                            category       10    15 27.73110  <.0001

TOTAL~category+MONTH                      numDF   denDF   F-value   p-value
                            (Intercept)        1    167  33.76328   <.0001
                            category       10    15 27.45656  <.0001
                            MONTH              2    167  0.08919    0.9147


                            Fixed effects: TOTAL ~ category
                                 Value Std.Error  DF   t-value p-value
                 (Intercept)    44.7714  39.98302 169  1.119761  0.2644
                 categoryI     -21.3169  81.76325  15 -0.260715  0.7979
                 CategoryM/I   -26.9857  74.80138  15 -0.360765  0.7233
                 categoryI/P    -4.9714  84.81679  15 -0.058614  0.9540
                 categoryI/Y   -26.0361  56.95878  15 -0.457105  0.6541
                 categoryM      -2.6945  76.82889  15 -0.035072  0.9725
                 categoryM/P    12.6730  88.40578  15  0.143351  0.8879
                 categoryM/Y   -14.3660  55.77518  15 -0.257570  0.8002
                 categorySlge 1333.4508  88.40578  15 15.083298  0.0000
                 categoryTR/P   52.5363  76.82889  15  0.683809  0.5045
                 categoryY/P   -12.5714  84.81679  15 -0.148219  0.8841
```

Appendix S2. Model selection and significance for native bird abundance in Kaingaroa Forest.

```
Model                      N    Marginal   Conditional      AIC        dAIC
native~category+MONTH     173  0.31961487   0.3415989     1425.099    0.000
native~category           173  0.25271511   0.3260302     1437.429   12.329
native~MONTH              173  0.04611528   0.3457874     1442.306   17.206

                                       numDF denDF   F-value p-value
native~category+MONTH     (Intercept)     1   150 133.46840  <.0001
                          category        8    12   6.68501  0.0019
                          MONTH           2   150   7.53103  0.0008

                       Fixed effects: native ~ category + MONTH
                                Value Std.Error  DF   t-value p-value
                (Intercept) 11.419935  3.177955 150  3.593485  0.0004
                categoryI    8.687677  5.444218  12  1.595762  0.1365
                categoryM/I  6.198794  5.110159  12  1.213033  0.2485
                categoryI/P  0.695892  5.639465  12  0.123397  0.9038
                categoryI/Y  0.273268  4.014441  12  0.068071  0.9468
                categoryM   24.793452  5.169002  12  4.796564  0.0004
                categoryM/P 25.724630  5.807768  12  4.429349  0.0008
                categoryM/Y 15.297359  3.948784  12  3.873941  0.0022
                categoryY/P  2.757858  5.672424  12  0.486187  0.6356
                MONTHJULY   -7.539704  2.570404 150 -2.933276  0.0039
                MONTHJUNE   -9.825201  2.795097 150 -3.515156  0.0006
```

Appendix S3. Model selection and significance for introduced bird abundance in Kaingaroa Forest.

```
Model                           N     Marginal    Conditional      AIC      dAIC
exotic~CorE                     173  0.04085920   0.3465921     1727.730    0.000
exotic~MONTH+CorE               173  0.04705940   0.3571461     1730.556    2.826
exotic~MONTH                    173  0.00506657   0.3167301     1731.011    3.281
exotic~category                 173  0.10727533   0.4151764     1737.109    9.370
exotic~category+MONTH           173  0.11007221   0.4244360     1740.070   12.340

exotic~CorE                                 numDF denDF   F-value p-value
                                (Intercept)     1   151 12.600961  0.0005
                                CorE            1   151  2.343586  0.1279

exotic~MONTH+CorE                numDF denDF   F-value p-value
                                (Intercept)     1   149 12.286668  0.0006
                                MONTH           2   149  0.564338  0.5699
                                CorE            1   149  2.414271  0.1224

                            Fixed effects: exotic ~ CorE
                               Value Std.Error  DF   t-value p-value
               (Intercept)  30.59391  9.155882 151  3.341448  0.0011
               CorEE       -16.88837 11.031825 151 -1.530878  0.1279
```

Appendix S4. Model selection and significance for bird abundance in open habitat and the border to mature aged pine stands in Kaingaroa Forest.

Model	N	Marginal	Conditional	AIC	dAIC
total~CorE+HARVEST	251	0.04122447	0.2084762	2526.965	0.000
total~CorE	251	0.02507417	0.1992758	2527.257	0.291
total~HARVEST	251	0.01641044	0.1948746	2528.428	1.463
total~SIZE+CorE*SIZE+HARVEST*SIZE+SIZE*CorE	251	0.06160925	0.2229442	2529.864	2.898
total~CorE*SIZE+HARVEST*SIZE+SIZE*CorE	251	0.06160925	0.2229442	2529.864	2.898
total~CorE*SIZE+HARVEST*SIZE	251	0.06160925	0.2229442	2529.864	2.898
total~MONTH+SIZE+CorE*HARVEST+CorE*MONTH+ CorE*SIZE+HARVEST*SIZE+HARVEST*CorE+SIZE*CorE	251	0.08613136	0.2468730	2531.518	4.552
total~SIZE+CorE*HARVEST+CorE*MONTH+CorE*SIZE+ HARVEST*SIZE+HARVEST*CorE+SIZE*CorE	251	0.08613136	0.2468730	2531.518	4.552
total~SIZE+CorE*HARVEST+CorE*SIZE+ HARVEST*SIZE+HARVEST*CorE+SIZE*CorE	251	0.06259382	0.2276132	2531.538	4.572
total~SIZE+CorE*SIZE+HARVEST*SIZE+ HARVEST*CorE+SIZE*CorE	251	0.06259382	0.2276132	2531.538	4.572
total~CorE*SIZE	251	0.03201360	0.2114447	2530.371	3.405
total~MONTH+SIZE+CATEGORY+CorE*CATEGORY+ CorE*HARVEST+CorE*MONTH+CorE*SIZE+ HARVEST*SIZE+HARVEST*CorE+SIZE*CorE	251	0.08525980	0.2535486	2539.328	12.363
total~MONTH+SIZE+CorE*CATEGORY+CorE*HARVEST+ CorE*MONTH+CorE*SIZE+HARVEST*SIZE+HARVEST*CorE+SIZE*CorE	251	0.08525980	0.2535486	2539.328	12.363
total~MONTH+SIZE+CATEGORY+CorE*CATEGORY+ CorE*HARVEST+CorE*MONTH+CorE*SIZE+CATEGORY*SIZE+ HARVEST*SIZE+HARVEST*CorE+SIZE*CorE	251	0.08825569	0.2578231	2542.198	15.233
total~SIZE+HARVEST+CATEGORY+MONTH+ SIZE*HARVEST+MONTH*HARVEST+MONTH*SIZE+CorE	251	0.06034091	0.2195739	2543.016	16.050

total~CorE+HARVEST

```
            numDF denDF  F-value p-value
(Intercept)     1   210 47.93657  <.0001
CorE            1    38  3.29834  0.0772
HARVEST         1    38  2.20525  0.1458
```

```
Fixed effects: total ~ CorE + HARVEST
               Value Std.Error  DF  t-value p-value
(Intercept) 12.80977  5.492544 210 2.332210  0.0206
CorEE       12.22466  6.662125  38 1.834949  0.0744
HARVESTW    10.10864  6.807118  38 1.485010  0.1458
```

Appendix S5. Model selection and significance for native bird abundance in open habitats and the ecotone between the open habitats and mature aged pine stands in Kaingaroa Forest.

Model	N	Marginal	Conditional	AIC	dAIC
native~MONTH+CorE*MONTH	251	0.2942479	0.2942480	2043.978	0.000
native~MONTH+SIZE+CATEGORY+HARVEST+ CorE*CATEGORY+CorE*HARVEST+CorE*MONTH+ CorE*SIZE+CATEGORY*SIZE+HARVEST*SIZE	251	0.3149522	0.3228153	2054.972	1.099
native~CorE+MONTH	251	0.2741187	0.2741187	2047.705	3.727
native~MONTH+CATEGORY+ CorE*CATEGORY+CorE*MONTH	251	0.3022770	0.3022771	2047.791	3.813
native~MONTH+CorE*CATEGORY+CorE*MONTH	251	0.3022770	0.3022771	2047.791	3.813
native~MONTH+CATEGORY+CorE*CATEGORY+ CorE*HARVEST+CorE*MONTH	251	0.3095419	0.3095419	2048.431	4.453
native~CorE	251	0.2617340	0.2617344	2048.522	4.544
native~MONTH+SIZE+CATEGORY+HARVEST+CorE*CATEGORY+ CorE*HARVEST+CorE*MONTH+CATEGORY*SIZE	251	0.3158908	0.3158925	2051.003	7.025050e+00
native~MONTH+CATEGORY+HARVEST+CorE*CATEGORY+ CorE*HARVEST+CorE*MONTH+CATEGORY*SIZE	251	0.3158908	0.3158925	2051.003	7.025050e+00
native~MONTH+CATEGORY+CorE*CATEGORY+ CorE*HARVEST+CorE*MONTH+CATEGORY*SIZE	251	0.3158908	0.3158925	2051.003	7.025050e+00
native~CorE*MONTH	251	0.2942479	0.2942480	2043.978	8.799361e-10
native~MONTH+SIZE+CATEGORY+HARVEST+CorE*CATEGORY+ CorE*HARVEST+CorE*MONTH+CATEGORY*SIZE+HARVEST*SIZE	251	0.3154220	0.3187448	2052.980	9.002271e+00

native~MONTH+CorE*MONTH		numDF	denDF	F-value	p-value
	(Intercept)	1	206	166.31195	<.0001
	CorE	**1**	**39**	**91.67648**	**<.0001**
	MONTH	2	206	2.44782	0.0890
	CorE:MONTH	**2**	**206**	**3.82990**	**0.0233**

native~MONTH+SIZE+CATEGORY+HARVEST+ CorE*CATEGORY+CorE*HARVEST+CorE*MONTH+ CorE*SIZE+CATEGORY*SIZE+HARVEST*SIZE		numDF	denDF	F-value	p-value
	(Intercept)	1	200	155.76830	<.0001
	MONTH	2	200	1.81205	0.1660
	SIZE	1	34	0.28016	0.6000
	CATEGORY	2	200	0.98507	0.3752
	HARVEST	1	34	0.34359	0.5616
	CorE	**1**	**34**	**87.48077**	**<.0001**
	CATEGORY:CorE	**2**	**200**	**3.12772**	**0.0460**

```
HARVEST:CorE      1    34   2.52376  0.1214
MONTH:CorE        2   200   1.65932  0.1929
SIZE:CorE         1    34   0.00268  0.9590
SIZE:CATEGORY     2   200   1.52545  0.2200
SIZE:HARVEST      1    34   0.01337  0.9086
```

```
Fixed effects: native ~ CorE * MONTH
                        Value Std.Error  DF   t-value p-value
(Intercept)          1.717948  2.228157 206  0.771018  0.4416
CorEE               22.843028  3.112425  39  7.339303  0.0000
MONTHJULY            1.682051  3.131333 206  0.537168  0.5917
MONTHJUNE            1.350233  3.060261 206  0.441215  0.6595
CorEE:MONTHJULY    -11.868027  4.308312 206 -2.754681  0.0064
CorEE:MONTHJUNE     -5.193262  4.364903 206 -1.189777  0.2355
```

Appendix S6. Model selection and significance for introduced bird abundance in open habitats and the ecotone between the open habitats and mature aged pine stands in Kaingaroa Forest.

Model	N	Marginal	Conditional	AIC	dAIC
exotic~HARVEST	251	0.01418331	0.2111858	2442.089	0.000
exotic~HARVEST+CorE	251	0.02043294	0.2153312	2443.260	1.171
exotic~HARVEST+SIZE	251	0.01687904	0.2174337	2443.768	1.678
exotic~HARVEST+HARVEST*CorE	251	0.02933115	0.2218662	2444.101	2.011
exotic~HARVEST+CorE*MONTH	251	0.03562297	0.2270874	2446.324	4.234
exotic~HARVEST+CorE*MONTH+HARVEST*SIZE	251	0.06200593	0.2370896	2446.414	4.324
exotic~HARVEST+CorE*HARVEST+CorE*MONTH+HARVEST*SIZE	251	0.07021303	0.2408639	2446.916	4.827
exotic~HARVEST+CorE*MONTH+HARVEST*CorE	251	0.04425840	0.2334394	2447.158	5.068
exotic~SIZE+HARVEST+CATEGORY+MONTH+SIZE*HARVEST+MONTH*HARVEST	251	0.04684873	0.2256376	2452.360	10.270
exotic~MONTH+SIZE+CATEGORY+HARVEST+CorE*CATEGORY+CorE*HARVEST+CorE*MONTH+CorE*SIZE+HARVEST*SIZE	251	0.07720208	0.2533187	2455.219	13.129
exotic~MONTH+SIZE+HARVEST+CorE*CATEGORY+CorE*HARVEST+CorE*MONTH+CorE*SIZE+HARVEST*SIZE	251	0.07720208	0.2533187	2455.219	13.129
exotic~MONTH+HARVEST+CorE*CATEGORY+CorE*HARVEST+CorE*MONTH+CorE*SIZE+HARVEST*SIZE	251	0.07720208	0.2533187	2455.219	13.129
exotic~HARVEST+CorE*CATEGORY+CorE*HARVEST+CorE*MONTH+CorE*SIZE+HARVEST*SIZE	251	0.07720208	0.2533187	2455.219	13.129
exotic~SIZE+HARVEST+CATEGORY+MONTH+SIZE*HARVEST+MONTH*HARVEST+MONTH*SIZE	251	0.04711090	0.2249094	2456.189	14.099
exotic~MONTH+SIZE+CATEGORY+HARVEST+CorE*CATEGORY+CorE*HARVEST+CorE*MONTH+CorE*SIZE+CATEGORY*SIZE+HARVEST*SIZE	251	0.07775569	0.2592203	2458.803	16.713

exotic~HARVEST

	numDF	denDF	F-value	p-value
(Intercept)	1	210	15.36727	0.0001
HARVEST	1	39	1.70845	0.1988

exotic~HARVEST+SIZE

	numDF	denDF	F-value	p-value
(Intercept)	1	210	15.112767	0.0001
HARVEST	1	38	1.683225	0.2023
SIZE	1	38	0.304385	0.5844

exotic~HARVEST+CorE

	numDF	denDF	F-value	p-value
(Intercept)	1	210	15.397979	0.0001
HARVEST	1	38	1.711197	0.1987
CorE	1	38	0.769016	0.3860

```
Fixed effects: exotic ~ HARVEST
                Value Std.Error  DF  t-value p-value
(Intercept) 8.397611  3.778077 210 2.222721  0.0273
HARVESTW    7.843580  6.000855  39 1.307077  0.1988
```

Appendix S7. Model selection and significance for New Zealand falcon activity level in relation to various weather conditions, Kaingaroa Forest, 2012–2014.

Model	N	Marginal	Conditional	AIC	dAIC
MIN~habitat+weather+month*day+factor(year)	5748	0.06499233	0.08783512	51941.51	0.000
MIN~habitat+weather+month*day	5748	0.06052196	0.08759205	51949.51	8.009
MIN~habitat+weather+month+sex+nickname+ factor(year)+day	5748	0.05851465	0.08042564	51967.43	25.925
MIN~habitat+weather+month+nickname+ factor(year)+day	5748	0.05877304	0.07996030	51965.87	24.367
MIN~habitat+weather+month+factor(year)+day	5748	0.05907039	0.07976572	51964.07	22.565
MIN~habitat+weather+month+day	5748	0.05461884	0.08011765	51971.77	30.261
MIN~habitat+weather	5748	0.03974073	0.07252216	52037.63	96.123

MIN~habitat+weather+month*day+factor(year)		numDF	denDF	F-value	p-value
	(Intercept)	1	5686	972.7221	<.0001
	habitat	**11**	**5686**	**16.3578**	**<.0001**
	weather	**7**	**5686**	**7.0575**	**<.0001**
	month	**4**	**5686**	**17.0453**	**<.0001**
	day	**2**	**5686**	**5.5927**	**0.0037**
	factor(year)	**2**	**5686**	**5.6948**	**0.0034**
	month:day	**8**	**5686**	**4.8374**	**<.0001**

MIN~habitat+weather+month*day		numDF	denDF	F-value	p-value
	(Intercept)	1	5696	889.6151	<.0001
	habitat	**11**	**5696**	**16.2407**	**<.0001**
	weather	**7**	**5696**	**7.0114**	**<.0001**
	month	**4**	**5696**	**16.8141**	**<.0001**
	day	**2**	**5696**	**5.5360**	**0.004**

Fixed effects: MIN ~ habitat + weather + month * day + factor(year)

	Value	Std.Error	DF	t-value	p-value
(Intercept)	23.280951	1.742670	5686	13.359355	0.0000
habitatI	5.102134	1.318205	5686	3.870516	0.0001
habitatI/P	12.548138	5.127215	5686	2.447360	0.0144
habitatM	9.054568	1.271201	5686	7.122848	0.0000
habitatM/I	6.994980	1.571258	5686	4.451834	0.0000
habitatM/P	18.392217	3.239622	5686	5.677272	0.0000
habitatP	-1.059042	1.900003	5686	-0.557390	0.5773
habitatSilage	-6.092347	2.228475	5686	-2.733864	0.0063

habitatTR/P	4.845049	1.417232	5686	3.418669	0.0006
habitatY/I	2.951986	1.304186	5686	2.263470	0.0236
habitatY/M	7.544005	0.787789	5686	9.576175	0.0000
habitatY/P	-2.685940	4.230006	5686	-0.634973	0.5255
weathercloudy	0.844908	0.710590	5686	1.189022	0.2345
weatherdrizzling	14.887688	2.714333	5686	5.484843	0.0000
weatherfoggy	2.279240	1.944655	5686	1.172053	0.2412
weatherhail	11.078564	6.786860	5686	1.632355	0.1027
weatherrain	4.927925	1.453570	5686	3.390223	0.0007
weathershower	2.833570	1.770429	5686	1.600499	0.1095
weatherstormy	-4.086240	4.699079	5686	-0.869583	0.3846
monthAPRL	-6.383684	2.605428	5686	-2.450148	0.0143
monthAUG	-7.691070	1.371956	5686	-5.605918	0.0000
monthJULY	-7.837293	1.369246	5686	-5.723800	0.0000
monthMAY	2.934483	2.221862	5686	1.320732	0.1866
dayam	-0.374417	1.434269	5686	-0.261051	0.7941
daypm	-5.902749	1.308466	5686	-4.511197	0.0000
factor(year)2013	2.710175	1.640622	5686	1.651919	0.0986
factor(year)2014	-0.637207	1.633078	5686	-0.390188	0.6964
monthAPRL:dayam	-5.398226	3.499557	5686	-1.542546	0.1230
monthAUG:dayam	-0.796091	1.907987	5686	-0.417241	0.6765
monthJULY:dayam	0.239618	1.971804	5686	0.121522	0.9033
monthMAY:dayam	-5.469321	3.097194	5686	-1.765896	0.0775
monthAPRL:daypm	10.018588	3.415124	5686	2.933595	0.0034
monthAUG:daypm	6.984586	1.884177	5686	3.706969	0.0002
monthJULY:daypm	5.700663	1.840198	5686	3.097853	0.0020
monthMAY:daypm	-1.454049	2.750077	5686	-0.528730	0.5970

Appendix S8. Model selection and significance for New Zealand falcon activity level in relation to wind speed in Kaingaroa Forest, 2012–2014.

Model	df	AIC	BIC	dAIC
MIN~habitat_windrank+YEAR+SEX+ month+Day+CorE+temprank+rainrank	89	51755.73	52346.92	0.00
MIN~habitat_windrank+YEAR+ month+Day+CorE+temprank+rainrank	88	51756.77	52341.34	1.04
MIN~habitat_windrank+YEAR+ month+Day+CorE+rainrank	84	51764.32	52322.37	8.59
MIN~habitat_windrank+YEAR+month+CorE+rainrank	82	51768.57	52313.36	12.84
MIN~habitat_windrank+YEAR+month+rainrank	81	51774.01	52312.18	18.25
MIN~habitat_windrank+YEAR+month	77	51791.81	52303.45	36.08

MIN~habitat_windrank+YEAR+SEX+month+ Day+CorE+temprank+rainrank

	numDF	denDF	F-value	p-value
(Intercept)	1	5641	984.5894	<.0001
habitat_windrank	**69**	**5641**	**3.7236**	**<.0001**
YEAR	**1**	**5641**	**23.0422**	**<.0001**
SEX	1	27	0.2520	0.6198
month	**4**	**5641**	**19.4489**	**<.0001**
Day	**2**	**5641**	**2.9948**	**0.0501**
CorE	**1**	**5641**	**3.9694**	**0.0464**
temprank	4	5641	0.7640	0.5486
rainrank	4	5641	3.0922	0.0149

MIN~habitat_windrank+YEAR+month+CorE+rainrank

	numDF	denDF	F-value	p-value
(Intercept)	1	5646	1031.4630	<.0001
habitat_windrank	**69**	**5646**	**3.7218**	**<.0001**
factor(YEAR)	**2**	**5646**	**12.2165**	**<.0001**
month	**4**	**5646**	**19.8659**	**<.0001**
CorE	**1**	**5646**	**4.2727**	**0.0388**
rainrank	**4**	**5646**	**2.9728**	**0.0183**

Fixed effects: MIN ~ habitat_windrank+factor(YEAR)+SEX+month+Day+CorE+temprank+rainrank

	Value	Std.Error	DF	t-value	p-value
(Intercept)	27.004257	3.532811	5646	7.643844	0.0000
habitat_windrankI.0	1.413238	7.730475	5646	0.182814	0.8550
habitat_windrankI/P.0	-20.431746	22.357351	5646	-0.913871	0.3608
habitat_windrankM.0	-0.641562	7.737505	5646	-0.082916	0.9339
habitat_windrankM/I.0	-10.369073	8.394537	5646	-1.235217	0.2168
habitat_windrankM/P.0	-18.933892	11.569157	5646	-1.636584	0.1018

habitat_windrankP.0	3.644068	6.589216	5646	0.553035	0.5803
habitat_windrankTR/P.0	-5.990136	7.127467	5646	-0.840430	0.4007
habitat_windrankY.0	-7.042676	2.883925	5646	-2.442045	0.0146
habitat_windrankY/I.0	-6.663829	5.338253	5646	-1.248317	0.2120
habitat_windrankY/M.0	-2.869597	4.060165	5646	-0.706768	0.4797
habitat_windrankY/P.0	-20.723495	11.496123	5646	-1.802651	0.0715
habitat_windrankI.1	-1.015963	3.773363	5646	-0.269246	0.7878
habitat_windrankI/P.1	19.179107	15.920539	5646	1.204677	0.2284
habitat_windrankM.1	-0.738421	3.605713	5646	-0.204792	0.8377
habitat_windrankM/I.1	-10.329240	4.277799	5646	-2.414616	0.0158
habitat_windrankM/P.1	-0.335328	13.123661	5646	-0.025551	0.9796
habitat_windrankP.1	-16.405345	3.675890	5646	-4.462959	0.0000
habitat_windrankSilage.1	-10.693828	6.988838	5646	-1.530130	0.1260
habitat_windrankTR/P.1	-4.068223	3.879010	5646	-1.048779	0.2943
habitat_windrankY.1	-7.542429	2.405583	5646	-3.135385	0.0017
habitat_windrankY/I.1	-5.461808	4.137029	5646	-1.320225	0.1868
habitat_windrankY/M.1	-5.542997	3.058534	5646	-1.812305	0.0700
habitat_windrankY/P.1	-11.292097	7.018623	5646	-1.608876	0.1077
habitat_windrankI.2	-1.198405	3.043711	5646	-0.393732	0.6938
habitat_windrankI/P.2	-9.100700	11.450795	5646	-0.794766	0.4268
habitat_windrankM.2	1.115732	3.118050	5646	0.357830	0.7205
habitat_windrankM/I.2	-5.613877	3.887141	5646	-1.444217	0.1487
habitat_windrankM/P.2	-0.489498	6.589817	5646	-0.074281	0.9408
habitat_windrankP.2	-10.600371	4.386460	5646	-2.416612	0.0157
habitat_windrankSilage.2	-23.502825	4.535783	5646	-5.181646	0.0000
habitat_windrankTR/P.2	-10.415207	3.440866	5646	-3.026915	0.0025
habitat_windrankY.2	-8.167243	2.356844	5646	-3.465331	0.0005
habitat_windrankY/I.2	-8.488659	3.621508	5646	-2.343957	0.0191
habitat_windrankY/M.2	-3.713340	2.992460	5646	-1.240899	0.2147
habitat_windrankY/P.2	-12.233243	8.359631	5646	-1.463371	0.1434
habitat_windrankI.3	-5.106674	2.951229	5646	-1.730355	0.0836
habitat_windrankI/P.3	8.737059	7.895369	5646	1.106606	0.2685
habitat_windrankM.3	-0.591756	3.003224	5646	-0.197040	0.8438
habitat_windrankM/I.3	-5.486269	4.260590	5646	-1.287678	0.1979
habitat_windrankM/P.3	17.007974	6.117935	5646	2.780019	0.0055
habitat_windrankP.3	-2.296699	4.723799	5646	-0.486197	0.6268
habitat_windrankSilage.3	-15.474818	4.320184	5646	-3.581982	0.0003
habitat_windrankTR/P.3	-7.617175	3.539217	5646	-2.152221	0.0314
habitat_windrankY.3	-8.758353	2.326083	5646	-3.765280	0.0002

habitat_windrankY/I.3	-9.116649	3.331503	5646	-2.736498	0.0062
habitat_windrankY/M.3	-3.342071	2.986824	5646	-1.118938	0.2632
habitat_windrankY/P.3	-11.448296	10.350042	5646	-1.106111	0.2687
habitat_windrankI.4	-4.743841	3.456752	5646	-1.372341	0.1700
habitat_windrankI/P.4	-8.137987	15.929615	5646	-0.510872	0.6095
habitat_windrankM.4	-1.241024	3.115770	5646	-0.398304	0.6904
habitat_windrankM/I.4	-0.008301	4.209765	5646	-0.001972	0.9984
habitat_windrankM/P.4	-5.677607	10.299187	5646	-0.551267	0.5815
habitat_windrankP.4	-5.873781	4.556175	5646	-1.289191	0.1974
habitat_windrankSilage.4	-20.822842	4.781263	5646	-4.355093	0.0000
habitat_windrankTR/P.4	-4.378433	4.502861	5646	-0.972367	0.3309
habitat_windrankY.4	-9.294709	2.447373	5646	-3.797831	0.0001
habitat_windrankY/I.4	-8.522849	3.866967	5646	-2.204014	0.0276
habitat_windrankY/M.4	-4.758128	3.017151	5646	-1.577027	0.1148
habitat_windrankY/P.4	-19.268601	22.376876	5646	-0.861094	0.3892
habitat_windrankI.5	0.020013	7.700316	5646	0.002599	0.9979
habitat_windrankI/P.5	-25.181510	22.366787	5646	-1.125844	0.2603
habitat_windrankM.5	14.214484	4.996829	5646	2.844701	0.0045
habitat_windrankM/I.5	4.708956	5.666232	5646	0.831056	0.4060
habitat_windrankM/P.5	-8.592162	15.948537	5646	-0.538743	0.5901
habitat_windrankP.5	-14.221418	22.299630	5646	-0.637742	0.5237
habitat_windrankSilage.5	-14.909521	10.308749	5646	-1.446298	0.1481
habitat_windrankTR/P.5	-10.697282	7.258330	5646	-1.473794	0.1406
habitat_windrankY/I.5	-14.916583	5.334475	5646	-2.796261	0.0052
habitat_windrankY/M.5	-0.345222	3.554501	5646	-0.097122	0.9226
factor(YEAR)2013	-0.018961	1.106370	5646	-0.017138	0.9863
factor(YEAR)2014	-2.954178	0.992002	5646	-2.977997	0.0029
SEXM	-1.058204	1.450103	27	-0.729744	0.4718
monthAUG	0.585185	1.802559	5646	0.324641	0.7455
monthJULY	-0.596915	1.844366	5646	-0.323642	0.7462
monthJUNE	5.890593	1.706274	5646	3.452314	0.0006
monthMAY	4.975363	1.788868	5646	2.781291	0.0054
Daymid-day	1.086121	0.853257	5646	1.272912	0.2031
Daypm	-0.632817	0.879161	5646	-0.719796	0.4717
CorEE	4.043680	1.913936	5646	2.112757	0.0347
temprank	-0.230398	0.583526	5646	-0.394838	0.6930
rainrank	1.565367	0.500930	5646	3.124920	0.0018

Appendix S9. Model selection and significance for New Zealand falcon activity level in relation to precipitation in Kaingaroa Forest, 2012–2014.

Model	df	AIC	BIC	dAIC
MIN~habitat_rainrank+YEAR+SEX+month+ Day+CorE+temprank+windrank	68	51827.94	52279.89	0.00
MIN~habitat_rainrank+YEAR+month+ Day+CorE+temprank+windrank	67	51828.98	52274.29	1.04
MIN~habitat_rainrank+YEAR+ month+Day+CorE+windrank	63	51836.86	52255.63	8.92
MIN~habitat_rainrank+YEAR+ month+CorE+windran	61	51841.17	52246.67	13.23
MIN~habitat_rainrank+YEAR+ month+windrank	60	51847.69	52246.55	19.75
MIN~habitat_rainrank+YEAR+month	55	51862.77	52228.44	34.83
MIN~month_rainrank+YEAR+SEX+ habitat+Day+CorE+temprank+windrank	49	51912.33	52238.17	84.39
(MIN~month_rainrank+YEAR+ SEX+habitat+Day+CorE+windrank	45	51920.03	52219.30	92.09
MIN~month_rainrank+YEAR+ habitat+Day+CorE+windrank	44	51920.99	52213.61	93.05
MIN~month_rainrank+YEAR+habitat+Day+windrank	43	51927.07	52213.05	99.13
MIN~month_rainrank+YEAR+habitat+windrank	41	51932.62	52205.31	104.68
MIN~month_rainrank+YEAR+habitat	36	51947.69	52187.16	119.75
MIN~habitat+rainrank+YEAR+SEX+month+ Day+CorE+temprank+windrank	36	52010.48	52249.95	182.54
MIN~habitat+rainrank+YEAR+ month+Day+CorE+temprank+windrank	35	52011.50	52244.32	183.56
MIN~habitat+rainrank+YEAR+month+Day+CorE+windrank	31	52019.14	52225.38	191.20
MIN~habitat+rainrank+YEAR+month+Day+windrank	30	52025.38	52224.97	197.44
MIN~habitat+rainrank+YEAR+month+windrank	28	52030.36	52216.65	202.42

MIN~habitat_rainrank+YEAR+SEX +month+Day+CorE+temprank+windrank

	numDF	denDF	F-value	p-value
(Intercept)	1	5662	1068.4825	<.0001
habitat_rainrank	**47**	**5662**	**4.9344**	**<.0001**
YEAR	**1**	**5662**	**20.2893**	**<.0001**
SEX	1	27	0.3692	0.5485
month	**4**	**5662**	**17.8628**	**<.0001**
Day	**2**	**5662**	**3.4430**	**0.0320**
CorE	**1**	**5662**	**5.3883**	**0.0203**
temprank	4	5662	1.0153	0.3979
windrank	**5**	**5662**	**2.9149**	**0.0124**

MIN~habitat_rainrank+YEAR
+month+Day+CorE+windrank

	numDF	denDF	F-value	p-value
(Intercept)	1	5666	1085.2803	<.0001
habitat_rainrank	**47**	**5666**	**4.9353**	**<.0001**
YEAR	**1**	**5666**	**20.4348**	**<.0001**
month	**4**	**5666**	**17.8337**	**<.0001**
Day	**2**	**5666**	**3.3992**	**0.0335**
CorE	**1**	**5666**	**5.5124**	**0.0189**
windrank	**5**	**5666**	**2.9723**	**0.0110**

Fixed effects: MIN ~ habitat_rainrank+factor(YEAR +SEX+month+Day+CorE+temprank+windrank

	Value	Std.Error	DF	t-value	p-value
(Intercept)	48.20980	10.556949	5664	4.566641	0.0000
habitat_rainrankY/M.0	-24.45035	9.963531	5664	-2.453984	0.0142
habitat_rainrankY.0	-27.89294	10.130381	5664	-2.753395	0.0059
habitat_rainrankI.0	-22.60648	10.179199	5664	-2.220851	0.0264
habitat_rainrankI/P.0	-23.99923	11.411388	5664	-2.103095	0.0355
habitat_rainrankM.0	-18.94175	10.202660	5664	-1.856550	0.0634
habitat_rainrankM/I.0	-24.95174	10.066621	5664	-2.478661	0.0132
habitat_rainrankM/P.0	-16.48281	10.531142	5664	-1.565150	0.1176
habitat_rainrankP.0	-28.42328	10.268738	5664	-2.767942	0.0057
habitat_rainrankSilage.0	-37.67935	10.203059	5664	-3.692946	0.0002
habitat_rainrankTR/P.0	-27.04901	10.041116	5664	-2.693825	0.0071
habitat_rainrankY/I.0	-27.84502	10.037513	5664	-2.774096	0.0056
habitat_rainrankY/P.0	-32.98058	10.834653	5664	-3.043990	0.0023
habitat_rainrankY.1	-25.89742	10.337989	5664	-2.505073	0.0123
habitat_rainrankI.1	-19.27021	11.350418	5664	-1.697754	0.0896
habitat_rainrankI/P.1	5.95391	16.229121	5664	0.366866	0.7137
habitat_rainrankM.1	-14.16600	11.994105	5664	-1.181080	0.2376
habitat_rainrankM/I.1	-27.19621	12.713128	5664	-2.139223	0.0325
habitat_rainrankM/P.1	-26.08137	18.622989	5664	-1.400493	0.1614
habitat_rainrankP.1	-31.49762	14.242801	5664	-2.211477	0.0270
habitat_rainrankSilage.1	-42.39998	13.035338	5664	-3.252695	0.0011
habitat_rainrankTR/P.1	-30.03773	13.063095	5664	-2.299434	0.0215
habitat_rainrankY/I.1	-37.38985	10.920557	5664	-3.423804	0.0006
habitat_rainrankY/M.1	-19.34630	10.269182	5664	-1.883918	0.0596
habitat_rainrankY/P.1	-36.92544	18.651901	5664	-1.979715	0.0478
habitat_rainrankY.2	-21.21836	10.525584	5664	-2.015884	0.0439
habitat_rainrankI.2	-24.03153	14.263482	5664	-1.684829	0.0921

habitat_rainrankM.2	-13.95019	11.199867	5664	-1.245568	0.2130
habitat_rainrankM/I.2	-24.72330	13.578904	5664	-1.820714	0.0687
habitat_rainrankP.2	-43.12067	24.444804	5664	-1.764002	0.0778
habitat_rainrankSilage.2	-27.44304	18.590963	5664	-1.476150	0.1400
habitat_rainrankTR/P.2	-32.72983	11.716725	5664	-2.793428	0.0052
habitat_rainrankY/I.2	-28.44218	12.029174	5664	-2.364433	0.0181
habitat_rainrankY/M.2	-21.11073	10.521031	5664	-2.006527	0.0448
habitat_rainrankY.3	-15.27263	10.985684	5664	-1.390231	0.1645
habitat_rainrankI.3	-16.65739	12.835532	5664	-1.297756	0.1944
habitat_rainrankM.3	-26.98318	11.854143	5664	-2.276266	0.0229
habitat_rainrankM/I.3	-14.20094	14.100666	5664	-1.007111	0.3139
habitat_rainrankP.3	-45.82679	24.453504	5664	-1.874038	0.0610
habitat_rainrankSilage.3	-51.37690	13.516746	5664	-3.800981	0.0001
habitat_rainrankTR/P.3	-29.39634	11.863555	5664	-2.477869	0.0132
habitat_rainrankY/I.3	-27.63053	12.182709	5664	-2.268012	0.0234
habitat_rainrankY/M.3	-21.34045	10.584739	5664	-2.016153	0.0438
habitat_rainrankY.4	13.56608	16.354636	5664	0.829494	0.4069
habitat_rainrankI.4	-24.71759	18.692155	5664	-1.322351	0.1861
habitat_rainrankM.4	-22.32519	16.336103	5664	-1.366617	0.1718
habitat_rainrankTR/P.4	-37.66689	18.636728	5664	-2.021111	0.0433
habitat_rainrankY/I.4	-28.17831	18.636750	5664	-1.511976	0.1306
factor(YEAR)2013	0.09530	1.100539	5664	0.086590	0.9310
factor(YEAR)2014	-2.83619	0.988293	5664	-2.869788	0.0041
SEXM	-1.08316	1.404201	27	-0.771372	0.4472
monthAUG	0.14925	1.801436	5664	0.082849	0.9340
monthJULY	-0.70428	1.844052	5664	-0.381918	0.7025
monthJUNE	5.79154	1.707979	5664	3.390877	0.0007
monthMAY	4.92574	1.793491	5664	2.746453	0.0060
Daymid-day	1.30844	0.851409	5664	1.536791	0.1244
Daypm	-0.38232	0.878630	5664	-0.435133	0.6635
CorEE	4.46626	1.888991	5664	2.364361	0.0181
temprank	-0.40085	0.579069	5664	-0.692234	0.4888
windrank1	-1.50913	1.506399	5664	-1.001814	0.3165
windrank2	-1.26802	1.545719	5664	-0.820344	0.4121
windrank3	-0.98114	1.582530	5664	-0.619985	0.5353
windrank4	-1.63068	1.680087	5664	-0.970594	0.3318
windrank5	3.97234	2.047494	5664	1.940101	0.0524

Appendix S10. Model selection and significance for New Zealand falcon activity level in relation to temperature in Kaingaroa Forest, 2012–2014.

Model	df	AIC	BIC	dAIC
MIN~habitat_temprank+factor(YEAR)+SEX+month+Day+ rainrank+windrank	67	51860.98	52306.30	0.00
MIN~habitat_temprank+factor(YEAR)+month+Day+ rainrank+windrank	66	51862.11	52300.79	1.13
MIN~habitat_temprank+factor(YEAR)+month+ rainrank+windrank	64	51867.86	52293.27	6.88
MIN~habitat_temprank+factor(YEAR)+month+windrank	60	51885.17	52284.03	24.19
MIN~habitat_temprank+factor(YEAR)+month	55	51905.04	52270.71	44.06
MIN~month_temprank+factor(YEAR)+SEX+habitat+ Day+rainrank+windrank	46	51967.18	52273.08	106.20
MIN~month_temprank+factor(YEAR)+habitat+ Day+rainrank+windrank	45	51968.20	52267.46	107.22
MIN~month_temprank+factor(YEAR)+habitat+ rainrank+windrank	43	51973.42	52259.40	112.44

MIN~habitat_temprank+factor(YEAR)+SEX+month+Day+rainrank+windrank

	numDF	denDF	F-value	p-value
(Intercept)	1	5663	1106.3292	<.0001
habitat_temprank	**46**	**5663**	**4.5956**	**<.0001**
factor(YEAR)	**2**	**5663**	**10.7812**	**<.0001**
SEX	1	27	0.2775	0.6026
month	**4**	**5663**	**18.9732**	**<.0001**
Day	**2**	**5663**	**4.0260**	**0.0179**
rainrank	**4**	**5663**	**3.7276**	**0.0049**
windrank	**5**	**5663**	**3.1782**	**0.0072**

MIN~habitat_temprank+factor(YEAR)+month+Day+rainrank+windrank

	numDF	denDF	F-value	p-value
(Intercept)	1	5663	1109.1782	<.0001
habitat_temprank	**46**	**5663**	**4.5960**	**<.0001**
factor(YEAR)	**2**	**5663**	**10.7941**	**<.0001**
month	**4**	**5663**	**18.9419**	**<.0001**
Day	**2**	**5663**	**3.9904**	**0.0185**
rainrank	**4**	**5663**	**3.7066**	**0.0051**
windrank	**5**	**5663**	**3.1699**	**0.0073**

```
Fixed effects: MIN ~ habitat_temprank+factor(YEAR)+SEX month+Day+rainrank+windrank
                                       Value Std.Error   DF   t-value p-value
(Intercept)                 50.56042  7.767484 5663  6.509240  0.0000
habitat_temprankM.5         23.36083 17.504081 5663  1.334594  0.1821
habitat_temprankY.1        -28.18505  8.624667 5663 -3.267958  0.0011
habitat_temprankM.1        -16.81406 17.505214 5663 -0.960517  0.3368
habitat_temprankM/I.1      -30.56931 15.013851 5663 -2.036074  0.0418
habitat_temprankTR/P.1     -34.64577 23.531912 5663 -1.472289  0.1410
habitat_temprankY/I.1      -19.32858 12.031085 5663 -1.606553  0.1082
habitat_temprankY/M.1      -27.98775  9.268074 5663 -3.019802  0.0025
habitat_temprankY.2        -32.19966  7.815334 5663 -4.120061  0.0000
habitat_temprankI.2        -26.66688  8.665861 5663 -3.077234  0.0021
habitat_temprankM.2        -27.63919  8.237176 5663 -3.355420  0.0008
habitat_temprankM/I.2      -25.48434  8.568159 5663 -2.974308  0.0029
habitat_temprankM/P.2      -16.14499 10.245541 5663 -1.575806  0.1151
habitat_temprankP.2        -22.85663  9.656447 5663 -2.366981  0.0180
habitat_temprankSilage.2 -29.18796 11.060001 5663 -2.639056  0.0083
habitat_temprankTR/P.2     -24.44455  8.597600 5663 -2.843183  0.0045
habitat_temprankY/I.2      -27.90844  8.748405 5663 -3.190118  0.0014
habitat_temprankY/M.2      -23.98178  7.902730 5663 -3.034619  0.0024
habitat_temprankY/P.2      -46.41933 23.572682 5663 -1.969200  0.0490
habitat_temprankY.3        -32.61110  7.694392 5663 -4.238295  0.0000
habitat_temprankI.3        -26.75037  7.784748 5663 -3.436254  0.0006
habitat_temprankI/P.3      -16.99723  9.484958 5663 -1.792019  0.0732
habitat_temprankM.3        -23.04045  7.805086 5663 -2.951979  0.0032
habitat_temprankM/I.3      -24.65758  7.892681 5663 -3.124107  0.0018
habitat_temprankM/P.3      -18.54719  8.929295 5663 -2.077117  0.0378
habitat_temprankP.3        -33.26811  7.999623 5663 -4.158709  0.0000
habitat_temprankSilage.3 -39.51728  8.036107 5663 -4.917466  0.0000
habitat_temprankTR/P.3     -27.32275  7.834364 5663 -3.487552  0.0005
habitat_temprankY/I.3      -28.63178  7.779998 5663 -3.680179  0.0002
habitat_temprankY/M.3      -24.86497  7.701649 5663 -3.228525  0.0013
habitat_temprankY/P.3      -34.72092  9.070706 5663 -3.827808  0.0001
habitat_temprankY.4        -31.59057  7.694291 5663 -4.105715  0.0000
habitat_temprankI.4        -26.58460  7.868102 5663 -3.378782  0.0007
habitat_temprankI/P.4      -34.89723 14.978446 5663 -2.329830  0.0199
habitat_temprankM.4        -25.42760  7.944059 5663 -3.200833  0.0014
habitat_temprankM/I.4      -27.66054  8.289139 5663 -3.336961  0.0009
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habitat_temprankM/P.4	-15.42832	10.419033	5663	-1.480782	0.1387
habitat_temprankP.4	-36.40664	8.352776	5663	-4.358627	0.0000
habitat_temprankSilage.4	-40.76930	8.758643	5663	-4.654750	0.0000
habitat_temprankTR/P.4	-31.07136	7.970102	5663	-3.898490	0.0001
habitat_temprankY/I.4	-32.54108	8.056053	5663	-4.039333	0.0001
habitat_temprankY/M.4	-24.68930	7.697977	5663	-3.207246	0.0013
habitat_temprankY/P.4	-28.27056	11.425232	5663	-2.474397	0.0134
habitat_temprankY.5	-35.82248	10.265531	5663	-3.489589	0.0005
habitat_temprankI.5	-40.80853	12.424715	5663	-3.284464	0.0010
habitat_temprankM/I.5	-29.07227	23.500654	5663	-1.237084	0.2161
habitat_temprankY/I.5	-33.65910	23.491240	5663	-1.432836	0.1520
factor(YEAR)2013	-0.11129	1.100905	5663	-0.101086	0.9195
factor(YEAR)2014	-2.95337	0.988755	5663	-2.986963	0.0028
SEXM	-1.09701	1.405358	27	-0.780595	0.4418
monthAUG	1.14831	1.865699	5663	0.615485	0.5383
monthJULY	0.00165	1.899287	5663	0.000869	0.9993
monthJUNE	6.45066	1.772398	5663	3.639509	0.0003
monthMAY	5.82075	1.848069	5663	3.149636	0.0016
Daymid-day	1.43028	0.875905	5663	1.632912	0.1025
Daypm	-0.47247	0.897436	5663	-0.526470	0.5986
rainrank1	1.45459	1.400313	5663	1.038764	0.2990
rainrank2	3.54676	1.834713	5663	1.933141	0.0533
rainrank3	2.87266	2.093521	5663	1.372168	0.1701
rainrank4	12.87896	5.444246	5663	2.365609	0.0180
windrank1	-0.63399	1.553295	5663	-0.408157	0.6832
windrank2	-0.72650	1.575206	5663	-0.461207	0.6447
windrank3	-0.54485	1.621120	5663	-0.336093	0.7368
windrank4	-1.01615	1.714775	5663	-0.592586	0.5535
windrank5	4.71025	2.075760	5663	2.269168	0.0233

CHAPTER 3

Logging influences winter home-range size and home-range overlap of New Zealand falcons in a mosaic landscape: a test of the Resource Dispersion Hypothesis

For submission

Co-authors: Phil F. Battley and Edward O. Minot


Black Stallion Photography

Laid Black 2014/2015

Abstract

Several studies in plantation forests have documented the ecological benefits of limited timber harvesting on diversities of avian species. However, large-scale harvesting may decrease habitat heterogeneity and negatively affect populations. One indicator of declining habitat quality can be increases in home-range sizes of animals. We assessed how changes in forest structure by timber harvesting affected the home range size of New Zealand falcons (*Falco novaeseelandiae ferox*) in Kaingaroa forest in the North Island of New Zealand by testing two predictions of the Resource Dispersion Hypothesis (RDH). The RDH predicts that (1) resource dispersion determines the home-range size, with smaller home ranges when resources are concentrated, and larger ranges when resources are dispersed, and (2) resource richness within home ranges influences home-range overlap, with greater overlap where resources are abundant and concentrated, and less overlap where resources are insufficient and dispersed. Using the key resources associated with prey availability for New Zealand falcons, namely patch size of logged areas (*Open-patch*) and extent of *Edge-habitat* (the ecotone between mature-pine trees and *Open-patches*), we examined the home-range size and overlap of 28 falcons. The distribution of *Edge-habitats* was strongly correlated with falcon home-range size ($R^2 > 0.83$), supporting the first RDH prediction. Home-range overlap was greater over the falcons' key habitats. More falcons used small *Open-patches* (< 3 km^2) and especially when these were concentrated (greater richness of the *Edge-habitat*), and fewer used large *Open-patches* (> 3 km^2; less richness of the *Edge-habitat*), supporting the second RDH prediction. Our results indicate that timber forests could hold a greater number of falcons by increasing falcon habitat quality through the

creation of *Open-patches* < 4 km^2 in size that are distributed < 3 km apart throughout the mature forest. A well-designed harvesting regime could enable the timber industry to contribute importantly to the conservation of this threatened New Zealand raptor.

Introduction

Rotational timber harvesting in large timber forests creates habitat heterogeneity that provides ecological benefits facilitating avian species diversity in New Zealand (Drapeau et al. 2000; Seaton 2010b). For instance, open-patches created by timber harvesting attract early successional birds (i.e. exotic small passerines) providing a prey base for raptor species such as New Zealand falcons (*Falco novaeseelandiae ferox*; Chapter 2). Nevertheless, habitat heterogeneity decreases when trees are harvested in large-scale clear-cuts, and such timber harvesting practice is the prevalent method in forest operations in New Zealand (Pawson et al. 2006). Numerous studies report that the loss of habitat heterogeneity reduces habitat quality for birds (Emmerich & Vohs 1982; Yahner & Scott 1988) that, depending on scale, results in a population sink (Pulliam & Danielson 1991). Therefore, it is important to understand how changes in forest structure by timber harvesting affect habitat quality for forest-dwelling species.

Habitat quality can be evaluated by examining home-range size of animals. Animals respond to declining habitat quality (i.e., reduced resources per unit area) by expanding their home ranges to obtain the same total resources as provided by a richer habitat (Carr & Macdonald 1986). Hence, increases in home-range sizes can be an indicator of declining habitat quality (Reid et al. 2007). Because habitat quality is directly correlated with the carrying capacity of a wildlife population, improving landscape structure by land management may lead to increasing the carrying capacity of a population (Reid et al. 2007). Therefore, maintaining habitat quality is one goal in conserving and managing species of concern.

New Zealand falcon (hereafter 'falcon') is the only extant endemic diurnal raptor in New Zealand, and is widely distributed in various habitat throughout New Zealand, from dry tussock land in South Island (Fox 1977, Bell and Lawrence 2009) to native podocarp forests in the North Island (Barea et al. 1997). In the last decade, several studies have described the breeding ecology and non-breeding ecology, habitat use, and home range sizes, and behaviour of falcons living in a pine plantation, Kaingaroa forest (Seaton 2007; Thomas 2008; Thomas et al. 2010; Chapter 2). The forest (c. 1800 km^2) is large enough to comprise different aged tree stands ranging from clear-cut to mature trees (> 25 years old), which create a mosaic-like landscape (Seaton 2010a). Such a heterogeneous landscape provides food (passerine birds) to falcons throughout the year. However, in recent years the annual harvest rate of timber has been drastically increased (by 109% from 2007 to 2014, Timberlands Ltd. pers. comm.), and trees harvested in groups or adjacent to an existing open-patch (e.g. clear-cut stands) result in the loss of habitat heterogeneity (C.H. pers. obs.), which may negatively influence the falcon population. A well-designed harvesting scheme including the size of cleared areas and the spatial arrangement of open-patches can be vital to conserve this widespread but threatened species.

We used the Resource Dispersion Hypothesis (RDH) as a tool to understand how timber harvesting regimes influence habitat quality and spatial organization of the falcon population in Kaingaroa forest. The RDH predicts that (1) resource dispersion determines the home-range size, with home-range size increasing as resource dispersion expands and decreasing as resource dispersion concentrated (Macdonald 1983), and (2) resource richness within home ranges influence home-range overlap of individuals (Eide et al. 1994), with degree of overlap increasing as resource abundance becomes spatially and/or temporally concentrated and decreasing as resource abundance becomes insufficient and scattered. The concept is that when resource patches are spatially and/or temporally concentrated and rich, the territory will support the minimum social unit (e.g. a pair) and also can support additional individuals at a minimal extra cost to the primary occupants (Johnson et al. 2002). Eide et al. (2004) documented the presence of relaxed territorially in Arctic fox (*Alopex lagopus*) and concluded that the relaxed territoriality could be explained by the RDH framework. The relaxed territoriality is driven by the fitness benefits obtained by tolerating overlapping home ranges with neighbouring animals and sharing resources when resources are not limited but spatially concentrated, as opposed to risking the costs of resource defence or seeking another foraging site (Carr & Macdonald 1986; Johnson et al. 2002). To date, the RDH has been used to explain spatial organization of various species, mostly mammalian carnivores, such as *Panthera* sp. (Hayward et al. 2009; Valeix et al. 2012), *Canis* sp. (Marino et al. 2012; Newsome et al. 2013), and badgers (*Meles meles*: Kruuk and Parish 1987, Rodríguez et al. 1996), but also some birds such as eastern wild turkeys (*Meleagris gallopavo silvestris*; Marable et al. 2012) and white-throated magpie-jays (*Calocitta formosa*; Langen & Vehrencamp 1998).

Resources for falcons

In 2013–2014 transect surveys conducted in Kaingaroa forest during the winter period (June–August) found that prey abundance (passerine birds) for falcons did not vary across different forest habitats (i.e. stand ages and ecotones) or sizes of open-patches (clear-cut stand and planted pine stands < 3 years old, and/or farmland pasture; Chapter 2), indicating that food abundance was probably not limiting the study population. A radio-tracking study during the non-breeding season (April to August 2012–2014) found that falcons used edge-habitat (i.e., the ecotone between mature-pine stands and open-patches) the most, followed by open-patches (feeding ground, Chapter 2, Fig. 1). These two key habitats were dispersed in different ratios and different sizes throughout Kaingaroa forest. For example, a high proportion of edge habitat occurs where small scale open-patches are concentrated among mature tree stands, whereas a low proportion of edge-habitat occurs where small scale open-patches are scattered among mature tree stands, and also where large open-patches are situated adjacent to intermediate-aged pine stands. Variation in the extent and distribution of open-patches in Kaingaroa forest makes it a suitable ecological setting for testing the RDH predictions.

Figure 1. The key habitats of New Zealand falcons in an exotic pine plantation, Kaingaroa Forest. Left: *The Edge-habitat*. Right: A large *Open-patch*.

We measured how distributions of the edge-habitat and open-patches influenced home-range size and the overlap of falcons. In small open-patches, distances between edge-habitats are small, whereas in large patches the distances are correspondingly larger. Therefore, we predicted that home-ranges of falcons will be smaller where edge-habitats are concentrated (i.e. a few smaller open-patches are distributed closely among mature-pine stands, which refers to ‘greater resource richness’), and larger where edge-habitats are scattered (i.e. a few larger open-patches are situated among mixture of mature-pine and intermediate-pine stands, which refers to ‘low resource richness’; **hypothesis 1**). We predicted that home-range overlap of falcons or a total number of falcons would be the greatest over the areas with greater resources richness, and home-range overlap or the total number of falcons would be minimal over the areas with little or no resources richness (**hypothesis 2**).

Methods

Study Area

Kaingaroa forest covers 1,800 km^2 of the volcanic plateau of the Central North Island of New Zealand (from NE corner at 38°27' S, 176°74' E to SW corner at 38°83' S, 176°09' E). Broadly, Kaingaroa is bordered by dairy farms and lakes to the north, indigenous podocarp forest to the east, small forest plantations to the south and southwest, and dairy farms to the west and south (Fig. 2).

Kaingaroa forest consists of 1342 harvestable stands, each approximately 1 km^2. *Pinus radiata* is the predominant pine species (Seaton 2007). These are typically clear-cut as mature stands 26–32 years after planting. When adjoining stands are harvested, the area of clear cut increases to several km^2. The annual harvest rate averaged 5.2 km^2 monthly from 2012–2014 (C. Hindle, Timberlands Ltd., pers. comm.). Details of forestry operational cycles, weather information, and methods for trapping of the falcons are found in Chapter 2. The falcon is apparently only threatened species found in Kaingaroa forest (Seaton et al. 2010b, Chapter 2).

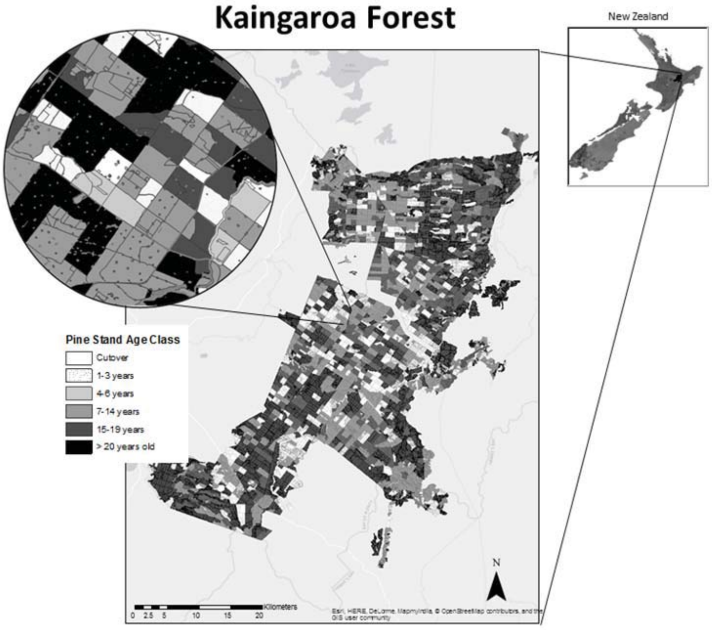

Figure 2. Map of the study area – Kaingaroa forest in the Central Plateau of the North Island, New Zealand. The mosaic landscape consists of different-aged pine stands from clear-cut to mature (> 20 years).

Radio tracking and home-range size

Radio-tracking was conducted by two trackers per season from April–June in 2012 and from June–August in 2013 and 2014 using triangulation methods (White & Garrott 1990) and visual verification when possible (Seaton et al. 2013). For obtaining a fix, each tracker followed a focal falcon by vehicle and measured up to three different bearings by quickly moving around the falcon either by vehicle or foot, depending on road conditions. In 2012, each falcon was tracked continuously for 8 h daily between dawn and dusk. In 2013 and 2014, each falcon was tracked continuously for 6 h daily based on two shifts – from dawn to early afternoon and early afternoon to dusk – with shifts alternated weekly. We obtained a mean of 159 ± 63(SD) fixes per falcon, ranging between 53 and 254 fixes. The mean total tracking duration per falcon was 60 ± 20 (SD) h, ranging between 8 and 91 h from 28 (14 males and 14 females) falcons.

We acquired shapefiles of Kaingaroa forest, containing information on stand age and boundaries, with permission from the Kaingaroa forest management company (Timberlands Ltd., Rotorua, New Zealand). We used a Geographic Information System (GIS, ArcGIS 9.3; ERSI, Redlands, California, U.S.A) that included depicting tree age classes of a single season: *Open-patch*, which consists of *Cutover* (clear-cut stands without pine seedlings) and *Young* (tree age 1–2 year-old pine stand), *Intermediate* (> 3 and < 14-year-old pine stand), and *Mature* (> 15-year-old pine stand). *Edge-habitat* was calculated by measuring the length of each habitat edge multiplied by 100 m (50 m either side of the border between *Mature* and *Open-patch*; Seaton et al. 2013). Stand interiors were defined as being over 50 m from the boundary.

The home-range size of falcons was calculated by Kernel Density Estimates (KDE) using Hawth's Analysis Tools 3.27 for ArcGIS (Beyer 2004). A reference smoothing parameter (Gitzen et al. 2006) was used to estimate core home- range size (50% KDE; Samuel et al. 1985) and the entire home range size (95% KDE; Seaman & Powell 1996). Means are reported as ± SE unless otherwise noted.

Seven falcons were tracked over multiple non-breeding seasons. They were one female from 2012–2014, one female in 2012 and 2014, one male in 2012 and 2013, and four females in 2013 and 2014. Therefore, in total, 36 falcon-seasons (15 males and 21 females) from 28 individuals (14 males and 14 females) were tracked by two trackers per season. Twenty-five falcons used mainly Kaingaroa forest and used neighbouring farmland less than 10% of the total sampling locations. We call these ‘forest falcons’. Eleven falcons used neighbouring farmland for over 10% of the total sampling locations, and we refer to these as ‘farmland falcons’ (Chapter 2). We analyzed forest and farmland falcons separately. The mean winter home-range size (95% KDE) and the winter core-home range size (50% KDE) of forest falcons were 19 ± 5 km^2 and 4 ± 0.8 km^2 respectively, and that of farmland falcons was 38 ± 6 km^2 and 7 ± 1.0 km^2 respectively; Chapter 2).

Hypothesis 1 - Factors influencing falcon home-range size

For each home range, we assessed seven factors that might have influenced falcon home range sizes (95% KDE): (1) the mean length (km) of all *Open-patch* (that includes *Cutover*, *Young,* and *Pasture*) perimeters within the home range of each falcon (hereafter we omit ‘within the home range of each falcon’), (2) the total length (km) of all *Edge-habitat* borders, (3) the percentage of *Mature* habitat, (4) the percentage of *Open-patch* habitat, (5) the mean *Open-patch* size (km^2), calculated as the total area of *Open-patch* (km^2) divided by the number of *Open-patches*, and (6) a density measure of edge length, calculated as the total edge length (km) divided by the total area of open patches (km^2). The final factor (7), the index of *Edge-habitat* distribution, was calculated by averaging the distances (km) between the centers of all *Open-patches* that bordered *Mature* within the home range of each falcon. Some falcons used arboreal windbreaks or mature-pine trees established along streams situated in pastures, and these were the second-most selected habitat by farmland falcons (Chapter 2). The role of mature trees in the pasture appeared to be equivalent to *Edge-habitat* in the forest. Therefore, we included mature trees in the pasture as *Edge-habitat* when the trees were located on a block of over 0.5 km^2 in size. We chose this index (the mean of the distances of all *Open-patches* within home range of each falcon) rather than the distances between only nearest neighbours (e.g. as done with water holes for lions *Panthera leo* in Valeix et al. 2012) because falcons can range widely and move quickly between distant resources and are not restricted to moving sequentially between neighbouring resources. We also examined sex variations in home-range size and statistically significant variables that influence the home-range size of falcons.

We used generalized linear mixed models (GLMMs; Pinheiro & Bates 2000) to identify factors influencing the home-range sizes of falcons. We constructed a multivariable regression model for each group of falcons (forest and farmland) to test the association between their entire home-range sizes and each variable (1) to (7). The association between the variables and the core home-range size (50% KDE) was not assessed because there were not enough comparable variables within the falcons' core home ranges due to their small size (e.g. 4–7 km^2). We constructed a suite of plausible candidate models for each analysis of home-range size in relation to the multiple independent variables using the stepwise regression with backward elimination method, removing non-significant variables until there was no improvement in model fit. We determined the best-fit models using the 'piecewiseSEM' package (version 1.2.0, Letcheck 2016) in R based on the Akaike Information Criterion (AIC). To account for repeated observations of the same individuals in multiple years, we included Falcon ID as a random effect in analyses identifying factors that affect falcon home-range sizes. We assessed the normality of residuals of each variable in the final multivariable regression models by constructing diagnostic plots. There was no evidence of high collinearity in these variables.

We calculated mean ± SE Open-patch size (km2) within home ranges of forest and farmland falcons. In this analysis, *Pasture* within home ranges of farmland falcons was not included in the *Open-patch* category in order to assess an association between the mean *Open-patch* size and the edge distance within Kaingaroa forest. To identify the threshold for the edge distance that induces an enlargement of falcon home-range size, we assessed relationships of falcon home-range sizes with the mean edge distance (km) and the mean *Open-patch* size (km^2). The median home-range size of all falcons (17 km^2) was used to evaluate the threshold. We chose the mean *Open-patch* size, not the total *Open-patch* size, in this analysis because the size of each available *Open-patch* within the home range of each falcon is directly related to the edge distance (even though not all *Open-patch* borders were aligned with *Mature* as being the *Edge-habitat*), whereas the total *Open-patch* size does not directly associate with the edge distance.

We also calculated mean ± SE total *Open-patch* size (km^2) for forest and farmland falcons. We included *Pasture* in the total *Open-patch* category of farmland falcons. We assessed that an upper limit of *Open-patch* size as a reference to the logging scale by contrasting the threshold of the edge distance (km) and total *Open-patch* size (km^2). We chose the total *Open-patch* size of forest falcons for this analysis because the total *Open-patch* size is the maximum patch size that forest falcons included in their home ranges. To simplify for the purpose of display, we selected forest falcons with data consisting of more than 150 observation points (*n* = 17).

Hypothesis 2 – Resource richness and home-range overlap

For each falcon home range, we separated the area of overlap from the area of non-overlap. Within each categorised area, we then calculated sizes of five habitat classes: *Edge-habitat*, *Cutover*, *Young*, *Intermediate*, and *Mature* for forest falcons and the size of six habitat classes (the five habitat classes plus farmland pasture '*Pasture*') for farmland falcons. The proportion of each habitat class was then calculated within each categorised area. To determine the rank order of habitats overlapped from most to least within home ranges of falcons, we used compositional analysis (Aebischer et al. 1993) in the 'adehabitat' package (version 1.8.18, Calenge 2006) in R.

We repeatedly observed several leg-banded males (n = 9) and unmarked males (n = 17) when they interacted with the radio-tagged females throughout the radio-tracking period. We assumed the unmarked males were the same individuals. This assumption is justified because marked (radio-tagged or leg-banded) males (*n* = 21/22) had high site fidelity (95%), remaining throughout the winter period in the areas where they bred in the previous breeding season. Moreover, the leg-banded males interacted with the same tagged females in the same *Open-patches* and *Edge-habitat* throughout the study period. Therefore, the maximum number of falcons that potentially used each *Open-patch* was based on combining all of the radio-tagged, the leg-banded, and the unmarked individuals. We did not include unmarked falcons that were found randomly in the analysis.

Results

The mean distance between *Edge-habitat*s was shorter n the home ranges of forest falcons (2.6 ± 0.3 km, range 0.4–15.0 km) than farmland falcons (3.9 ± 0.3 km, range 0.8–21.5 km, $t_{24,10} = 3.16$, $P = 0.0046$). The mean distance between *Edge-habitat*s (i.e. the distribution of the *Edge-habitat*) was correlated with home-range size for both forest falcons ($\beta = 16 \pm 1.3$ (SE), $R^2 = 0.87$, df = 23, $P < 0.0001$) and farmland falcons ($\beta = 15 \pm 2.5$ (SE), $R^2 = 0.83$, df = 9, $P = 0.0001$; Fig. 3).

The home-range size of falcons was not correlated with any of the other factors we examined, namely the mean length of *Open-patch* perimeter, the total length of the *Edge-habitat*, the percentage of the *Mature* and *Open-patch* habitat, the mean *Open-patch* size, or the density of the edge length (Table 1). We did not find sex variations in home-range size or in the *Edge-habitat* distribution.

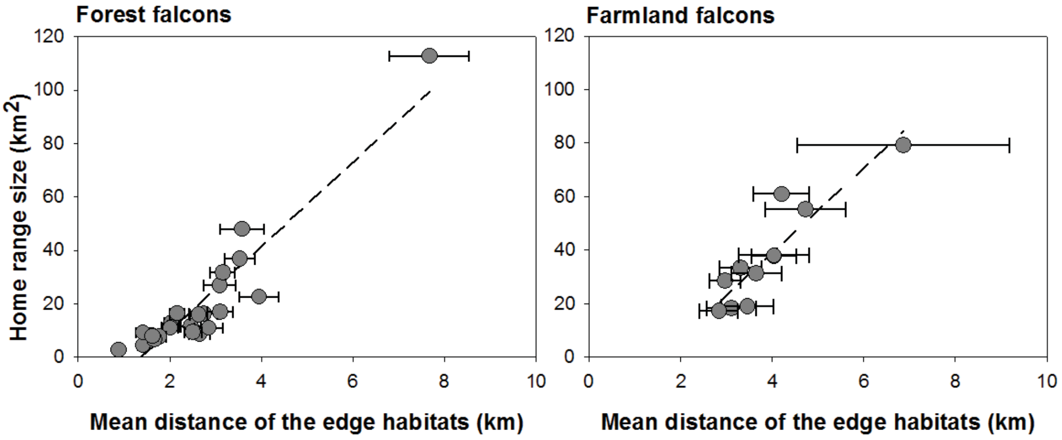

Figure 3. The relationship between the index of edge-habitat (open-patches bordering mature-aged pine stand) dispersion and New Zealand falcon home range size during the non-breeding season (April–August), 2012–2014. Forest falcons (n = 25) are birds with > 90% of the total sampling locations in Kaingaroa forest; farmland falcons (n = 11) are birds with > 10% of the total sampling locations in farmland.

The size of available *Open-patches* in Kaingaroa forest was larger in size within home ranges of farmland falcons (4.0 ± 1.0 km^2, range 0.9–7 km^2) than of forest falcons (2.6 ± 0.5 km^2, range 0.2–8.7 km^2). Most falcons maintained a home-range size < 17 km^2 when the mean edge distance was < 3 km irrespective of the mean *Open-patch* size (Fig. 4A). Smaller *Open-patches* (< 1 km^2) that were dispersed amongst *Mature* stands also induced an enlargement of home-range sizes. The total *Open-patch* sizes were much smaller in the home ranges of forest falcons (5.2 ± 0.7 km^2, range 0.7–18.5 km^2) than of farmland falcons, (56.2 ± 5.8 km^2, range 11.5–81.3 km^2). The home-range size of most falcons increased over 17 km^2 (as an indicator range size) when the total *Open-patch* size exceeded 4 km^2 (the dashed line) and the 3 km edge-distance threshold (Fig. 4B).

Table 1. Results of generalized linear mixed models examining the factors influencing home-range size of New Zealand falcons in Kaingaroa forest.

	Forest falcon (*n* = 25)				Farmland falcon (*n* = 11)			
Independent variable: Home-range size	Full model AIC: 190.3		Best fit model AIC: 181.9		Full model AIC: 84.1		Best fit model AIC: 83.4	
dependent variable	Estimate ± SE	*P*	Estimate ± SE	*P*	Estimate ± SE	*P*	Estimate ± SE	*P*
Intercept	−21.74 ± 1.26		−2.27 ± 16.76		−4.94 ± 26.67		10.70 ± 14.39	
Mean distance (km) between neighboring *Open-patches*	*17.03* ± 1.78	< 0.0001	15.78 ± 1.26	< 0.0001	14.96 ± 3.96	0.0633	13.40 ± 2.07	0.0006
Mean length (km) of all *Open-patch* perimeters	−0.01 ± 0.06	0.9834			1.61 ± 2.08	0.5177		
Total length (km) of *Edge-habitat* border	−0.04 ± 0.06	0.5279			0.03 ± 0.95	0.9755		
% area of *Mature*	−0.44 ± 0.26	0.1123			−0.40 ± 0.78	0.6598	−0.47 ± 0.39	0.2735
% area of *Open-patch*	−0.13 ± 0.22	0.5507			−0.24 ± .019	0.3391	−0.24 ± 0.11	0.0649
Mean *Open-patch* size (km^2)	−1.43 ± 1.90	0.3841			−2.97 ± 4.21	0.5541		
Density of *Edge-habitat*/*Open-patch* area	−1.17 ± 9.77	0.9059			13.87 ± 36.90	0.7430		
							−7.22 ± 4.50	0.1599
Sex	−3.33 ± 4.13	0.4326			−5.25 ± 9.02	0.6194		

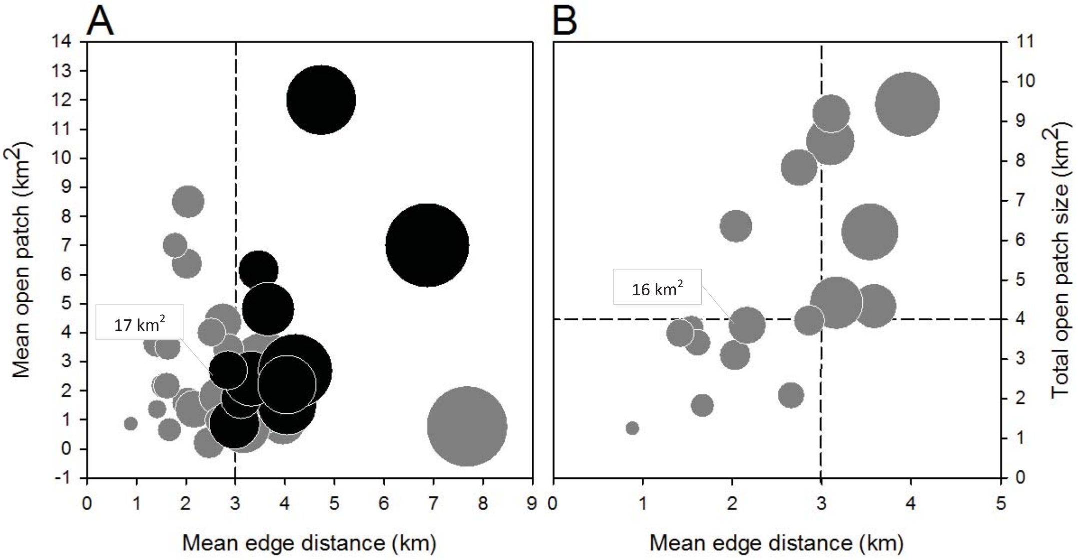

Figure 4. A: Relationships of home-range size, the mean edge-distance (km): distance between the *Edge-habitats*, and the mean *Open-patch* (km^2) within home ranges of forest falcons (gray circle, *n* = 25) that used Kaingaroa forest more than 90% of radio-tracking durations and farmland falcons (black circle, *n* = 11) that used farmland adjacent to Kaingaroa forest more than 10% of radio-tracking durations. The edge distance is the index of edge habitat (mature tree stands bordering *Open-patches*) distribution within the home range of each falcon. Farmland pasture within home ranges of farmland falcons was not included in the measurement of the mean *Open-patch* size for this analysis. The threshold for the edge distance is 3 km (dashed line). Home-range sizes near 17 km^2 (the median home-range size of all 36 falcons) are denoted as a reference. B: Relationships of home-range size, the mean edge distance, and total *Open-patch* size (km^2) within home ranges of forest falcons. To simplify, only data of forest falcons with more than 150 observation points (*n* = 17) are presented in this panel. The total *Open-patch* size at 4 km^2 (the dashed line) indicates as the upper limit of *Open-patch* size that is linked to an increased home-range size of most falcons (> 17 km^2) with the edge distance > 3 km.

Hypothesis 2 - Resource richness and falcon home-range overlap

Results of the compositional analysis showed that the greatest home-range overlap occurred in two key falcon habitats, *Edge-habitat* and *Open-patch* (*Cutover* and *Young*, Fig. 5). Core home-range overlap occurred in 16 individuals: 3 pairs (2 of 3 pairs were the same individuals over two years) and 10 unpaired individuals (both intra- inter-sexual). The core home-range overlap was greater (69 ± 6.8%) in pairs than in unpaired individuals (31 ± 8.8%). Some degree of home-range (95% KDE) overlap of falcons was found in 5 pairs (2 of 5 pairs were the same individuals over two years) and 26 unpaired individuals. The mean home-range overlap of pairs was greater (54 ± 7.7%) than of unpaired individuals (32 ± 5.1%).

The number of falcons that overlapped their home ranges or used the same areas was negatively related to the increased area of *Open-patches* from 2012–2014. For the purpose of displaying the number of falcons using *Open-patches* and the changes in the patch size, we include the GPS locations of banded and unmarked falcons in Fig. 6. In 2012, one to six falcons (a mixture of pairs and unpaired individuals) used the areas where *Edge-habitats* were concentrated (Fig. 6 and Table 2). After *Edge-habitats* were dispersed further by timber harvesting between winters (2012 and 2013 and 2013 and 2014), only up to three falcons (a single, a pair, or a pair and extra-pair male) used the area.

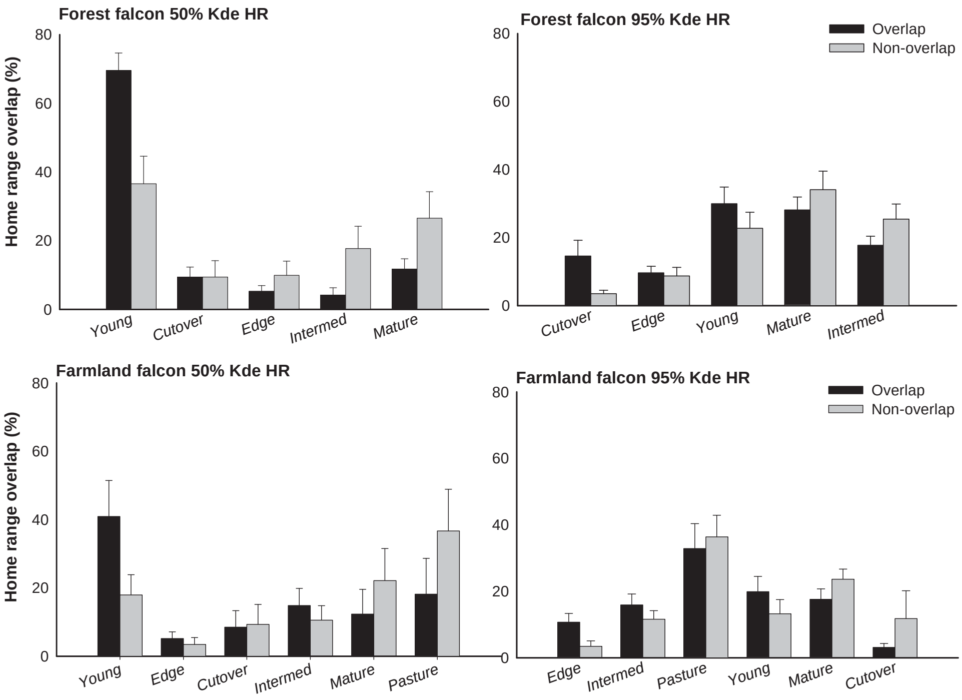

Figure 5. The proportion of habitat classes within overlapping and non-overlapping portions of falcon home ranges. Left-hand panels are the 50% KDE ranges (n = 10 forest and 4 farmland birds); right-hand panels are 95% KDE ranges (n = 18 forest and 9 farmland birds). *Edge* stands for *Edge-habitat*. Habitat classes are arranged from the most to least overlapped by falcons based on the results of the compositional analysis, except for the core home range of farmland falcons (where the sample size was too small for compositional analysis). Bars denote SE.

Figure 6. Examples of changes in forest structure by timber harvesting, the number of falcons and their home-range overlap from 2012 to 2014. Solid lines represent the entire home-range (95% KDE) of radio-tracked falcons. Dots represent locations of banded and unmarked falcons that interacted with some of the radio-tracked females throughout the study period. Note that the white blank spaces outside Kaingaroa forest are farmland pasture.

Table 2. Examples of changes in *Open-patch* sizes (km^2) by year (2012–2014) and the numbers of New Zealand falcons (marked and unmarked) that used these *Open-patches*. The merged cells shown in 2014 indicate that the area of *Open-patch* increased by further timber harvesting of mature-pine stands located between smaller *Open-patches* in 2012 and 2013. "↑" represents increased, "↓" denotes decreased, and "↔ " indicates no change.

	2012		**2013**		**2014**		**Δ 2012–2014**	
Open-patch ID	Size (Km^2)	No. falcon	Size (Km^2)	No. falcon	Size (Km^2)	No. falcon	Size (Km^2)	No. falcon
a	2.7	5	3.2	2	9.3	3	↑	↓
b	1.0	3	2.1	3				
c			3.4	3				
d	2.9	3	3.0	2	8.8	2	↑	↓
e	2.4	4	3.0	3				
f	0.7	0	2.6	2	5.6	3	↑	↓
g			1.3	2				
h	3.1	3	6.7	3	8.1	2	↑	↓
i	7.7	1	7.7	0	7.7	2	↔	↔

Discussion

Factors influencing falcon home-range size

We found that the distribution of the *Edge-habitat* was a determinant of falcon home-range size in Kaingaroa forest; a strong positive correlation (R^2 > 0.83) was found between home-range sizes of Kaingaroa falcons and the distances between the *Edge-habitats* (the dispersion of the key resources). Smaller home ranges of forest falcons included smaller mean *Open-patches* (2.6 km^2) with shorter distances between the Edge-habitats (2.6 km) compared with those of farmland falcons (4.0 km^2 and 3.9 km respectively). Therefore, our results supported the first prediction of the RDH (Hypothesis 1).

Several studies report that prey abundance is the factor most likely to influence the home-range size of raptors such as goshawk (*Accipiter gentilis*; Kenward 1982), European sparrowhawk (*A. nisus*; Marquiss & Newton 1982), and golden eagle (*Aquila chrysaetos*; Marzluff et al. 1997), or that prey abundance played some definitive role in influencing spatial patterns (e.g. prairie falcon, *F. mexicanus*; Steenhof et al. 1999 and peregrine falcon, *F. peregrinus*; Ganusevich et al. 2004). In our study, prey abundance was not the primary determinant of the falcons' home range size (Chapter 2), but instead, the dynamic changes to forest structure created by clear-cutting and its effect on prey accessibility are the determinant factors of home-range size of Kaingaroa falcons.

Clear-cutting occurred within the home ranges of all falcons we tracked, covering 4.6% in total of the falcons' home ranges. In general, falcons did not use all available *Edge-habitat*s equally. They tended to use segments of the *Edge-habitat* border that receives direct solar radiation for sun basking (typically northerly or north-east aspects; CH. unpublished data). Therefore, even though the proportion of the mature stands being harvested within home ranges of falcons appeared small (approximately 4.3–5.4%), when these harvested stands included the favoured segments of the *Edge-habitat*, falcons would need to find alternative *Edge-habitats* that would provide similar ecological conditions. Hence, the availability of the suitable *Edge-habitat* for falcons (actually preferred and used) might have been much lower than the apparent availability of the habitat (the proportion of the *Edge-habitat* available within the home range of each falcon). As a result, subtle changes of the forest structure are expected to influence falcons' habitat use as they compensate for their loss of the preferred *Edge-habitat*.

Our argument is based on the premise that falcons enlarge their home ranges in order to encompass a greater area of key resources. It is also generally true, however, that enlargement of a home range will inevitably result in more of those key resources being encompassed, regardless of the cause behind the territory enlargement. For instance, an alternative explanation could be that falcon home-ranges sizes are not set by resource levels, but by the density of other falcons in the forest, and that birds will maintain the largest ranges possible. Where densities are low, larger ranges will be possible. In this scenario, home-range size would be set by the level of agonistic encounters along boundaries, and the relationship between the *Edge-habitat* distribution and the home-range size shifts from being a cause to a consequence. We find this to be a less likely explanation for the Kaingaroa falcons. For seven falcons tracked over multiple years, their home-range sizes fluctuated with the availability of the edge-habits regardless of presence or absence of falcons on the borders (C.H. unpublished data). For instance, between the winter of 2013 and 2014, timber harvesting within home ranges of falcons enlarged sizes of *Open-patches* by removing mature stands directly adjacent to existing *Open-patches* and this removal included their favoured segments of *Edge-habitats* (CH pers. obs.). This resulted in an increase in home-range size (by 83–914%) for all five falcons tracked subsequently for the following two winters (2013 and 2014; CH unpublished data). In particular, the falcons with home ranges near the border of farmland expanded their use of arboreal windbreaks or mature-pine trees established along streams situated in pastures (shown in Fig. 5). A compatible result was found in a study of eastern wild turkey (*Meleagris gallapovo silverstris*) in which turkeys had smaller home-range sizes in less fragmented areas where availability of food resources was richer than in fragmented areas (Marable et al. 2012).

The mature portion of the *Edge-habitat* appeared to play important roles for falcons during the winter period. Falcons use the mature trees as a shelter from severe winter weather (i.e. cold rain and strong wind), as a vantage point for hunting opportunities in neighbouring *Open-patches*, and as a perch for sun basking and pair interaction (Chapter 2). Several diurnal raptors, such as roadside hawk (*Rupornis magnirostris*), Plumbeous kite (*Ictinia plumbea*; Jullien and Thiollay 1996, Anderson 2001), grey hawk (*Asturina nitida*), bat falcon (*F. rufigularis*; Jullien and Thiollay 1996), American black vulture (*Coragyps atratus;* Anderson 2001), and goshawk (Kenward 1982) are known to preferably use areas with high landscape heterogeneity as they provide greater prey diversity. Sergio and Bogliani (1999) documented that habitat heterogeneity that consists of poplar plantations and farmland not only offer Eurasian hobby (*F. subbuteo*) hunting fields but also breeding sites through providing breeding habitat for hooded crow (*Corvus corone cornix*), as the hobbies used unused crow nests in tall trees.

Edge-habitat availability may be important in summer as well as in winter. Among our study falcons, the winter home ranges of falcons substantially overlapped their breeding territories. Males, in particular, showed stronger site fidelity (96%) than females (63%) from the breeding season to the following non-breeding season (Unpublished data). We observed these males using the same features of the *Edge-habitat* in both breeding and non-breeding seasons. Male falcons might have needed to protect the potential breeding habitat from conspecific competitors by occupying the area throughout the seasons. The presence of mature-pine stands, near potential nest sites appeared to be the most influential element for nest site selection by falcons because the mature trees near nests provide a vantage point for guarding their nest during the day and roosting at night (pers. obs.). These observations during the breeding season were consistent with the results of a breeding study of the same falcon population (Seaton et al. 2010a).

Resources richness and falcons' home-range overlap

Our results showed that home-range overlap was more extensive over two key habitat types, the *Edge-habitat* and *Open-patch* but the patterns of overlap differed slightly between forest and farmland falcons. The largest home-range overlap occurred over the *Open-patches* (*Young* and *Cutover*) in both entire and core home-ranges of forest falcons but not the *Edge-habitat*, suggesting that forest falcons shared the same *Open-patches*, probably for hunting. In contrast, farmland falcons overlapped over *Young* within their core home ranges but the *Edge habitat* within their entire home ranges.

We found that the areas with high resource richness were used by pairs as well as unpaired individuals, whilst the areas with low resource richness were limited to pairs. The use of an area by more than a unit of a pair suggests the area has a greater ecological value. Our observations indicated that falcons, especially males, occupied *Open-patches* and the *Edge-habitats* throughout the non-breeding season as potential breeding sites for the subsequent season. When a male formed a pair with a female, the pair would use a particular *Open-patch* more than the other *Open-patch*es in their territories. If a female interacted with an extra-pair male, the same *Open-patch* could be used by three falcons (the pair and an extra-male). Pairs use *Open-patches* for various purposes such as hunting and feeding, courtship displays and resting (Chapter 5). Unpaired individuals use *Open-patches* mainly for hunting and or resting but the use of an *Open-patch* that was already occupied by a pair (the primary occupants) was not frequently observed unless an individual formed a pair with a resident female. Where resource patches are heterogeneous, primary animals may require more than one resource patch to acquire adequate resources, and where patches are rich, it may contain an excess of resources that can support additional individuals (Johnson et al. 2002). Therefore, an area that was used by unpaired individuals as well as by pairs suggests that the area offers an abundance of prey. All these observations and results clearly support the second prediction of the RDH (Hypothesis 2), which is that as resource richness increases, greater home range overlap will be possible.

Although I document in Chapter 2 that prey bird abundance did not differ among *Open-patch* sizes, the surveys were conducted in patch sizes up to 4 km^2. Prey birds may have been widely dispersed in larger *Open-patches* (> 4 km^2), resulting in fewer falcons sharing the same *Open-patch*. Furthermore, a limited availability of the *Edge-habitat* in Kaingaroa forest may have resulted in falcons expanding their ranges to farmland, leading to the greater home-range overlap of farmland falcons over the limited *Edge-habitat*, mostly trees in the pasture. In addition to the roles of the *Edge-habitat* for falcons explained above (i.e. vantage point for territorial defence, shelter from severe weather, or basking, etc.), the use of edge habitat might be partly explained by the ecological features related to falcons' hunting strategies. *Open-patches* in the forest include piles of wood slash, tall sticks, medium-sized logs and tree stumps that falcons also use as vantage points for hunting (CH. unpublished data).

Some of the farmland falcons used fence posts for hunting in the pasture where the landscape is slightly elevated. Nevertheless, the height of tall trees should have facilitated hunting as it provides a better vantage point (Jullien & Thiollay 1996; Steenhof et al. 1999) than the objects available in the pasture. Hence, farmland falcons might have preferentially used the limited tall trees available in farmland pasture. Moreover, these well-used trees might have some associated features attractive to falcons such as silage pits where prey birds were concentrated or a segment of the *Edge-habitat* that receives direct solar radiation for basking (Chapter 2).

Similar results were documented by Eide et al. (2004) in a study of Arctic fox for which the spatial distribution and richness of prey and its predictability explained the variation in spatial and temporal organization of home ranges. The foxes had small home ranges with large overlap in coastal areas where prey was predictable and concentrated in small patches. Medium home ranges and overlap were found inland where prey was less predictable and gathered in larger patches, and large home ranges with little overlap occurred inland where prey was unpredictable and widely distributed.

Management implications

The application of the RDH was useful to identify the determinant factor influencing the home-range size of falcons and to understand the importance of the *Edge-habitat* available for them within the timber forest. Our study provided strong evidence that the distribution of the *Edge-habitat* determines the home-range size of falcons in Kaingaroa forest. This indicates that if Kaingaroa forest provides a greater proportion of the *Edge-habitat* created by having *Open-patch* no larger than 4.0 km^2 in size that ideally borders to *Mature* and distributed closely (< 3.0 km apart) throughout the pine forest, falcons are expected maintain smaller winter home ranges (< 17 km^2) and more potential nest sites close to edges to mature stands will be available. As a result, the carrying capacity of the Kaingaroa falcon population could be increased. Note that the *Open-patch* size < 4 km^2 is not a clear-cut size created at a time. It is the cumulative size of an *Open-patch* that can be created by timber harvesting over multiple years that the patch may consist of 0–3-year-old pine stands.

It is possible that the population has declined in the decade since Seaton et al. (2010a) studied the breeding season ecology of the same falcon population in 2003–2006. In that time, Seaton et al. found a mean of 30 nests per year, while we found a mean of 17 nests within the same pine forest in the years 2011–2014. This coincided with a doubling of the harvesting rate since 2007 (C. Hindle, Timberlands Ltd. pers. comm.), possibly due to increased international demands for timber.

The New Zealand falcon is currently listed as At Risk by Department of Conservation in New Zealand (Robertson et al. 2016) and Near Threatened by IUCN (IUCN 2012). For the conservation of this threatened New Zealand raptor, the sizes and distribution of *Open-patches* in the landscape should be considered in the forest management regimes because the consequences of harvesting patterns influence future forest cycles, and thus will persist in the forest system for long-term (Franklin & Forman 1987). Well-designed harvesting regimes that will benefit both falcon populations and timber industries are urgently needed for assuring long-term sustainability of this nationally vulnerable raptor in New Zealand commercial forests. In an effort to improve conservation on a large scale, based on our findings, we recommend that forestry companies should develop logging protocols to limit a size of total *Open-patch* up to 4.0 km^2 and remain small blocks of mature stands in the way that *Open-patches* can be distributed closely (< 3.0 km apart) throughout the pine forest. The protocol should be integrated into the forestry management regimes, and can be expanded to pine forest managements for the conservation of other raptor species in worldwide.

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CHAPTER 4

Annual survival estimates and risk of 1080 secondary poisoning for New Zealand falcons in a managed exotic forest

Wildlife Research, in revision.

Co-authors: Phil F. Battley and Edward O. Minot

A male chick of Vicious and Kizzy 2014/2015

Abstract

Context. Since the 1970s, sodium fluoroacetate (1080) has been applied annually for pest control throughout Kaingaroa forest, a pine plantation forest in New Zealand. The near-threatened New Zealand falcon (*Falco novaeseelandiae*) breeds in Kaingaroa, yet the extent to which these falcons are susceptible to indirect 1080 poisoning, their causes of mortality, and annual survival rate are not well documented.

Aims. We investigated the survival of adult falcons during 1080 poisoning operations in 2013–2014, assessed causes of mortality, and estimated the annual survival rate for Kaingaroa falcons.

Methods. Using radio-telemetry and visual observations, we monitored marked adult falcons before and after 1080 operations in 2013–2014 and assessed mortality causes through post-mortem examinations. Using Program MARK, the annual survival rates for adults and juveniles were estimated from long-term banding data (2003–2014).

Key results.

Sixteen adult falcons were potentially exposed to 1080-affected prey during carrot-bait ground operations in May–July 2013 and 2014, and all bar one survived (95% CI for survival = 68–100%). The exception was a radio-tagged male that died within a fortnight of the 2014 operation, of unknown cause. Additionally, 21 marked adult falcons were potentially exposed to 1080-affected prey from cereal-bait aerial operations in February 2013 and November 2014; all survived (95% CI = 81–100%). Three falcons were depredated by introduced mammals. One falcon was found dead in emaciated condition but evidently died from head injury through Australasian magpie

(*Cracticus tibicen*) attack. The annual survival rate of falcons estimated from long-term banding was 80 ± 13% for adults and 29 ± 5% for juveniles.

Conclusions. The risk to adult falcons in Kaingaroa forest from 1080 secondary poisoning was low. Identifiable mortalities were attributable to depredation by introduced mammals and head injury by Australasian magpie attack. The annual survival rate of Kaingaroa falcons was comparable to those of other raptor species in different regions.

Implications. While adult New Zealand falcons do not seem to be affected negatively by 1080 operations, whether this is true for juveniles is unknown. Studies of juvenile falcons to document mortality levels and causes and emigration rates are recommended.

Additional keywords: *Falco novaeseelandiae*, sodium fluoroacetate, 1080, annual survival, pine plantation forest, mortality, predation, post-mortem

Introduction

Introduced predatory mammals have caused catastrophic devastation of New Zealand's native bird populations (King 1984). Feral cats (*Felis catus*), ferrets (*Mustela furo*), possums (*Trichosurus vulpecula*), rats (*Rattus rattus, R. norvegicus, and R. exulans*), and stoats (*Mustela erminea*) prey on eggs, chicks, and adult native birds (Courchamp *et al.* 2003; King 2005). Eradication or management of these predatory mammals is routinely conducted by government and land management agencies (Innes and Barker 1999). The traditional method of predator control using traps is labour intensive, expensive, terrain-limited and species- or guild-specific. For instance, the removal of one trophic level (e.g. top predators such as feral cats and stoats) from an ecosystem can result in an outbreak of mid-ranking predators, such as rats (Soule *et al.* 1988) that can lead to further reduction of threatened species (Courchamp *et al.* 1999; Crooks and Soulé 1999). Several studies have demonstrated how partial predator control operations potentially generate such paradoxical outcomes (Moller *et al.* 1992; Courchamp *et al.* 1999; Crooks and Soulé 1999; Girardet *et al.* 2001; Courchamp *et al.* 2003; Tompkins and Veltman 2006; Rayner *et al.* 2007). Predator control using vertebrate toxins can manage multiple species with the through direct and indirect (secondary) poisoning (Alterio *et al.* 1997; Gillies and Pierce 1999; Innes *et al.* 1999; Murphy *et al.* 1999; Alterio 2000).

Nevertheless, the risk of secondary poisoning on non-target native biodiversity is an ongoing global issue (Stephenson *et al.* 1999; Cowan and Crowell 2017). Raptors are potentially exposed to dying prey that has ingested toxin as well as carcasses with the residual toxin. The New Zealand falcon (*Falco novaeseelandiae*) is the only extant diurnal endemic raptor of New Zealand and is listed as near-threatened by the IUCN (2012) and ‘At Risk’ by the New Zealand Department of Conservation (Robertson *et al.* 2016). It is widely distributed in various habitats throughout New Zealand, from native podocarp forests in the North Island (Barea 1995; Barea *et al.* 1997) to dry tussock land in the South Island (Fox 1977; Heather and Robertson 2005; Bell and Lawrence 2009). They feed primarily on small passerine birds (Seaton *et al.* 2008a; Kross *et al*. 2013b) and small mammals such as mice (*Mus musculus*), European rabbit (*Oryctolagus cuniculus*), rats, stoats (Kross *et al.* 2013a) and hedgehogs (*Erinaceus europaeus*, CH. Unpublished data). In general, New Zealand falcons are active-pursuit foragers that feed on live prey but they also have been documented feeding on carrion (Taylor 1977, Fisher *et al*. 2015, Poupart 2016).

The use of sodium fluoroacetate (commonly known as 1080) is prevalent throughout New Zealand due to cost effectiveness and its non-persistence in live animals that ingested sub-lethal dose (it can be eliminated from an animal’s body within 1–4 days) and it is not cumulative (Eason *et al.* 1994; Eason *et al.* 1997). However, when a mammal receives a lethal dose of 1080, most display symptoms between 30 minutes and 3 hours (Eason *et al.* 1997; Martin and Twigg 2002, Littin et al. 2010) but can take up to 12 hours (Martin and Twigg 2002). Most deaths occur within 6–18 hours (Eason *et al.* 1997; Littin et al. 2010), but some may take up to 2 days (Martin and Twigg 2002). In contrast, 1080 persists in carcasses for one week to several months (King *et al.* 1994; Gooneratne *et al.* 1995; Meenken and Booth 1997; Eason *et al*. 2013) depending on weather conditions. Warmer ambient temperatures increase the rate of carcass decay whereas carcasses may persist longer in cooler (winter) conditions.

The New Zealand falcon has been identified as a high priority for study to understand the possible impact of 1080 (Spurr and Powlesland 1997; Veltman *et al.* 2014). The hypothetical risk is that New Zealand falcon can either scavenge carcasses or kill and eat poisoned animals and ingest poison. Exposure to dying poisoned animals for such prolonged periods of hours or days is of concern because prey vulnerability may be a fundamental drive in the hunting behaviour of raptors. Currently, the extent to which the New Zealand falcon is susceptible to indirect 1080 poisoning is not well documented (Veltman *et al*. 2014).

The vulnerability of different bird species to 1080 poisoning varies but a wide range of species has been documented with 1080 residues in tissues after poisoning operations, including species potentially preyed upon by falcons (Spurr 1994; Spurr and Powlesland 1997; van Klink *et al.* 2013; van Klink and Crowell 2015; and Morriss *et al.* 2016). Of particular concern is the high susceptibility of Blackbirds (*Turdus merula*) to 1080 poisoning (Morriss *et al.* 2016), as Blackbirds are widespread and common in forests and known in the diet of falcons (Seaton et al. 2008a; Kross *et al*. 2013b). Other species frequent in the diet of falcons that are known to have been affected by 1080 include chaffinch (*Fringilla coelebs*), song thrush (*Turdus philomelos*) and dunnock (*Prunella modularis*). Additionally, small mammals such as mice (*Mus musculus*), rats (*Rattus rattus*) and hedgehogs (*Erinaceus europaeus*) have also been found dead in 1080 poisoned blocks (Morriss *et al*. 2016).

Since 2003, several studies have focused on the falcons in Kaingaroa forest (hereafter 'Kaingaroa falcon population') situated in central North Island, to understand their breeding behaviour (Thomas 2008), and their habitat use in relation to prey abundance and distribution in both the breeding (Seaton 2007) and the non-breeding seasons (Chapter 2). These studies included intensive nest surveys and banding of both adult and nestling falcons. Throughout Kaingaroa forest, 1080 is used annually to control rabbit and possums, including in areas with resident falcons (Seaton 2007; CH. pers. obs.). Adults that breed within Kaingaroa forest remain in the area through the non-breeding season (Chapter 2). Therefore, they may be exposed to 1080 poison during poisoning operations that typically occur during the winter months (June to August) through ingesting poisoned prey.

A thorough investigation of the effect that secondary 1080 poisoning has on New Zealand falcons is required if any negative impacts are to be managed effectively. Knowledge of the annual survival rate and the extent and causes of mortality will allow for a projection of population changes and, in turn, assist in the prioritisation of management options of falcon populations in these pine plantations (Williams *et al.* 2002; McIntyre 2012).

In this study, we monitor the fate of adult New Zealand falcons in Kaingaroa forest through 1080 poison operations in 2013–2014 using radio-telemetry and visual confirmation of leg-banded adult falcons and determine the cause of mortality for adult falcons found dead during our study (2013–2014). We also analyse long-term banding data (2003–2014) to report juvenile and adult apparent survival rates.

Methods

Study Area

The study was conducted in the Kaingaroa forest (from NE corner at 38°27' S, 176°74' E to SW corner at 38°83' S, 176°09' E) located in the central plateau of the North Island of New Zealand (Fig. 1). The elevation range is 400–900 m (Washbourn 1978), the annual precipitation averages 1555 mm, and average monthly temperatures range from 5.5–16.3°C, averaging 10.9°C (YR 2014). Broadly, Kaingaroa forest is bordered by dairy farms to the west and south, dairy farms and lakes to the north, small forest plantations to the south and southwest and indigenous podocarp forest to the east. Kaingaroa forest is the largest pine plantation forest in the southern hemisphere (1,800 km^2) and encompasses 1,342 harvestable stands (ca. 1 km^2 per stand). The dominant tree species is *Pinus radiata*, which is harvested after 26 years of planting, typically in stands or groups of several stands.

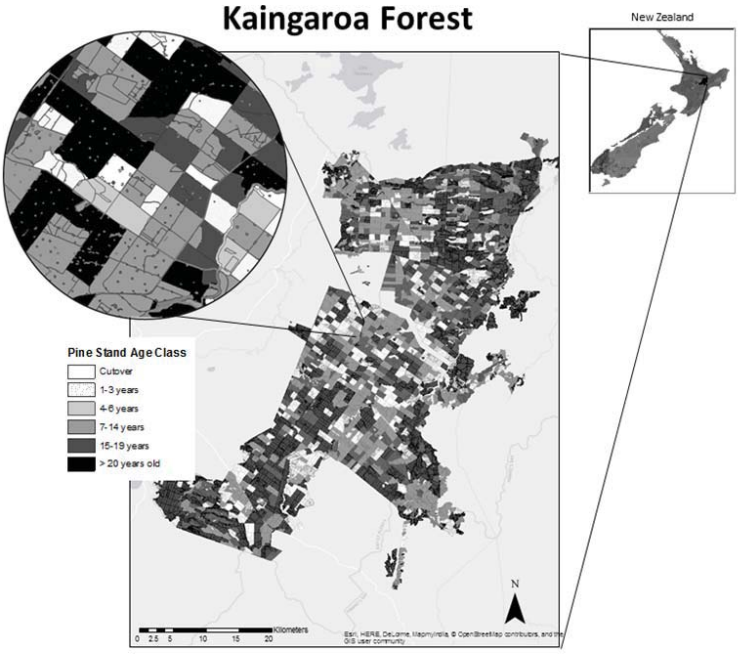

Fig. 1. Map of the study area – Kaingaroa forest in the Central Plateau of the North Island, New Zealand. The enlargements show the mosaic landscape consisting of different-aged pine stands from clear-cut to mature (> 20 years).

1080 baiting operations

Carrot bait – Timberlands Ltd. annually conducts 1080 ground operations from late May to July for controlling numbers of rabbit and brushtail possums. Pre-feeding was done by distributing pieces (ca. 2 cm^3) of carrot by hand along the perimeter of clear-cut stands (open and unplanted stands after timber harvesting) where land preparation for planting seedlings has been completed. Approximately two weeks after pre-feeding, 1080 poison (0.08% w.w., dyed green) was laid by hand at the same stand perimeters, on average at 3 kg ha^{-1}. Total areas with carrot-bait poisoning operations were 6185 ha in 2013 and 1100 ha in 2014. The area of the carrot-bait 1080 operation was smaller 2014 due to the annual operation being replaced by the cereal-bait 1080 operation (Kurt Edward, Timberlands Ltd. pers. comm.) conducted by OSPRI (see below).

Cereal bait – In addition to the annual ground 1080 poison operation, OSPRI occasionally conducts 1080 aerial operations for targeting brushtail possums, a vector of bovine tuberculosis (TB), under the national bovine TB eradication programme. Target areas and date of operations were determined by OSPRI. The 1080 cereal bait (0.15% w.w.) was aerially pre-fed and applied at 2kg ha^{-1} in the central part of Kaingaroa forest (10 000 ha) in February 2013 and in the southwest part (7200 ha) and the south part of the forest (23 000 ha) in November 2014.

Radio telemetry

Using a Bal-Chatri trap or Dho-gaza net (Fox 1977; Bloom *et al.* 2007), we captured adult New Zealand falcons in their nesting territories for radio transmitter attachment during the summer months (November to January) in 2012–2013 and 2013–2014. Adult New Zealand falcon pairs with chicks less than 14 days old or at the incubation stage were avoided in order to prevent nest abandonment (Seaton 2007). New Zealand falcons were fitted with a Holohil (Carp, Ontario, Canada) RI-2CM transmitter (7.5–12.8 g) using a backpack harness with a weak-link. Transmitters weighed 3.6 ± 0.2% of the body mass of the tagged males and 2.8 ± 0.1% of the body mass of the tagged females. We placed a piece of 2-mm thick neoprene material on the bottom of a transmitter using standard contact adhesive glue in order to prevent cold stress by direct contact of the transmitter with the bird's dorsum (K. Meyer and R. Thorstrom, pers. comm.). To minimize the chance of the neoprene material detaching from a transmitter, the surface of each transmitter was scrubbed using sandpaper before attachment of the neoprene. All captured unbanded New Zealand falcons were also given a metal band and a unique combination of colour bands.

For each 1080 poison operation, we surveyed the survival of marked (radio-tagged or banded) adult New Zealand falcons by radio-telemetry and visual confirmation at four-day intervals before and after the 1080 operation. The duration of the pre-1080 monitoring was 3 weeks and the post-1080 monitoring lasted 5 weeks. Potential exposure to 1080 poison by falcons is defined here as being when marked falcons used poison blocks in which they could potentially consume prey that had ingested carrot or cereal-bait 1080 poison.

Falcon survival through 1080 operations

Thirty adult falcons (13 females and 17 males) were monitored through carrot-bait and cereal-bait 1080 operation periods in 2013–2014, for a total of 37 individual exposure periods. Twenty-four birds (10 females and 14 males) were monitored through one operation, five individuals (three females and two males) for two operations and one male for three operations. Twenty-three adult falcons were radio-tracked (15 for carrot-bait and 8 for cereal bait operations) and 14 were confirmed via leg bands (one carrot-bait and 13 cereal-bait operations). Most of these banded falcons interacted with radio-tagged falcons, and some were previously monitored individually or along with radio-tagged falcons (males, in particular, had strong site fidelity throughout seasons, Chapter 5). These facts facilitated locating them and confirming the use of the

1080 operations blocks during the 1080 monitoring periods. We used the confidence interval (95%) of a proportion to estimate survival rate of the 1080 poison operations (Wilson 1927).

Causes of mortality

Mortality signals in the radio-transmitters identified the death of tagged falcons, which were then retrieved. Details of the carcass situation and the external body condition were recorded for each falcon in the field. Initial post-mortems were conducted by N. Hyde at Wingspan Birds of Prey Trust in Rotorua, New Zealand and the first author (C.H.) through examining tissue and skull damage by removing the entire skin from the body. A tissue sample from each organ (i.e. brain, heart, intestine, kidney, liver, lung, reproductive glands, and stomach) was preserved in 95% ethanol for histopathology. Further post-mortems and histopathology were conducted by S. Hunter, DVM. at the Massey University Institute of Veterinary, Animal and Biomedical Sciences, in Palmerston North, New Zealand. A radio-tagged male falcon died during the 2014 carrot-bait 1080 monitoring period. Most of his muscle tissues were scavenged and less than 10 g of muscle tissue was collected for a 1080 residue analysis (> 10 g was recommended), which was examined at the Landcare Research Toxicology Laboratory (Gerald Street, Lincoln 7460).

Annual Survival and re-capture rates with the long-term band recovery data

Band recovery data for Kaingaroa falcons go back to 1998 when Wingspan Birds of Prey Trust (Rotorua) commenced banding Kaingaroa falcons, though annual survival rates are estimated here from three intensive nest survey periods conducted by Massey University and Wingspan Birds of Prey Trust over 11 years between 2003 and 2014: 2003–2005, 2007–2008, and 2011–2014. We estimated apparent survival rates of juvenile (< 1-yr-old) and adult (≥ 1-yr-old) falcons from these dates, using the Live-Recaptures (CJS) model in Program MARK 8.1 (White and Burnham 1999). We pooled the band recovery data into two groups: breeding falcons that were banded as adults at their nesting area ($n = 88$; female = 41 and male = 47) and falcons that were banded as nestlings ($n = 263$; female = 127 and male = 136). We constructed a binary matrix that includes the re-sighting history for each banded individual during the breeding seasons (October to February) in 2003–2014. We assumed that banded nestlings that were not recaptured were dead or emigrated. We specified nine encounters that include breaks of two years between 2005 and 2007 and three years between 2008 and 2011. We constructed a global model to determine juvenile survival (the first year survival) and adult survival: $\{\phi(_{2a-./t*Sex}; P_{t*Sex}\}$, where '$\phi$' denotes apparent survival rate, 'P' denotes encounter probability (recapture rate), '2a' denotes an age effect over two age classes (< 1-yr-old and ≥ 1-yr-old), '.', denotes a time effect constant throughout the first-year study period, 't' denotes a time effect over the study period, and *'Sex'* denotes sex as determined from morphometrics at the time of banding.

We report the oldest falcon and estimated the mean age of Kaingaroa falcon population with the band recovery data of nestlings from the earliest record in 1998 to 2015. To avoid underestimation, we excluded nestlings that were banded after 2011 from the analysis of falcon age. We calculated the mean age of marked falcons in each sex by taking at the latest recaptured year of each individual divided by numbers of the marked individuals.

Results

Falcon survival through 1080 poison operations

Fifteen of the 16 adult falcons (15 radio-tagged and 1 banded) potentially exposed to carrot-bait 1080 poison survived during the monitoring periods (CI = 68–100%, Table 1). A single radio-tagged male died of unknown causes within a fortnight of the 2014 carrot-bait 1080 poison operation. All the 21 adult falcons (eight radio-tagged and 13 banded) that were potentially exposed to cereal-bait 1080 poison also survived during the monitoring periods (CI = 81–100%). In total, 36 of the 37 adult falcons survived over the 1080 monitoring periods (CI = 84–100%).

Table 1. The numbers of radio-tagged and banded adult New Zealand falcons that were potentially exposed to carrot-bait and cereal-bait 1080 poisons and that survived over the 1080 operations, and the 95% confidence interval for survival, and the area of 1080 poison per bait type in 2013–2014. Potential exposure to 1080 means that an individual was known to be using an area when 1080 was applied during a pest control operation.

	Carrot bait			Cereal bait			
	Radio-tracked	Banded	Total	Radio-tracked	Banded	Total	Grand Total
2013	13	1	14	1	0	1	15
2014	2	0	2	7	13	20	22
Potentially exposed	15	1	16	8	13	21	37
Survived	14	1	15	8	13	21	36
95% *CI* (%) Including continuity correction	68–100			81–100			84–100
Poison area (ha)	12 493			38 700			51 193

Causes of mortality

The bodies of five adult falcons were retrieved for post-mortem examination during the study period 2013–2014, and four of the five deaths occurred within 1080 operation blocks but outside of the time period when 1080 was applied or effective. Of these four, one radio-tagged adult female falcon (unknown age) and one banded adult male falcon (3 years old) were depredated by stoats during the non-breeding season and the breeding season respectively. These falcons each had a canine bite mark (6 mm in width) on the rear of their skulls. Post-mortems indicated that these recovered bodies had good body fat reserves, and histopathology examinations found no obvious abnormalities.

One radio-tagged female (4 years old) was found dead in June 2014. The body was emaciated, with a 30% drop in body mass in the 6 months since we re-fitted a radio-transmitter in December 2013. A post-mortem examination indicated that the direct cause of death was head trauma. There were three sets of 1–2 mm holes (5–7 mm apart) on the top of the skull associated with severe internal haemorrhage on the skull and brain. These sets of holes did not resemble canine bite marks but indicated beak marks made by Australasian magpie (*Cracticus tibicen*). Histopathology examinations did not find obvious abnormalities. The cause of emaciation is unknown. One radio-tagged male (unknown age) was depredated during the 2013/2014 breeding season. Only plucked feathers, two leg bands, and the transmitter of the adult male falcon were found approximately 70 m from his nest. A small piece of falcon leg was all that remained within the metal band, suggesting depredation by a feral cat may have been his cause of death.

The last retrieved falcon was a radio-tagged male (unknown age) that died of unknown causes. His body was found in July 2014, two weeks after the 1080 carrot-bait operation within his feeding ground but appeared to be freshly dead. The internal organs were found intact, but most of his pectoral, triceps and biceps muscles were scavenged, likely by Australasian harrier (*Circus approximans*). A post-mortem examination and histopathology did not detect structural and internal abnormalities. The body was in good condition and had decent fat reserves. Muscle tissue sample of < 10 g was sent to a 1080 toxicology analysis. The result found no 1080 residue (the method detection limit (MDL) is 0.001 µg/g with the 9% uncertainty (95% C.I).

Annual Survival and re-capture rates with the long-term banding data

The estimated mean annual survival rate of adult New Zealand falcons from the long-term band recovery data was 80 ± 13% (mean ± s.e.; by sex rates were female = 78 ± 7% and male = 82 ± 5%), and for juveniles was 29 ± 5% (female = 27 ± 0.05% and male 31 ± 0.06%). Re-sighting rates differed between the sexes with 61 ± 5% for females and 44 ± 5% for males. The mean known-age of female falcons was 3.8 ± 2.5 years old (mean ± s.d., *n* = 25) and of males was 4.3 ± 2.5 years old (*n* = 19). The oldest females were eight years old (*n* = 4), and the oldest male was 10 years old.

Discussion

Falcon survival through 1080 operations

We monitored radio-tagged or banded falcons through 37 periods of potential exposure to 1080 in 2013–2014. All falcons survived with the exception of the male falcon that died during the carrot-bait 1080 monitoring period in 2014. 1080 residue was not detected in his muscle tissue, though as the sensitivity of analysis decreases with samples of less than 10 g (Spurr and Powlesland 2000) and we were unable to collect 10 g of muscle tissue. Thus the ability to detect 1080 if present may have been low. Post-mortem and histopathological analyses found no abnormalities, the body had good fat reserves, and the cause of death remains unknown.

The annual survival rate of adult Kaingaroa falcons of 80 ± 13% was comparable to those of other raptor species in different regions without known poison operations, which ranged from 60 to 87% (e.g. Eleonora's falcon *F. eleonorae*, Ristow *et al*. 1989; Cooper's hawks *Accipiter cooperii*, Roth *et al.* 2005; sharp-shinned hawks *A. striatus*, Roth *et al.* 2005; Northern goshawks *A. gentilis*, Squires and Reynolds 1997; Kenward *et al*. 1999; Tornberg and Colpaert 2001; and sparrowhawks *A. nisus*, Newton 1975; Newton *et al*. 1983). The evidence from our study and the viability of the Kaingaroa falcon population after many years of 1080 baiting operations indicates that the risk of secondary poisoning of 1080 on adult Kaingaroa falcons is low.

However, recent falcon nest surveys (2011–2015) indicate that the Kaingaroa falcon population has declined in the last decade (Chapter 3). Seaton (2007) studied the breeding season ecology of the same falcon population in 2003–2006 and reported finding a mean of 29 breeding pairs per season. In contrast, I found a mean of only 17 nests within the same study site in 2011–2014. One change that could be influencing the numbers of birds present is an increase in the forest harvesting rate, resulting in a reduction in the edge habitats favoured by falcons and a reduction in habitat quality

(Chapter 3). Juvenile emigration and low survival rates may also be influencing the Kaingaroa falcon population.

The risk to New Zealand falcons from 1080 is that falcons might scavenge carcasses or kill and eat poisoned animals (Fisher 2013). Juvenile birds may develop foraging proficiency over time (Marchetti and Price 1989; Kitowski 2003), and we suspect that the risk to juvenile falcons (independent first-year chicks) may be greater than the risk to adults if juveniles have lower foraging success and are therefore more likely to scavenge or take ailing prey. To date, there has been no intensive study of juvenile New Zealand falcon feeding behaviour and survival during a 1080 poison operation conducted in Kaingaroa forest or anywhere else. Monitoring juvenile survival through 1080 operations will be more challenging than for adults, as juveniles potentially disperse out of Kaingaroa forest, limiting the effectiveness of VHF radio-tracking for determining the fate of individuals (R. Seaton, pers. comm.).

1080 can persist for several weeks to several months under less favourable conditions, such as extreme cold and drought (Eason *et al.* 2013). Annual carrot bait 1080 operations are typically conducted during the winter months when biodegradation will be slow, which suggests that in winter there may be prolonged accessibility of carcasses (rabbits, possums, and passerine birds) to predatory birds (New Zealand falcons and Australasian harriers) following a 1080 poison operation. Seaton *et al*. (2009) surveyed the breeding success of Kaingaroa falcons in relation to the use of 1080 during the breeding season 2003–2006, and found that breeding success was not related to the time since 1080 application (one month to > 3 years), bait type (carrot or cereal), or application method (ground vs aerial), and concluded that there was no evidence of a negative impact of the 1080 poison applications on the falcon population during the breeding seasons. In that study, however, 1080 was applied more than a month before the breeding season, and as 1080 in baits or in soil breaks down within two weeks in favourable environmental conditions (11–20 ^{o}C and 8–15% moisture, King *et al.* 1994) such as those that occur during the breeding season of falcons (October–February, range 10.6–16.3 ^{o}C, humidity > 65%, YR 2014), any 1080 had most likely decomposed by the time of their study.

The extensive, regular, and long-term use of 1080 poison in Kaingaroa forest may benefit the survival of Kaingaroa falcons by both controlling numbers of mammalian predators such as stoats and feral cats through secondary poisoning and through increases in prey abundance (Powlesland *et al*. 1999). However, as no comparisons have been of falcon demography and potential prey numbers in a similar habitat in the absence of 1080 operations (either before and after treatment, or in control blocks) it is not clear how much the success of falcons at Kaingaroa can be attributed to pest control versus habitat management. In general, creating open habitats by clear-cutting mature tree stands by timber harvesting attracts insectivorous and generalist bird species (i.e. falcon prey) because deep-forest insect fauna become available to them (Clout and Gaze 1984; Moorman and Guynn 2001; Pawson *et al*. 2006). Moreover, cleared open habitats promote colonisation of forbs and grasses, which produce seeds eaten by generalist birds (Pawson *et al*. 2006; Moorman and Guynn 2001). With the constant rotation of clear-cutting and planting trees, Kaingaroa forest can maintain relatively high numbers of passerine birds during the winter season (Chapter 2), though of course our measurements of passerine bird numbers have been made only in a forest subject to 1080 operations. The rotational harvesting scheme in operation at Kaingaroa also ensures a continual availability of the clear-cut and young stands that nesting is confined to (Thomas 2008, Seaton et al. 2009, Chapter 5). Studies of movements of predatory mammals in plantation forests might reveal whether these young stands are used less than mature stands, in which case falcons might benefit from direct habitat management independent of any benefits accruing from predator control.

Causes of mortality

High rates of falcon nest predation by introduced mammals have been reported in several studies (Lawrence and Gay 1991, Barea 1995, Gaze and Hutzler 2004, Seaton *et al.* 2009, Kross *et al.* 2013a), though, to our knowledge, predation on adult New Zealand falcon by introduced mammals has not been reported. Post-mortem examinations found puncture wounds (6–7 mm apart) in the skin and musculature at the base of the skull of the radio-tagged female (age unknown) and the banded male (3 years old), indicating these falcons were attacked by stoats. The body of the female was found in a prone position under a blackberry bush located at the base of a tall mature tree. A part of left shoulder was taken and the left humerus was crushed. This female could have been attacked while roosting at night or even during the day while perching in the tree. The body of the banded male was found in a 3-year-old pine forest stand during the morning hours by a forest contract worker (G. Jenkins, pers. comm.). He saw the falcon leap up vertically and then fall to the ground. Later examination revealed stoat bite marks on the back of the falcon's head so the observed movements were likely to be its death throes. The death of another breeding male was consistent with depredation by a feral cat, possibly if the bird dive-bombed the cat as a form of nest defense rather than being attacked when at his nest. This male had been monitored intensively for 12 months starting November 2012. We frequently observed him incubating over the two consecutive breeding attempts (CH. pers. obs.), though his two nestlings were about 14 days old at the time of his death. A nestling over 14 days old no longer requires intensive parental care, and this male was unlikely to have been attacked at his nest.

The emaciated 4-year-old female found dead had previously been monitored for 18 months starting November 2012, and she successfully raised three nestlings each breeding season in 2012–13 and 2013–14. The result of histopathology did not find any abnormality so the cause of emaciation remains unknown. The direct mortality cause was head injury, most likely due to Australasian magpie attacks. Australasian magpies are found throughout Kaingaroa forest but are concentrated in forest stands bordering farmland. Throughout the study period, we regularly observed magpies attacking New Zealand falcons, including this female, but all falcons appeared to manage to avoid physical contact by the magpies. Her emaciated body condition may have made her vulnerable to attack.

Documented causes of mortality in the genus *Falco* in other regions include predation (McFadzen and Marzluff 1996), electrocution (Gombobaatar *et al*. 2004; Dixon *et al.* 2013; Fox and Wynn 2010; Kross 2014), collisions with buildings, aircraft, vehicles or trains (Faccio *et al*. 2013), and shooting (Gombobaatar *et al*. 2004; Fox and Wynn 2010; Faccio *et al.* 2013; Cianchetti-Benedetti *et al*. 2016).

Annual Survival and re-capture rates with the long-term banding data

The apparent survival rate of adult falcons in Kaingaroa was comparable to those of raptors elsewhere (see above). The encounter probability (recapture rate) of falcons was higher in females (61%) than in males (45%). Two reasons for this may be that (1) females exhibit greater natal philopatry than males, and/or (2) females have higher detectability at nests than males because breeding females generally remain at their nests more than males (Thomas 2008) and the band recovery data heavily rely on finding nests during the breeding seasons.

The apparent survival rate (incorporating survival and natal philopatry) of juvenile falcons was low (29%). Lower survival rates of juveniles are expected as dispersing individuals face risks when exposed to new sites (Johnson *et al.* 2009). With limited knowledge of juvenile dispersal for the Kaingaroa population, we were not able to distinguish mortality from emigration for juveniles in our study. Seaton *et al.* (2008b) monitored eleven juvenile falcons (five female and six male) from the same population for 3 months using radio telemetry in 2006 and found that four of the five females remained in Kaingaroa forest, but none of the males was found within the study site after the 3-month tracking period. The study concluded that these juvenile falcons emigrated out of Kaingaroa forest. Thomas *et al.* (2010) monitored three juvenile Kaingaroa falcons (one female and two males < 7 months old) for 5 months (between December and June) using satellite telemetry. The study found that two falcons remained continuously in Kaingaroa forest, and one male traveled ca. 50 km out of the forest for two days and returned to the forest. Neither study monitored birds until they breed in successive breeding seasons. High mortality in the first year of life is commonly reported in raptor species (Zelenak and Rotella 1997; Harmata *et al*. 2001; Roth *et al*. 2005; Morgan Davies and Restani 2006; Ward and Conover 2013).

While VHF telemetry and visual observations were appropriate methods for studying the survival of adult falcons, future research into the survival and movements of juveniles would require GPS or satellite telemetry that is capable of distinguishing emigration from mortality. This would enable evaluation of how much the low apparent survival of juveniles represents mortality and/or dispersal, and allow direct investigation of juvenile survival through 1080 operations. Factors affecting natal philopatry might also shed light on whether philopatry is sex-biased (given that the current adult population appears to be male-biased; Chapter 5). Furthermore, continuous monitoring of adult falcons over 1080 operations with convincing information of bird mortality to increase sample size (n > 60) and using multiple control sites (if suitable), and quantitative measurement of any change in population size and identifying factors influencing the population change are recommended (Veltman and Westbrooke 2011).

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CHAPTER 5

Effects of logging-induced changes in habitat influencing the reproductive strategy of New Zealand falcons: causes and consequences of divorce

For submission

Co-authors: Phil F. Battley and Edward O. Minot

Chatri & Psyco 2012/2013

Abstract

We studied the reproductive strategy of a non-migratory raptor, the New Zealand falcon, living in a pine plantation forest. We investigated how the falcon's reproductive strategy was influenced by changes in forest structure through assessing causes of divorce. We used radio-tracking data (*N* = 36) and behavioural observations (*N* = 42 pairs) over three non-breeding seasons in 2012–14 and long-term (2003-2015) band recovery data to address five hypotheses: (1) the habitat mediated hypothesis, (2) the better option hypothesis, (3) the mate familiarity hypothesis, (4) the forced divorce hypothesis, and (5) the musical chair hypothesis. We also examined the timing of the male's mate-guarding behaviour in relation to early nesting. Our observations mainly supported hypotheses 4 (forced divorce) and 5 (musical chair). We found that falcons retain or divorce their partners based on nest site suitability, which is influenced by changes in forest structure and composition but is unrelated to reproductive success. The divorce rate was 40%, and all but one incidence were initiated by females leaving their territories regardless of reproductive outcomes. Extra-pair interactions occurred in females but not males of a pair. We found males that strongly exhibiting vigilant behavioural traits (e.g. chasing or attacking large birds entering and passing over their breeding territories) nested earlier in the season and outcompeted females from the territory occupants, suggesting they likely enhanced mate-guarding performance than males that express vigilant behavioural trait less strongly. Winter home-range overlap was greater for pairs that remaining together than pairs that divorced in the subsequent breeding season. Winter courtship displays were used for pair-formation (the process of establishing a social bond) rather than pair-bonding (the process of maintaining a social bond), and also used for intra-sexual competition over females. Sufficient prey availability in the study area might have promoted relatively stable reproductive outcomes, and with that foundation, falcons were able to adjust mating strategies to the rapid changes of habitat suitability.

Key words: New Zealand falcons, raptor, mating system, mating patterns, mate and site fidelity, reproductive strategy, reproductive success, extra-pair males, extra-pair copulation, divorce

Introduction

Environments are constantly changing, and animals need to adapt to environmental fluctuations by adjusting their morphology, physiology, and behaviour in order to maximise fitness (Wingfield, 2008). Intraspecific variation in the reproductive decision is considered as an adaptation to environmental circumstances (Both, Dingemanse, Drent, & Tinbergen, 2005; Rowley, 1983). The population demography and behavioural preferences for mate choice are also major factors shaping the mating system of animals (Waser, 1993).

Divorce is believed to be a reproductive strategy by an individual may maximise its own fitness, and birds are repeatedly faced with the decision to either stay with or divorce their partners (Choudhury, 1995; Coulson, 1972). Assessing the costs and benefits of mate fidelity is the key to understanding when the divorce will occur, which is largely determined by the life-history strategies of the species, population demography, and reproductive trade-offs (Choudhury, 1995).

Ecological constraints and an animal's biological parameters independently shape site fidelity as an optimal form of habitat selection (Switzer, 1993). Studies on raptors have found reproductive success to be related to site fidelity (Catlin, Rosenberg, & Haley, 2005; Marquiss & Newton, 1982), both mate and site fidelity (Bai & Severinghaus, 2012; McDonald, Olsen, & Baker-Gabb, 2003; Thorstrom, Morales, & Ramos, 2001) or mate fidelity alone (Boal, 2001; Martin, Koeslag, Curtis, & Amar, 2014; Naves, Cam, & Monnat, 2007). In contrast, nest success of merlins (*F. columbarius*; Warkentin, James,

& Oliphant, 1991) and black kites (*Milvus migrans*; Forero, Donázar, Blas & Hiraldo, 1999) was not related to site fidelity.

The non-migratory New Zealand falcon (*Falco novaeseelandiae*) occurs in native habitats, but also in large managed exotic timber forests. Birds in these exotic forests are inevitably faced with habitat alterations by timber harvesting, which affect both foraging areas (the favoured edge-mature ecotone) and nesting areas (most falcons nested in open ground, in newly clear-cut stands on stands with pines age up to three years old: Seaton, Holland, Minot, & Springett, 2009, CH. unpublished data). We studied New Zealand falcons in Kaingaroa forest, a plantation forest in the central North Island, in order to understand the impact of habitat alteration resulting from harvesting and general forest management on their reproductive strategies. Current information on the breeding behaviour of falcons in plantation forests is limited to the summer breeding season (September to March). The degree to which pairs interact year-round in the changing forest environment and how these interactions influence mating patterns during the breeding season is unknown.

We investigated how timber harvesting and the consequent changes in forest structure influence the mating patterns of falcons. Specifically, we assess causes of divorce in falcons by examining potential roles of (a) site fidelity, (b) mate fidelity and (c) extra-pair interaction. We test five hypotheses that explain causes of divorce in relation to habitat changes. (1) The habitat mediated hypothesis predicts that divorce is a by-product of territory choice, and the decision to divorce is made by at least one member of a pair based on previous breeding outcomes (Desrochers & Magrath, 1996). (2) The better option hypothesis is where divorce occurs when one member of a pair decides to desert for a better mate for its own benefit (Ens, Safriel, & Harris, 1993). (3) The mate familiarity hypothesis states that continual breeding with the same mate allows better behavioural coordination between the male and female, resulting in improving reproductive success (Boal 2001; Rowley 1983). (4) The forced divorce hypothesis applies where divorce is a result of a third individual who intrudes and outcompetes one member of a pair (Taborsky & Taborsky, 1999). (5) The musical chair hypothesis was proposed for migratory birds in which males and females settle on the best available territory upon arrival, and thus arrival timing of individuals determines whether to divorce or retain the same partner (Dhondt & Adriaensen, 1994). Although the musical chairs hypothesis was developed to explain divorce in migratory birds, the hypothesis may be applicable to our study population because potential nesting sites of falcons are constantly created by timber harvesting and newly available breeding territories may be filled on a first come first served basis. Hypotheses (1) to (3) are dependent on a reproductive outcome, whereas (4) and (5) are not.

We predict that reproductive success and suitability of nest site will play definitive roles in pairs' decisions about whether to retain or divorce their partner, and that early nesting will promote reproductive success. We expect that pairs will continue to breed in the same territories as long as the nest-site quality remains suitable and the previous breeding was successful (hypothesis 1), but that birds may replace partners after reproductive failure (hypothesis 2). We also expect that pairs will move together to a better breeding site if one becomes available nearby as long as their breeding attempt was successful in the previous season (hypothesis 3). Divorce likely occurs when a new breeding site becomes available but is already occupied by another falcon one bird of the opposite sex is able to then settle at the new site (hypothesis 5). Since male falcons appeared to be territorial, we do not expect to observe forced divorced (hypothesis 4).

Sex variations in mating strategies

Female falcons in our study site exhibited a high rate of extra-pair interaction and copulation (EPC), and some females interacted with their partners and extra-pair males in a similar intensity (CH pers. obs.). Areas rich in resources support year-round residency of both females and males and thus facilitate pair interactions in raptors outside the breeding season (Boggie, Mannan, & Wissler, 2015). Therefore, such environmental conditions would promote perennial pair bonds (Thorstrom, et al., 2001) and may permit the occurrence of extra-pair interaction/mating (Rosenfield, Sonsthagen, Stout, & Talbot, 2015). Extra-pair mating may be an extension of mate choice after pair-formation (the process of establishing a social bond) has occurred (Choudhury, 1995). A female may seek extra males in reserve, or a female could still attain 'better genes' for her offspring by engaging in EPC (Graves, Ortega-Ruano, & Slater, 1993; Houtman, 1992; Smith, 1988).

EPC occurs in many socially monogamous raptor species (Koopman, McDonald, & Hayward, 2007; Rosenfield, et al., 2015; Villarroel, Bird, & Kuhnlein, 1998; Warkentin et al., 1994) and can result in extra-pair paternity (Rosenfield et al., 2015). To minimise the risk of cuckoldry, male raptors may use two strategies to assure paternity: frequent copulations and mate guarding (Birkhead, Atkin, & Møller, 1987). Males copulate frequently to dilute or devalue inseminations from other males (Birkhead, 1987), and it usually occurs over extended periods, possibly well before the females are fertile

(Mougeot, 2004). Mate-guarding is a male's strategy to remain close to the female during the time she is fertile, limiting the female's opportunities for EPC (Birkhead, et al., 1987). However, raptor males cannot effectively guard their females as they usually hunt alone, and in many species, the females remain in the nest areas throughout the pre-laying period and are fed by males (Birkhead, 1987). To achieve paternity, male falcons may, therefore, need to establish a breeding territory, attract a female, and perform long-term mate-guarding by actively interacting with a female (i.e. closely associating with her, 'play' flying together, performing courtship displays) throughout the non-breeding season.

Variation in paternity and breeding success may be explained by unique behavioural traits. The shyness-boldness continuum is an essential axis of behavioural variation that appears in numerous species (Wilson, Clark, Coleman, & Dearstyne, 1994), an which can correlate with behavioural traits such as exploration, aggressiveness, risk taking, and feeding strategies (Goss-Custard, Durell, & Ens, 1982). Several extensive studies of personality in great tits (*Parus major*) reveal that exploratory behaviour is related to sexual selection (van Oers, Drent, Dingemanse, & Kempenaers, 2008) and reproductive success (Both, et al,. 2005; Hollander, Van Overveld, Tokka, & Matthysen, 2008). Hollander et al. (2008) found that the exploratory behaviour of great tits was positively correlated with alarm calling (vigilance) towards a human intruder but negatively related to nest defence behaviour (boldness). This finding indicated that there was a distinction between the boldness behaviour (nest defence performance) and vigilance performance (alarm calling).

Based on these findings, we predict that mate-guarding will be performed advantageously by a male falcon that possesses a persistent behavioural trait (pursue and engage female's attention effectively), which is regulated by a bold or vigilant behaviour. Males strongly exhibiting either of these behavioural traits could secure a better site, attract a female, and maintain a strong pair bond with the female and could breed earlier in the season, potentially increasing their reproductive success relative to males that express these traits less strongly (Newton & Marquiss, 1984; Sodhi, James, Warkentin, & Oliphant, 1992).

Furthermore, we examine the consequences of divorce by comparing winter home-range overlap of pairs that bred together in previous year and retained together in the subsequent year (namely 'retained pairs') and the pairs that bred together in previous year but divorced ('divorced pairs') in the subsequent year, and variations of courtship display of retained and pairs that newly formed (new pairs). We predict a greater winter home-range overlap by retained pairs than divorced pairs, and that the home-range overlap of retained pairs increase and that of divorced pairs decrease over time from mid-winter to late winter (June–August). We also predict variations of courtship display between retained pairs and new pairs, with new pairs commencing courtship display earlier in the breeding season and performing for a longer period compared to retained pairs.

Methods

Study site

The Kaingaroa forest (hereafter called "Kaingaroa") sits on a volcanic plateau in the central North Island of New Zealand. The forest covers 1,800 km^2, which comprises 1342 harvestable stands of approximately 1 km^2 each. The focal harvest species is *Pinus radiata* (Seaton, et al. 2009) what is typically harvested at 26–32 years after planting (Pawson, Ecroyd, Seaton, Shaw, & Brockerhoff, 2010). See details of the study site in Chapter 2.

Nest survey and radio tracking

We conducted nest surveys during the breeding season (October to January), mainly focused on the open grounds (clear-cut stands before planting seedlings to young pine-stands, which tree ages ≤ 3-yr-old tree stands) where Kaingaroa falcons typically nest (Seaton, et al. 2009; Stewart and Hyde, 2004). Breeding stage, nest location and stand age were recorded. An approximate distance of each nest from the nearest mature stand was also recorded in the field, and an exact distance was confirmed with ArcGIS maps.

We radio-tracked 28 falcons (14 female and 14 male) over three non-breeding seasons (April–June 2012, June–August 2013–2014; see Chapter 2 for details of falcon capturing and tracking). Of these 28, seven falcons (one male and six females) were tracked over multiple non-breeding seasons: one male in 2012 and 2013, one female in 2012 and 2014, one female from 2012–14, and four females in 2013 and 2014. Hence, in total, we tracked 36 falcon-seasons (15 males and 21 females) from 28 individuals.

We obtained 159 ± 63 (mean ± SD) fixes per falcon ranging between 33 and 275 fixes with a mean of 60 ± 20 h total tracking time per falcon (range 8 to 91 h).

Behavioural observation and analysis

To begin, we established an ethogram of breeding and courtship behaviour (Fox, 1977; Ratcliffe 2010; Table 1). Courtship display consists of Bow and Jerk-up, Flapping, Flittering-flight, Flying-display, Tippy-toed Running by males and Twitch-fly by both sexes (see Table 1 for definition). Copulation is generally led by Soft-whining by female and Food-passing by a male. Pair cooperation includes Cooperative-hunting, Following, and Play-flight. We also measured perching distance (< 25 m, < 300 m, and See-Each-Other-Distance) between the female and male. An activity budget was recorded for each pair, using focal sampling (Martin & Bateson, 2007) during the radio-tracking periods. In September 2013 and 2014, we observed each pair for 2–3 h day^{-1} at weekly intervals until pairs nested. We observed each pair for a total of 22 ± 2.4 h (mean ± SD) and a mean observation period of 2.9 ± 1.6 h pair^{-1}. We calculated the frequency and duration of each behaviour.

We used band recovery data from the Kaingaroa falcon population collected by Wingspan Birds of Prey Trust (Rotorua, New Zealand) and Massey University to analyse pair status and nesting dates. The band recovery data consist of three intensive nest surveys over 12 years (2003–2015): 2003–2005, 2007–2008, and 2011–2015. Falcons (nestlings or adults) were marked using leg bands with unique metal numbers and colour combinations at their nest sites. The data included 164 nests by 116 pairs, in

Table 1. Ethogram of falcon pre-breeding behaviours.

	Behaviours	Code	Sex	Description
Display	Bow and Jerk-up	**BJ**	♂♀	Bows head right down, may pick object with beak, and then jerk head up into an erect position. Repeats this sequence quickly several times.
	Flapping	**FP**	♂	Male holds his wings high with short wing-beats, keeps legs forward and tail depressed, resulting in a slow motion bouncing flight. The male flies in this manner around the female.
	Flittering-flight	**FF**	♂	A horizontal posture and flittering from branch to branch about 5 to 10 m from the feeding or waiting female.
	Flying-display	**FLYD**	♂	Male flies in a loop when the female is in sight, which includes diving down and/or quick wing flaps (like twitching) in the air.
	Tippy-toed Running	**TR**	♂♀	Jerky little runs between posturing and quick flittering flights or without flittering flights.
	Twitch-fly	**TF**	♂♀	While flying in circles, occasionally twists body from one side to another quickly like twitching, with short wing-beats.
Copulation	Food-passing	**FDPS**	♂	Male brings captured prey to the female and drops the prey in the air or places it on a stump when the female approaches him.
	Soft-whining	**SWN**	♀	Female whines gently while posturing horizontally and holding wings loosely.
	Copulation	**CPL**	♂♀	Male lands on the female's back and attempts to copulate. The female accepts the male.
Cooperation	Cooperative-hunting	**COPH**	♂♀	A pair chases a prey bird and they hunt cooperatively.
	Following	**FOL**	♂♀	A member of a pair moves within 3 min in the direction of the other member moved.
	Play-flight	**PLYF**	♂♀	A pair flies together in a playful manner, swooping up and down concurrently or attempting to attack each other gently in the air.
Perching	Perch-together (< 25 m)	**PT25**		A pair perches within 25 m of each other.
	Perch-together (< 300 m)	**PT300**		A pair perches within 300 m of each other.
	See-each-other-distance	**SEOD**		A pair perches more than 300 m apart but are in line of site.

which both members of a pair were marked in 59 pairs and only one member was marked in 57 pairs. We excluded records of pairs where neither of the members was marked. Note that the band recovery data are female biased as bandings were conducted during the breeding seasons by finding nests. Females, in general, remained at their nests while males in general move in and out of nest when hunting, therefore, females were inclined to be captured and banded and re-sighted in following years, more than males.

Breeding dispersal

We measured the mean breeding dispersal distance of 125 nests from 41 marked adult females and 60 nests from 26 marked adult males using GPS to measure distances between nests in successive years. The data consist of a mean of 3.0 successive breeding seasons for females (range from 2 to 5 breeding seasons) and 2.3 successive breeding seasons for males (range from 2 to 4 breeding seasons).

Fidelity, nest dates and pair status

The band recovery data (2003–2014) include 100 nesting attempts that included records of breeding success (not all data included records of nest success). A nest was regarded as successful if at least one nestling fledged. We defined divorce as occurring when both members of a pair were known to be alive but no longer paired in a subsequent season (this excludes situations in which the fate one partner was unknown). The Divorce data consist of 54 records from 86 nests of 30 marked adult females and 39 records from 67 nests of 27 marked adult males.

Site fidelity was assessed for nests in successive breeding seasons, with site referring to a commercial forest stand unit, and age being the years since clear-cutting. Site fidelity of radio-tracked falcons was assessed in 18 radio-tracked females and 15 radio-tracked males. Three of 21 radio-tracked females were removed as we were not able to determine their fates. Mate fidelity was assessed for each member of a pair in successive breeding seasons. We used the Mann-Whitney U-test to measure the relationship between nesting dates and pair social status (retained pairs versus new pairs).

Nest success

We also examined nest success in relation to mate or site fidelity between breeding seasons. Fisher's Poisson test was used to evaluate whether nest success was related to the fidelity. In addition, we evaluated the relationship between nest success and mate and/or site fidelity within a season using radio-tracking data and behavioural observations of 36 falcons (2012–2014).

Divorce and extra-male interaction by females

Within a radio-tracking period or a behavioural observation period, we counted each time a radio-tagged female interacted with extra-pair male(s) in addition to their original partners. We also noted when females interacted with a different male (between pair male and extra-pair males) from the end of the previous monitoring period to the beginning of the following monitoring period. We totalled the number of interactions between females and extra-pair males and standardised these as the number of interactions per min of observation. Fifteen of 21 total radio-tagged females interacted with extra-pair males (71%), and a total of 40 pairs, which include 21 original pairs and 19 extra-pairs were formed during the winters 2012–2014 (some females had more than one extra-pair male).

Male mate guarding strategy - Vigilant behavioural trait

Throughout the study period, we recorded the males' territorial calls and behaviour (e.g. chasing or attacking Australasian harriers (*Circus approximans*) or Australasian magpies (*Cracticus tibicen*) entering and passing over their breeding territories). We calculated the frequency of the territorial behaviour from 25 males, and the mean of the frequency was ranked into three categories: *strong* – mean percent frequency above the average, *moderate* – mean percent frequency between one occurrence and below average, and *weak* – no record of the behaviour.

Boldness-shyness behaviour was measured by the intensity of dive-bombing when the first author (CH) approached the nest. The intensity of nest defence should increase as nestlings get older (because it relates to the duration of parental investment; Sergio & Bogliani 2001), therefore, we collected data when chicks were over 15 days old. Nest defence intensity was classified into three categories: *bold* – male hit head of CH, *curious* – male swooped over CH's head but made no contact, and *shy* – male alarm called but did not approach CH. We collected the males' behavioural data before we captured them for transmitter attachment as trapping would likely alter their behaviour.

Although there were subtle variations in the timing of breeding commencement each year (e.g. the majority of falcons nested earlier in one year than the other years), we combined the nest initiation dates of the three breeding seasons and pooled them into fortnightly periods. We used the Kruskal-Wallis rank sum test to assess the statistical significance of the relation between nesting dates and ranks of boldness-shyness or vigilance of males.

Pair home-range overlap

We calculated winter home-range overlap of pairs who reproduced in the previous breeding season. Home-range size was calculated with kernel density estimates (KDE) with a reference smoothing parameter (Gitzen, Millspaugh, & Kernohan, 2006) for core home-range size (50% KDE; Samuel, Pierce, & Garton, 1985) and the entire home-range size (95% KDE; Seaman & Powell, 1996) of falcons using Hawth's Analysis Tools 3.27 for ArcGIS (ArcGIS 9.3; ERSI, Redlands, California, U.S.A). We chose the 50% and 95% KDE for compatibility with other home range studies. Mean ± SE core home-range size of females was 6 ± 1.0 km^2 and males was 3 ± 0.5 km^2, and the mean entire home-range size of females was 32 ± 6.4 km^2 and male was 15 ± 2.6 km^2 (Chapter 2).

We calculated the percentages of core and entire home-range overlaps of each member of eight pairs: one pair in 2012 (April–June), five pairs in 2013 and two pairs in 2014 (June–August). Of these, four pairs reproduced in subsequent years and four pairs divorced.

Pair interaction and courtship behaviour

We obtained activity budgets for 35 pairs over three years: six pairs in 2012, 15 pairs in 2013, and 14 pairs in 2014. We pooled these pairs into two categories based on their breeding status: retained pairs (*N* = 11) and new pairs (*N* = 24). We constructed generalised linear mixed models (GLM, Poisson distribution) to compare (1) percent of the frequency of extra-pair male interactions between divorced and retained females, and (2) for percent of the duration of each pair interaction or the frequency of each courtship behaviour between retained pairs and new pairs. Negative binominal modeling was used to fit over-dispersed regression models (McCullagh & Nelder, 1989).

Ethical Note

All bird handling procedures followed the Animal Ethics guidelines approved by Massey University (protocol No. 11/96) and the Department of Conservation National Permit (National Permit Number BP-32336-RES.).

Results

Fidelity, nest dates and pair status

Breeding dispersal between breeding seasons by females (*N* = 47) was slightly farther (mean ± SE = 1.9 ± 0.3 km) than by males (*N* = 31, 1.4 ± 0.3 km). Banding records showed that the majority (97%, *N* = 118) of falcons nested in a stand-pine age less than 3 years old and less than 3% (*N* = 4) of nests were found in stands over 4 years old.

We found that mate fidelity was not statistically associated with site fidelity of both females and males (Table 2). Both females and males had greater mate fidelity (65% of females and 82% of males) than site fidelity (37% of females and 46% of males). Lower site fidelity of males than females is inconsistent with the results of the radio-tracking analysis that males had greater site fidelity (14/15, 93%) than females (12/18, 67%). Replacement of a partner while staying in the same forest stand was infrequently observed (11% of females and 3% of males).

Table 2. Site and mate fidelity of New Zealand falcons, based on long-term band recovery data (2003–2014). Fidelity is measured with the data (female: *N* = 54, male: *N* = 39) that include only marked pairs and either member of separated pairs whose survival was confirmed in following years. Data presented as *N* (%).

	Female	**Mate**			**Male**	**Mate**		
		Retained	New	Total		Retained	New	Total
Site	Stayed	14 (26)	6 (11)	20 (37)	Stayed	17 (44)	1 (3)	18 (46)
	Moved	21 (39)	13 (24)	34 (44)	Moved	15 (38)	6 (15)	21 (54)
	Total	35 (65)	19 (35)	54	Total	32 (82)	7 (18)	39

Fisher's test: *P = 0.572*

Fisher's test: *P = 0.098*

Among all radio-tracked females (*N* = 21), only one female had strong site fidelity and she replaced her original partner with her extra-pair male. This female was located in her breeding territory throughout the tracking period June–August 2013 (100%) while the other 20 radio-tagged females spent an average of 29% (range 0–84%) in their breeding territories. This tagged female interacted with the extra-pair male (unmarked) in her previous breeding territory 29% of the total tracking duration of her. In contrast, the original male (radio-tracked) remained near the female for only 5% of the total tracking duration. Pair status (retained or divorced) did not influence nesting dates of marked females (U = 366.5, N = 57, P = 0.440) and marked males (U = 137.0, N = 35, P = 0.348).

Nest success

(a) Between breeding seasons

Both females and males had greater nest success (76% and 79% respectively) than nest fail (24% and 21% respectively, Table 3). Neither site nor mate fidelity was statistically related to nest success.

(b) Within breeding season

Seven tagged females failed their breeding attempts during the study period; for five of these, we have behavioural data from before and after the nest failure. Three females interacted with extra-pair males throughout the non-breeding season. After their initial nest attempts failed with their partners, all re-nested successfully with their extra-pair males. The other two did not have extra-pair male prior to nest failure. After their nests failed, they interacted with different males for a short period (including copulation attempts) but re-nested with their original partners. These different males were a first-year young male for one female, and the female's divorced partner from the previous breeding season in the other.

Divorce and extra-male interaction by females

Between the 2011/2012 and 2014/2015 breeding seasons, we determined the breeding status of 30 pairs in successive breeding seasons. These 30 pairs comprised 10 widowed pairs, nine divorced pairs and 11 retained pairs. Four females of the 11 retained pairs did not have extra-pair males and the remaining seven females interacted with extra-pair males: three females interacted with extra-pair males briefly (no more than two continuous radio-tracking durations), two females interacted with extra-pair males throughout the non-breeding season and two females did so to an unknown degree. Seven of the nine divorced females interacted with extra-pair males throughout the previous non-breeding season. We did not monitor presence/absence of extra-pair males for the remaining two females.

The divorce rate of radio-tracked falcons (N = 36) was 40%. Divorced females had a greater frequency of interaction with extra-pair males (mean ± SE = 78 ± 12%) than did females that retained the same partner (35 ± 19%, $Z_{15} = 11.2$, $P < 0.0001$; Fig 1).

Table 3. Mate and nest site fidelity of New Zealand falcon in relation to nest success by marked female nesting attempts (N = 54) and marked male nesting attempts (N = 39) between 2003 and 2014. Fidelity is measured with the data that include marked pairs and also either member of pairs that was separated but confirmed its survival.

		Female			**Male**		
		Nesting Outcome			Nesting Outcome		
		Success (%)	Fail (%)	Total (%)	Success (%)	Fail (%)	Total (%)
Mate	Retained	27 (43)	8 (13)	35 (65)	27 (39)	6 (15)	33 (85)
	New	14 (26)	5 (9)	19 (35)	4 (10)	2 (5)	6 (15)
	Total	41 (76)	13 (24)	54	31 (79)	8 (21)	39
Fisher's test		P = 1.00			P = 1.00		
Site	Stayed	15 (28)	5 (9)	20 (37)	13 (33)	4 (10)	17 (44)
	Moved	26 (48)	8 (15)	34 (63)	18 (46)	4 (10)	22 (56)
	Total	41 (76)	13 (24)	54	31 (79)	8 (21)	39
Fisher's test		P = 1.00			P = 0.71		

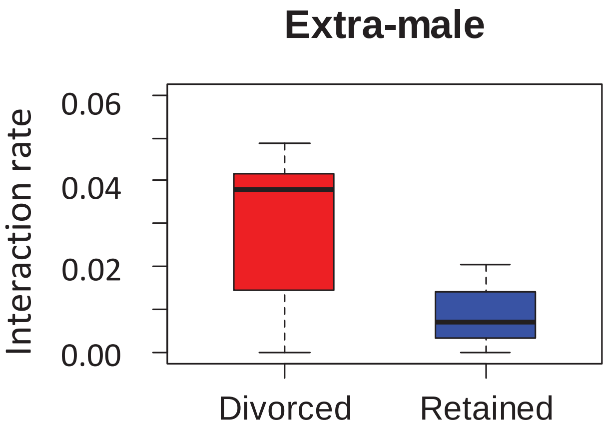

Figure 1. Interaction rate (number per min) of females who interacted with extra males in relation to pair status (divorced: mean = 0.04 ± 1.1 (SE) and retained: mean = 0.01 ± 0.2 (SE)) in the successive breeding season.

Male mate-guarding strategy and nesting dates

The male's vigilance level (strong, moderate, or weak) was related to nest initiation dates. Males with strong vigilance nested earlier (range 8–29 September) than males with moderate or weak vigilance (range 15 November–1 December 1; H_2= 7.88, P = 0.020). In contrast, there was no relationship between male boldness-shyness behaviour and nest initiation dates (H_2= 1.49, P = 0.476).

Pair home-range overlap

Both core and total winter home-range (HR) overlap were greater in the retained pairs than in divorced pairs (core HR *overlap,* mean ± SE = 42 ± 8.3% c.f. 9 ± 4.1%, respectively, Fig. 2A; total HR overlap = 57 ± 4.8 c.f. 23 ± 4.6 %, respectively).

We found a greater home-range overlap in retained pairs than divorced pairs throughout winter. Divorced pairs reduced their home-range overlap through the winter (31 ± 9.5%, 29 ± 9.6% and 8 ± 3.9%, respectively; Fig. 2B and 3A) while retained pairs maintained a high and increasing overlap of home ranges (57 ± 7.9%, 50 ± 10.6% and 70 ± 2.1% in June, July and August respectively; Fig. 2C and 3B).

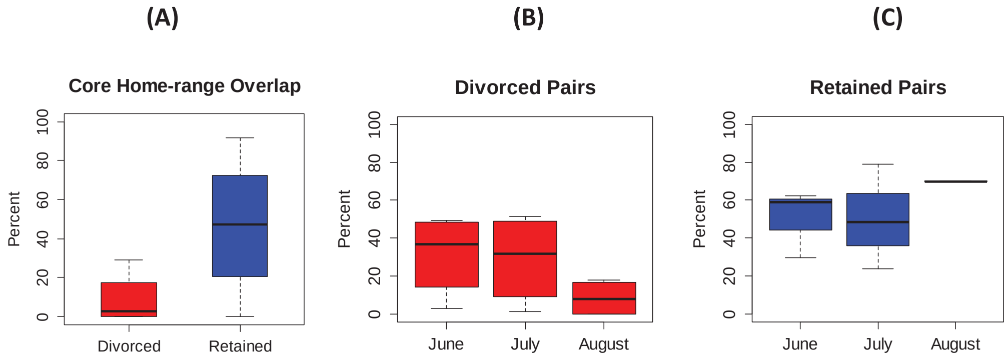

Figure 2. (A) Mean core home-range overlap (50% KDE) of New Zealand falcon pairs that divorced (*N* = 4) and pairs that were retained (*N* = 4) in winter, 2013–2014, and monthly change of mean home-range (95% KDE) overlaps of (B) the pairs that divorced (*N* = 12) and (C) the pairs that were retained (*N* = 9).

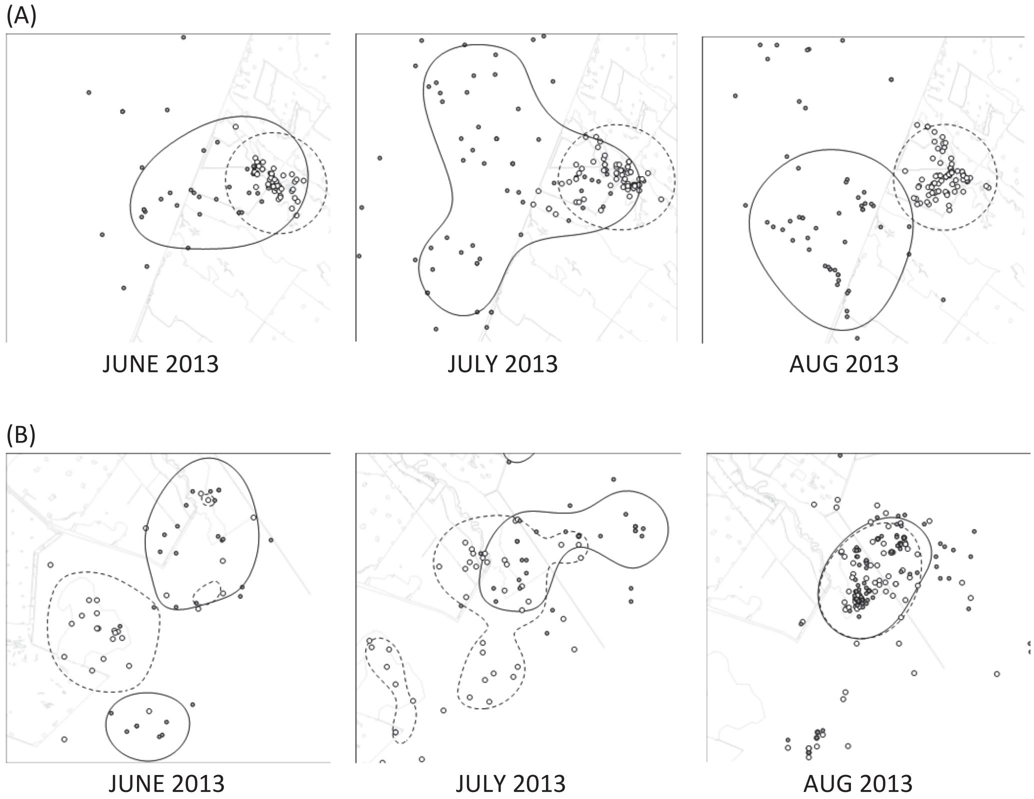

Figure 3. Monthly core home-range (50% KDE) overlaps of (A) a pair of New Zealand falcon, which divorced and (B) a pair, which retained together and reproduced in subsequent years. The solid line indicates core home-range of male and dash line indicates that of the female.

Pair interaction and courtship behaviour

Pair bonds in new pairs appeared to be reinforced behaviourally. New pairs perched within 25 m of each other longer than retained pairs did (though not quite statistically significantly so: $\beta = 0.7 \pm 0.4$, $Z_{34} = 1.9$, $P = 0.056$). Retained pairs perched within 300 m of each other longer than new pairs ($\beta = 1.2 \pm 0.04$, $Z_{34} = 28.4$, $P = < 0.0001$; Fig. 4). Males in new pairs followed females more frequently than males in retained pairs ($\beta = 1.2 \pm 0.4$, $Z_{34} = 3.0$, $P = 0.0003$), but there was no variation in females following males between retained and new pairs (β = 0.3 ± 0.4, Z_{34} = 0.7, P = 0.471). New pairs exhibited Play-fly more frequently than retained pairs (β = 3.3 ± 0.6, Z_{34} = 5.5, $P < 0.0001$), while retained pairs hunted cooperatively more frequently than new pairs (β = 1.8 ± 0.8, Z_{34} = 2.3, P = 0.020).

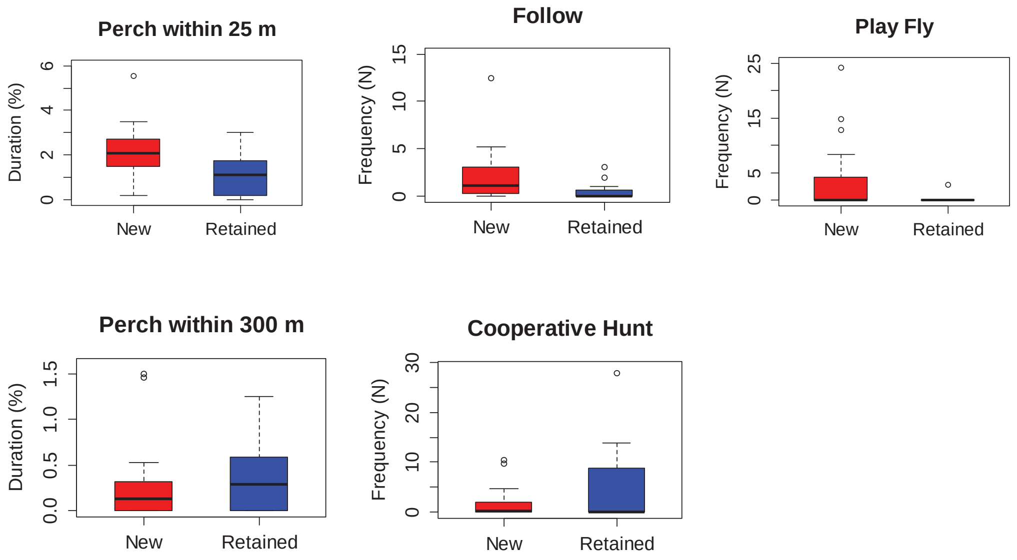

Figure 4. Interactions between males and females in new and retained pairs. All behaviours were statistically significant except perch within 25 m.

The first date on which we recorded courtship behaviour by a male in a new pair was 8 May, more than 3 months earlier than we first recorded male courtship in a retained pair (23 August). There was a greater frequency of courtship display by males in new pairs than in retained pairs, in particular Flittering-flight (β = 1.5 ± 0.7, Z_{34} =2.15, P = 0.032), Flapping (β= 1.5 ± 0.7, Z_{34} =2.15, P = 0.032), and Fly-display (β = 1.1 ± 0.2, Z_{34} = 4.7, $P < 0.0001$; Fig. 5). Furthermore, a greater frequency of Food-passing (β = 1.7± 0.4, Z_{34} = 4.0, $P < 0.0001$), Soft-whining (β = 1.4 ± 0.3, Z_{34} = 4.3, $P < 0.0001$) and Copulation

($\beta = 1.7 \pm 0.7$, $Z_{34} = 2.5$, $P = 0.013$) were also observed in the new pairs than retained pairs (Fig. 6).

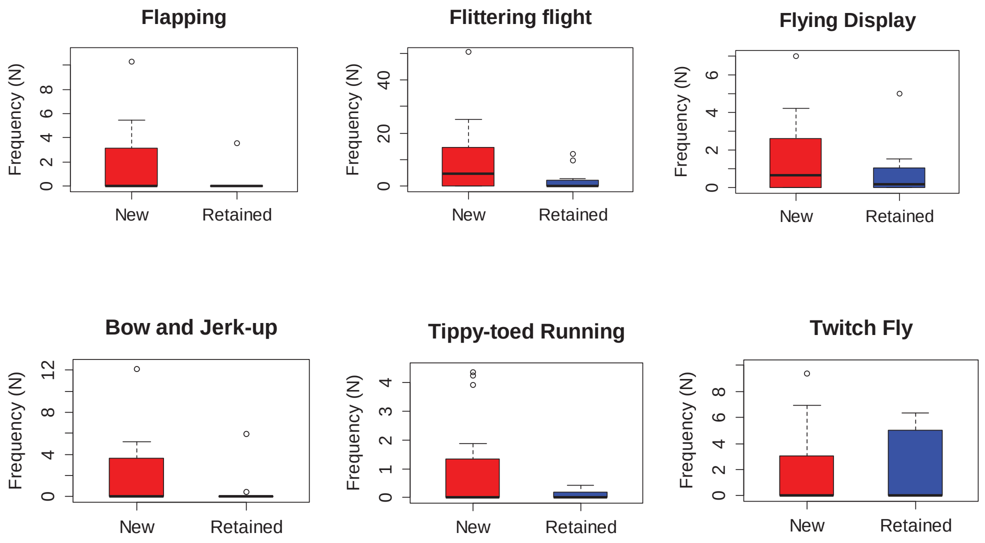

Figure 5 Frequency (N) of mate-display behaviours in new and retained pairs. All behaviours were performed by males. The top three behaviours had statistically significant differences.

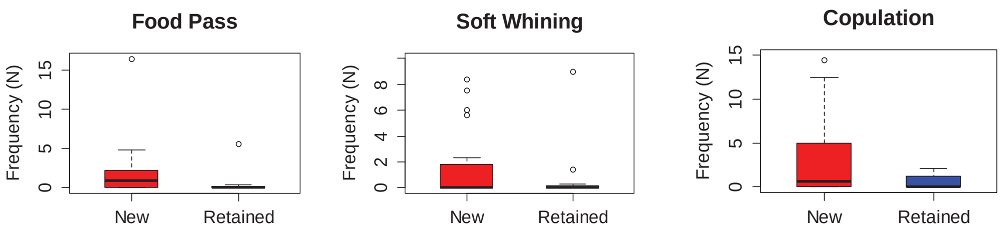

Figure 6. Frequency (N) of courtship and copulation behaviours compared between new and retained pairs. All displayed behaviours had statistically significant variations between the pair statuses. Food passes were made by males and soft whining and scrape check by females.

Discussion

New Zealand falcons living in the dynamic habitats created by on-going forest operations at Kaingaroa forest frequently divorced and changed their breeding sites. Among radio-tagged falcons (2012–14), the divorce rate was 40% and in all but one case this involved the females leaving their breeding territories and moving to other areas. The long-term banding data also indicate that females had lower site fidelity and moved slightly further than males between years. Females of other raptors such as merlins (Warkentin et al., 1991) and peregrine falcons (*F. peregrinus*; Court, Bradley, Gates, Boag, 1989) also exhibited greater breeding dispersal than males.

Fidelity in relation to nest site quality

Site fidelity was not significantly related to mate fidelity in either sex, though overall mate fidelity was higher than site fidelity (Table 2). This is likely a consequence of the ephemeral nature of the breeding habitat in the harvested forest. Unlike for raptors breeding in sites that scarcely change from year to year or even decades or centuries (e.g. large trees, rock overhangs; Burnham, Burnham, & Newton, 2009), nest site suitability for New Zealand falcons changes predictably with time. Young stands (up to 3 years old since harvest) contain several features that falcon pairs require (or favour) for breeding – nesting elements, prey availability, the height of pine-trees, and the presence of emergent trees in the vicinity. Selection of clear-cut stands may be related to the high abundance of debris left after harvesting and windrowing events (e.g., branches, underbrush, and upturned root clumps) because the debris creates various pockets for nest sites (Chapter 2). Moreover, clear-cut to 2-year-old pine stands offer high prey availability as the stands attract avian insectivores, early successional passerine birds and ground foraging seed eaters (Chapter 2). Those habitat features disappear within three years as grass grows over potential nesting pockets, and branches and underbrush undergo decomposition (CH pers. obs). The stand quality may decline further when the height of trees reaches 1 m or higher, usually around three years after planting. Trees over 1 m apparently interrupt a falcon’s nest defence, such as room to dive-bomb. Falcons may target intruders better in an open space where they can dive-bomb with full force (CH pers. obs.). The presence of mature tree stands near a potential nest site may be the most influential component for nest site selection of falcons because the tall trees provide a vantage point for guarding nests during the day and providing a roost at night (Chapter 2). Our records showed that over 62% of nests (N = 177) were found within 100 m of the nearest mature stand, and over 84% were located within 200 m of mature stands. Typically, if mature trees were removed from one nesting season to the next, most pairs shifted their nest locations towards the remaining mature trees within their breeding territories, indicating that complete removal of mature trees could induce desertion of a site and/or a mate. Consequently, changes in habitat suitability may promote divorce in less than or at 3-year-intervals. The significance of forest structural diversity and remaining mature forest around existing nests (at least 2 ha) for goshawks (*Accipiter gentilis*), honey buzzard (*Pernis apivorus*), and common buzzard (*Buteo buteo*) in timber forests were also reported as influencing the probability of nest reuse in successive years (Lohmus, 2005; Saga & Selås, 2012).

The analysis of band recovery data showed no sex variation in site fidelity, though results of the radio-tracking analysis revealed that males had greater site fidelity (93%) than females had (67%). This discrepancy is because the radio-tracking data represent the site fidelity of falcons over a period of less than three years, while the analysis of the band recovery data covers longer periods. Because nest site quality deteriorates within three years, falcons must move to new sites regardless of their sex. Male falcons, however, were more likely than females to remain in their breeding territories as long as the nest-site quality remained suitable.

We predicted that pairs were likely to breed together continuously in the same site when their previous nest was successful (hypothesis 1, habitat-mediated), and when their breeding history enabled behavioural coordination, resulting in retained pairs breeding earlier in the season, which led to breeding success (hypothesis 3, mate familiarity, Boal 2001; Rowley 1983). However, our results showed that reproductive success did not influence their mating pattern, or pair status did not correlate with nesting date. Our finding was somewhat compatible to a study of golden eagles (*Aquila chrysaetos*) that mate changes led to nest switching, which was independent of reproductive success (Kochert & Steenhof, 2012). Evidence from other studies suggests that these mechanisms can apply to similar species. A study of Cooper's hawks (*A. cooperii*) in Arizona supported the mate familiarity hypothesis, showing that pairs with both mate and site fidelity bred earlier in the season and produced larger broods and more fledglings than newly formed pairs that contained at least one sub-adult hawk (Boal, 2001). Another study of two forest-dwelling falcons, the barred forest-falcon (*Micrastur ruficollis*) and the collared forest-falcon (*M. seitorquatus*) in Guatemala, found 100% mate fidelity and a higher reproductive success in pairs that reused the same nest locations for a few years than in pairs that changed nest locations (Thorstrom et al., 2001).

Our observations of marked males indicated that they remained in the same breeding territories as long as the site quality was suitable. In contrast, females varied in their behaviour (CH, unpub. data). Some remained in their breeding territories, interacted with their original partners throughout the non-breeding season, and bred together in the subsequent breeding season. Others explored neighbouring hunting grounds, ranging from ca. 1–6 km away from their breeding territories soon after their fledglings became independent or dispersed from their natal areas (often between February and May, personal observation). These hunting grounds were newly created by clear-cutting and often occupied by other males (either marked or unmarked). These new clear-cut fields were evidently occupied by falcons soon after they were created. Divorce occurred when a male remained in his previous breeding territories but the female moved location and interacted with different males. Pair-formation began when a female and a male started to use a new hunting ground. This behavioural pattern, which was independent of previous breeding success, supported the prediction of the Hypothesis 5, musical chairs, which the sequence of arrival in a habitat affected subsequent mate choice. This divorce pattern appeared to occur in the Kaingaroa falcons because of the dynamic nature of the habitat in which new hunting and breeding grounds are constantly created by clear-cutting and disappearing through forest regrowth. Future studies could test whether other factors affect females' degree of site fidelity, such as age (Darley, Scott, & Taylor, 1977; Lifjeld & Slagsvold, 1988, Doherty et al., 2002), temperament (Harrison et al., 2015) or male fitness (Lifjeld & Slagsvold, 1988).

Male's mate-guarding strategy and nesting dates

We found that highly vigilant males nested earlier in the season than less vigilant males, but we found no such difference in boldness. Vigilant males pursued females and engaged in courtship displays, which appeared to attract the female's attention. They likely constrained a female's ability to leave the territory and interact with other males (Birkhead, 1987; Wagner, Shug, & Morton, 1996). Moreover, highly vigilant males may secure a better quality territory quicker than less vigilant males (Both et al., 2005). Consequently, they appeared to be proficient at obtaining and retaining a female, which is highly advantageous in a population with a high rate of female EPC and a male-biased sex ratio.

Vigilant males may have been able to displace resident males. For example, an unmarked male appeared in a breeding territory of a pair and interacted with the resident female to a greater extent than her original partner interacted with her. The extra-pair male eventually evicted the resident male and nested with the female in the successive breeding season within 40 m of her previous nest location. Mate replacement was independent of previous breeding success. This observation supports the forced divorce hypothesis (hypothesis 4). It appeared that the extra-pair male performed mate guarding more effectively than the original partner.

Extra pair interaction, food availability, and habitat alteration

There were no extra-pair females recorded with males, and eight males (seven radio-tagged and one banded) remained unaccompanied for successive years after their partners divorced or died. Adult sex ratio plays an essential role in social behaviours and mating systems of birds, and an unbalanced sex ratio likely influences pair bonds (Kokko & Jennions, 2008; McNamara, Szekely, Webb, & Houston, 2000). We did not systematically investigate the sex ratio of the Kaingaroa falcon population, but our observations suggest that the population was male-biased during the main intensive study period (2012–14). If so, the cost of divorce may be detrimental to male falcons. Hence, males maintain gain a greater benefit to assure reproductive opportunity by retaining partners. By exhibiting site fidelity, a male could increase the chance the female remains, and that would lead to a slight correlation between mate fidelity and site fidelity by females.

Females, on the other hand, had extensive extra-pair interactions throughout the non-breeding season; this was especially so for divorced females, which interacted with these males throughout the non-breeding season regardless of nest success with their original males. A high frequency of extra-pair paternity is expected when the risks of losing a male are high (Petrie & Kempenaers, 1998). In the managed timber forest, falcons live in an ephemeral habitat where divorce likely occurs frequently. Therefore, extra-pair interactions (including EPC) in this study population are likely to be a pre-existing conditional strategy for reducing the costs of male loss. A surplus of males may also have allowed females interact with multiple of males. An adequate availability of food in the forest may have promoted a high rate of extra-pair paternity (Rosenfield et al., 2015) because females had access to additional feeding sites of extra-pair males (Gray, 1997) or could get extra food through courtship feeding by extra-pair males (Rosenfield et al., 2015). Courtship feeding followed by copulation is typically observed during the pre-nesting period in raptors (Fox, 1977; Ratcliffe, 2010; Rosenfield, et al., 2015) and feeding will increase the females' energy intake, enhancing her breeding success (Newton, 1979). Courtship feeding may serve other purposes. In an urban environment where food availability was relatively high, the occurrence of courtship feeding throughout the non-breeding season was reported as pair-bonding in Cooper's hawks (Boggie, et al., 2015).

In our study population, new pairs repeatedly performed the copulation display throughout the non-breeding season, indicating that courtship feeding was employed for pair-formation in winter. It might also be used as a form of mate guarding by the male, to acquire a female's attention and prevent her from interacting with extra-pair males (Wagner, et al., 1996).

Although most of the avian mating hypotheses predict behavioural patterns between breeding seasons, our close observations of falcon mating patterns within a breeding season may support the better option hypothesis (hypothesis 2). We recorded short-term occurrences of EPCs by two radio-tracked females after their initial breeding failure. Neither had shown any association with an extra-pair male before the failure. Extra-pair copulations could mean offspring acquire better genes (Houtman, 1992; Kempenaers et al., 1992) or increased immune-competence (Johnsen, Andersen, Sunding, & Lifjeld, 2000). These females re-nested with their original partners in their breeding territories within the same breeding season. In contrast, three female falcons replaced their partners with an extra-pair male after the failure of their first breeding attempt, supporting the better option hypothesis. Each of these females likely had established a pair bond with an extra-pair male during the non-breeding season. These observations indicate the likely benefit of pair-bonding (irrespective of male status, original or extra-pair male) established prior to nesting season. Falcons perhaps respond to the constant changes in habitat as an environmental stimulus and adjust their mating patterns rapidly to maximise their reproductive output (Both et al., 2005).

Causes of nest failure were not determined in our study. Nests may be disturbed inadvertently by forestry operations such as windrowing and timber harvesting within the vicinity of nests and such disturbances may be frequent. Nevertheless, identifying breeding failure caused by forest operations is difficult because the failure occurs typically in the early incubation stage (within ca. 2–3 weeks), most likely causing nest abandonment by females (CH. unpublished data), therefore, these nests were often undetected (Newton, 1979). Nest failure by predation or other causes may be easier to detect as it has a longer time span for detection (ca. 60 days), and some noticeable remnants of nesting activities such as faecal build-up, shed down, and regurgitated pellets may be evident (Steenhof & Newton, 2007; CH. pers. obs.). Therefore determining the relationship between divorce and reproductive success of falcons in a managed forest would require intensive monitoring of pair interactions before and after nesting attempts. Further thorough monitoring is required to understand the falcons' divorce mechanisms, nest failures, and their mating patterns in relation to age or parent birds provisioning rates contributing to offspring.

Pair home-range overlap

Clear segregation of winter core home-range use among divorced pairs confirmed that the degree of pair interaction during the study period was minimal. Yet, their degree of overall home-range (95% KDE) overlap declined gradually, suggesting that the transition may be a slow process, perhaps while searching and assessing compatible breeding sites and partners. Retained pairs maintained a greater home-range overlap throughout the non-breeding season. By August, both new and retained pairs appeared to settle into breeding sites with their partners for the up-coming breeding season.

Courtship behaviour

We found compelling dissimilarities between retained pairs and new pairs in the degree of interaction and courtship display. The first courtship display by a new pair was seen in early May (autumn) whereas retained pairs courted in late August (early spring). Frequent courtship displays were observed among newly formed pairs in mid-winter but not in retained pairs. Thus, courtship displays were employed for pair-formation during the non-breeding season rather than for pair-bonding (the process of maintaining a social bond; McKinney, 1992).

Perching within 300 m of each other and occasional cooperative hunting were the major interactions performed by retained pairs. In contrast, new pairs demonstrated much closer interactions. For instance, a male in a new pair frequently followed a female within his territory and stayed within 25 m of her. The pairs also exhibited play-fly, frequently followed by chittering vocalisations, usually expressed for excitement (Cade, 1955). This type of flight was commonly seen among juvenile siblings as well (CH. pers. obs.). Cade (1955) reported comparable winter mating behaviour of American kestrels (*F. sparverius)*, including courtship feeding, cooperative hunting, mutual preening and billing, chittering vocalisation, and copulation. Temporal variation between pairs in the timing of the start of courtship was also documented, suggesting that the status (new or retained) of these pairs might have been different. Agonistic territorial behaviours during the non-breeding season were also reported in these kestrels. Kaingaroa male falcons, in lieu of aggressive interaction, used courtship display for intra-sexual competition or mate-guarding purposes. We observed mid-winter courtship displays by two males to their original females when their females had extra-pair males within or near the original males' breeding territories. These males appeared to compete with extra-pair males with courtship displays, possibly attempting to capture the female's attention thus preventing her from seeking extra-pair males or interacting with them (Birkhead & Møller, 1992, Wagner, et al., 1996).

The absence of aggression was ubiquitous among falcons throughout the seasons (CH. unpublished data). In an extreme case, we witnessed a male copulating with a radio-tagged female in front of an extra-pair male perched on a stick in an open field ca. 300 m away. During the following tracking period, these two males perched within 50 m of each other above the incubating female. Sodhi (1991) documented that male merlins (*F. columbarius*) often tolerated intruders during the non-fertile period but did not tolerate them during their females' fertile period. The nonviolent social system and relaxed territoriality may be driven by the fitness benefits obtained by tolerating sharing resources (e.g. food or females) when resources are not limited or when there is no risk of paternity interference (i.e. outside a female's fertile period), as opposed to risking the costs of resource defence or seeking another resource (Johnson, Kays, Blackwell, & Macdonald, 2002; Sodhi 1991).

The only agonistic behaviour observed was by a radio-tagged female who occasionally chased and dive-bombed an unmarked male near her breeding territory (CH.

unpublished data). The behaviour continued throughout our 8-hour continuous tracking periods for two weeks in late April 2012. Her radio-tagged mate remained in the vicinity but did not intervene. From week three and beyond, the female appeared to accept the male (we assumed the male was the same individual) as we recorded him courtship displaying and both individuals calmly perched in close proximity. Perhaps, such a behavioural transition occurs in every new pair in the initial process of pair-formation during the early non-breeding season.

Conclusions

Changes to forest structure caused by timber harvesting influenced the mating patterns of the Kaingaroa falcon population. Falcons assess nest site suitability and in deciding to move, a divorce may eventuate. We examined patterns of divorce, site-fidelity, and interactions between pairs and extra-pair males, in relation to five hypotheses that could explain why divorce occurs. Our observations mainly support two hypotheses, namely the musical chair hypothesis and the forced divorce hypothesis because mate fidelity of falcons was not influenced by their reproductive outcomes.

Females exhibited a high rate of extra-pair male interactions. A surplus of males might also have allowed females to have a selection of males, and additionally help to reduce the cost of male loss. Males, in contrast, likely experienced a lack of females. Therefore, the mate-guarding strategy may be the most effective male mating strategy in the Kaingaroa falcon population. Vigilant males were effective at mate guarding. Males also maintained their breeding sites as long as the nesting quality remained suitable.

That way, they secured their breeding opportunities by providing breeding territories to females. We suggest that a future study includes investigating whether this apparent sex bias is real. If so, for the purpose of conservation management, it is important to understand what drives a male bias, and if not, why EPC occurs in females exclusively. In place of aggression, courtship displays were also used for intra-sexual competition by males over females and may also be used for mate-guarding. Sufficient prey availability in the study area might have promoted relatively stable reproductive outcomes, and with that foundation, falcons were able to adjust mating strategies to the rapid changes of habitat suitability.

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CHAPTER 6

Synthesis

Psyco 2014/2015

The first time I exposed myself to receive fearless ‘*kamikaze*’ dive-bombs from New Zealand falcon pairs, I noticed that some pairs worked synchronously as a team while others did not. This raised simple questions, ‘Why are these two individuals paired up? What happens to them during the period when they are not nesting?’

The following broad research aims were established for my study based on these questions: (1) investigate the non-breeding seasonal ecology of New Zealand falcons in Kaingaroa forest, and (2) understand how landscape modifications shape the mating system of Kaingaroa falcons.

The first two research chapters (Chapter 2 and 3) set out to document the constraints (ecological and landscape) that Kaingaroa falcons face in relation to changes in forest structure resulting from on-going forestry operations. In Chapter 4, I documented mortality factors and survival rates of Kaingaroa falcons, and I explored the impact of 1080 operations on these factors. In the final chapter (Chapter 5), I investigated how changes in forest structure influenced breeding pair dynamics. In this chapter, I illustrated how ecological and landscape constraints shape the mating system of Kaingaroa falcons, by presenting specific observations of breeding pairs as examples. Lastly, I then outlined recommendations for forestry management practices and address possible directions for future research to further our understanding of this threatened species living in a modified landscape.

Ecological constraints

Ecological constraints are defined here as the limitation of resources that affects the fitness and productivity of falcons, such as the abundance and distribution of prey birds, shelter and nest site quality. Throughout the year, plantation forests provide hunting and nesting grounds for Kaingaroa falcons by clear-cutting (Seaton et al. 2009, Chapter 2), however, these management practices also mean that the habitat use of these of falcons is constrained by the number, distribution, and sizes of the open patches (Chapter 3). I found that exotic passerine birds were distributed throughout different habitats within the forest during the non-breeding season, while native birds were found more commonly in the edge-habitat (i.e., open-patch bordered to mature-pine stands) than interiors of classified stands (Chapter 2). Neither sizes (standard: ≤ 2 km^2 and large: > 2 and ≤ 4 km^2) nor harvest timing (summer or winter) influenced prey abundance. Based on these findings, I concluded that the dynamic changes of forest structure created by clear-cutting and its effect on prey accessibility drive spatial patterns of Kaingaroa falcons, as opposed to these being driven by overall prey abundance and distribution.

Degradation of habitat quality by growth of trees

We found that neither mate nor site fidelity of Kaingaroa falcons was affected by reproductive success but rather were restricted by degradation of nesting habitat quality due to the growth of trees and grass (Chapter 5). Pine-stands up to three years old contain several features that falcons require (or favour) for breeding – nesting elements, greater prey accessibility, and a suitable tree height for nest defence. These nesting features disappear within three years of a clear-cut event as grass grows over access to potential nesting pockets, branches and underbrush decompose, and the height of trees becomes taller than 1 metre (CH. pers. obs). Once this occurs, pairs must likely face leaving their breeding territory to find suitable breeding habitat. Divorce, therefore, occurs when the individuals that make up a pair do not move to the same site.

Kaingaroa Forest – a view from forest compartment 802

Landscape constraints

Kaingaroa falcons used the edge-habitat the most frequently of the 11 classified habitats in the forest (Chapter 2). The mature portion of the edge-habitat served important roles for falcons in winter such as providing shelter from severe winter weather, vantage points for territory defence, hunting ledges overlooking open-patchs, and basking spots (Chapter 2). This habitat was also selectively used by the same falcon population during the breeding season (Seaton et al. 2013). The mature trees of the edge-habitat provide a vantage point for guarding nests during the day and providing roosting site at night (CH pers. obs.). The preference for the edge-habitat is not limited to Kaingaroa falcons but it appears to be a characteristic of New Zealand falcons in other regions and other raptor species. Fox (1977) suggested that the density of New Zealand falcons and their prey found in the South Island can be greater when the native forest was partially felled, creating margins and clearings. Anderson (2001) examined habitat use of 18 diurnal raptors in a rain forest ecosystem in Honduras in relation to three degrees of habitat heterogeneities and found that density and diversity of 16 out of the 18 raptor species occurred greatest in survey plots with the highest landscape heterogeneity (Genera of the 16 species: *Buteo, Buteogallus, Cathartes, Chondroheirax, Coragyps, Elanoides, Falco, Herpetotheres, Ictinia, Leptodon, Micrastur, Sarcoramphus, Spizaetus*, see Table 1 in Anderson 2001). Several other diurnal raptors have also been reported as preferring habitat with high landscape heterogeneity in other regions: roadside hawk (*Buteogallus anthracinus*), Plumbeous kite (*Ictinia plumbea*), grey hawk (*Asturina nitida*), bat falcon (*Falco rufigularis*), black vulture (*Coragyps atratus*), and goshawk (Kenward 1996, Jullien and Thiollay 1996, Anderson 2001).

Degradation of habitat quality by removal of mature tree stands

Landscape constraints are defined here as the degradation of habitat by removal of the Kaingaroa falcon's preferred habitat (the edge-habitat). Although falcons preferentially used the edge-habitat, I found that falcons did not use all available edge-habitats equally (Chapter 3) but rather that they were inclined to use those segments receiving the best direct solar radiation for sun basking (typically northerly or north-east aspects) or located on the top of the hill (CH. unpublished data). Home ranges are determined by the availability of those favoured segments of the edge-habitat. During the breeding season, falcons preferred to nest near mature stands: over 62% of nests were found within 100 m of the nearest mature stand, and over 84% were located within 200 m of mature stands (Chapter 5). The removal of mature stands from the home-range of a falcon pair decreased the quality of a nest site (Chapter 5), and likely consequently affect pair-bonding (the process of maintaining a social bond). The majority of pairs I observed shifted their nest sites towards the remaining mature trees within their breeding territories after a harvest event. Complete removal of mature trees within the breeding territory could induce desertion of the territory and/or partner altogether.

An excellent example of this process was seen in a radio-tracked female, 'Guardian', and her partner, 'Feisty'. I radio-tracked Guardian for three consecutive winters from 2012–2014, and her partner Feisty for two consecutive winters from 2012–2013. I also monitored the breeding behaviour of this pair for four breeding seasons (2011/12–2014/2015) and recorded nest locations for five consecutive breeding seasons (2011/2012–2015/2016). All of their nesting attempts were successful (produced 2–3 fledglings each breeding season). The pair showed strong mate fidelity and site fidelity to one particular area from the 2011/2012 to 2014/2015 breeding seasons (Fig. 1). The pair nested on the ridge of a moderate hill by the mature stand. The mature stand on the north side of the territory was located in a shaded and low elevation area, which evidently made it unappealing to the pair to nest near. During the 2014 winter, an unmarked male appeared in a newly created open patch near Guardian's home range and interacted with her throughout the 2014 winter to the pre-breeding season, however, she chose to nest again with her previous partner, Feisty, in the following breeding season (2014/2015: Fig. 1D). After the last remaining mature stand located on the hill was harvested over the 2015 winter (see Fig. 1E), Guardian paired and nested with an unmarked male in the following breeding season (2015/2016). I suspect that this male was the same individual seen the previous winter. The area used by the new pair composed of Guardian and the unbanded male was created by timber harvesting during the 2015 winter. The new nest was also located on the upper portion of a moderate hill with a well-lit mature tree stand situated nearby, and thus somewhat resembled the previous nest site Guardian used with Feisty. I did not confirm the survival of Feisty nor radio track the pair during the 2015 winter. It is possible that Guardian might have lost Feisty over the winter season. However, considering all the evidence (i.e., extra-pair male event, an enlargement of the open patch to more than 3 km^2, a reduction of habitat heterogeneity, and availability of new territory), it is likely that the nest site degradation caused by the removal of all mature stands in the previous territory resulted in the desertion of the original breeding site and her four-year breeding partner, Feisty.

The most used habitat by Kaingaroa falcons was the edge-habitat. Using the Resource Dispersion Hypothesis as a tool, I tested whether availability of the edge-habitat was the primary determinant of home-range size, and found that dispersion patterns of the edge-habitat influenced their home-range sizes (Chapter 3). When smaller open-patches (< 3 km^2 each) are distributed closely (< 3.0 km apart) among mature stands (which creates plenty of the edge-habitat), falcons maintain smaller home-range sizes. Also when these conditions are met, more suitable breeding sites may be available. When an open patch was enlarged beyond 3 km^2, and several of these larger open patches were dispersed across a mixture of intermediate-aged-pine stands and mature-pine stands, there was less of the edge-habitat in a given area. These conditions subsequently required falcons to occupy larger home-ranges. This was shown in my home range analyses. Forest falcons that used Kaingaroa forest exclusively had smaller mean home-range sizes than farmland falcons that used farmland for more than 10% of the tracking duration (26 km^2 and 45 km^2 respectively, Chapter 2). The habitat of the farmland falcons enclosed larger open patches than that of the forest falcons. In contrast, Fox (1978) noted that New Zealand falcons in the South Island of New Zealand occupied smaller ranges in open country areas and larger ranges in native forests. Presumably, these native forests did not offer much habitat heterogeneity to falcons and/or sufficient prey numbers.

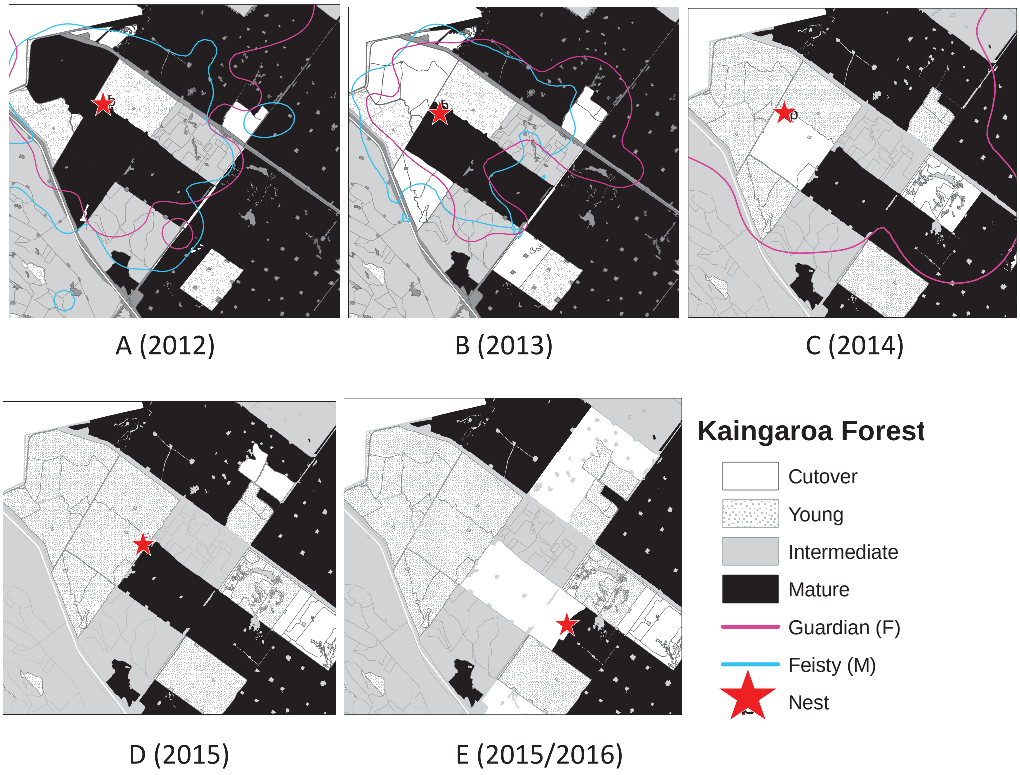
A (2012)
B (2013)
C (2014)
D (2015)
E (2015/2016)

Figure 1. Change of forest structures for five sequential years from 2012–2016. Nest locations of the previous breeding season and winter home ranges of a pair (Guardian (F) and Feisty (M)) are overlaid on the maps of the winter season (2012–2015) and the 2015/2016 breeding season. Guardian (pink line) was radio-tracked for the 2012–2014 winters and Feisty (blue line) for the 2012–2013 winters. They shifted nest locations corresponding with the removal of mature stands within their breeding territory. After the last mature stand was removed from their breeding territory, Guardian nested with a different male who occupied the south-east of Feisty's breeding territory (2015/2016 map). No radio-tracking was conducted after the 2014 winter.

Reproductive consequences of mating strategies in the ephemeral habitat

Balbal (behind) and Juvjuv 2014/2015

Non-breeding season pair interactions

I found that all divorces except one were initiated by females leaving the breeding territories. Since males are characteristically more territorial among the Kaingaroa falcons, it inevitably results in it being females that leave their breeding sites. Over the four breeding seasons during which this study occurred (2011/12–2014/15), I recorded locations of tagged falcons and survival data of fledglings during the post-fledgling period, and although anecdotal, I observed food delivery was only made by male parents, while tagged female parents were usually located ca. 1.0–5.5 km away from their nest sites (Chapter 5). Similar observations have been reported in studies of the Eurasian sparrowhawk (*Accipiter nisus*, Eldegard et al. 2003), and Tengmalm's owl (*Aegolius funereus*, Eldegard & Sonerud 2012). In these studies, researchers documented that males delivered food to fledglings at a higher rate than females throughout the post-fledging period. Female falcons explored neighbouring hunting grounds, and when they encountered with different males. Pair formation may begin immediately after a female and male meet, although some did not interact until the pre-breeding season (i.e., August) despite sharing divorced their original partners. Dhondt and Adriaensen (1994) noted that divorce rate increases when female familiarise themselves with a new range because the cost of searching the new range and the benefits of remaining in previous territories become equivalent.

Food pass: Feisty brought food to his offspring

Female chick chases a food drop

Taxonomic constraints on mating strategies

In mammals, the distribution of resources determines female spatial patterns, whereas the distribution of females regulates the spatial organization of males (Macdonald 1983; Clutton-Brock 1989). This is because males do not assist in the rearing of young in most mammalian species, however, pregnancy and lactation impose greater energetic demands on females (Gittleman and Thompson 1988). As a result, the availability of resources is directly tied to a female's reproductive success (Macdonald

1983; Clutton-Brock 1989). Males, on the other hand, can potentially inseminate many partners, hence an increased accessibility to females favours their reproductive success (Macdonald 1983, Clutton-Brock 1989, Sandell 1989).

In contrast to mammals, female-biased dispersal is common in resident birds (Clark et al. 1977, Greenwood 2012). The male defends a resource to attract a female. It is the male's ability to secure and hold a resource rather than their capacity to defend the female that females use as a means of assessing the quality of a male (Greenwood 1980). This has identified in the Kaingaroa falcon population. The majority of tagged male falcons exhibited strong site fidelity since the successful retention of territory increased breeding opportunity by attracting and retaining a female through the provision of food through courtship feeding (Chapter 5). Therefore, the availability of food is crucial to the breeding success of male falcons. As a result, habitat use of Kaingaroa male falcons is mostly influenced by changes in forest structure, which previously asserted, drive prey accessibility. A male would most likely breed with the same female as long as the female remained in his territory (Chapter 5). In contrast, habitat use of female Kaingaroa falcons appeared to be driven by the presence of territory holding male whose range provides adequate prey, food by courtship feeding, and suitable breeding habitat.

Female strategies

Guardian 2015/2016

Extra-pair males and abundance of food

Some females replaced their partners with the extra-pair males in the sequential breeding season, while females who retained the same partners in the sequential breeding season most likely did not establish a pair-bond with extra-pair males in the previous non-breeding season (Chapter 5). With the nest site being in an ephemeral habitat, nest site quality does not last for long and a pair may face divorce at relatively regular intervals (described above with the ecological and landscape constraints).

Potentially, the surplus of males available to Kaingaroa females allows them to reduce the costs of male loss by establishing pair-bonds through extra-pair male interaction (Chapter 5). Rosenfield et al. (2015) found that in an urban environment, Cooper's hawk (*Accipiter cooperii*) exhibited a high rate of extra-pair young (EPY: nestlings that carry the gene of an extra-pair male). They suggested that, in part, this was explained by the synergetic effects of the association between courtship feeding and copulations in an area with a high density of breeding adults. Sufficient food availability in the area likely allows floater males (young individuals that haven't established their territory) to provide prey to territorial females in exchange for copulation. This condition pertained to Kaingaroa falcons. Throughout the non-breeding season, I observed courtship feeding followed by copulation as a form of pair formation and mate-guarding strategy among Kaingaroa male falcons (Chapter 5).

I observed that a banded floater male (1-2-year-old who has not yet reproduced), named Brown (a male chick of another tagged female, Silence2) interacted with a tagged adult female, Survivor, two weeks after a failed nesting attempt with her partner, Curious. Brown appeared in the nesting territory of the pair and performed courtship display to Survivor. The courtship display by Brown included bow and jerk-up, flapping, flittering flight, tippy-toed running, and food delivery followed by copulation (see the ethogram table 1 in Chapter 5). Nest scrape was also performed by him (a courtship display by the male falcon running its breast through the substrate or nest depression, and pushing out with its legs behind, forming the nest scrape). I suspect that the scrape was originally made by the adult male, Curious, not by Brown because within a week, Survivor had laid eggs in the scrape and the pair (Survivor and Curious) successfully raised two nestlings to fledge in their second nesting attempt within the same breeding season. The adequate prey present in Kaingaroa forest enabled non-territorial males (both fully matured adults and young floater males) to interact with resident females and perform extra-pair copulation (EPC).

Several studies of various raptors documented a high rate of EPC existing in their populations: peregrine falcon (*F. peregrinus*), prairie falcon (*F. mexicanus*), American kestrel (*F. saprverius*), European kestrel (*F. tinnunculus*), goshawk (*Accipiter gentilis*), osprey (*Pandion haliaetus*: Balgooyen 1976, Ratcliffe 1980, Birkhead and Lessells 1988), as well as some mammals (Cohas and Allaine 2009, Reichard 1995). However, the evidence of extra-pair paternity (EPP) is uncommon (e.g. American kestrels, Villarroel et al. 1998; Marlin, *F. columbarius*, Warkentin et al. 1994; Boreal owls, *Aegolius funereus*, Koopmanc et al. 2007). A study of EPP* in the Kaingaroa falcon population is needed to elucidate whether food availability in the area correlates to the rate of EPP as shown in the study of Rosenfield et al. (2015). *The study has been conducted and results are in preparation for a publication.

Male strategies

Bro 2012/2013

Factors influencing mate guarding performance

Some falcons lost their partners from depredation, unknown causes, potentially by 1080 secondary poisoning (Chapter 4), or divorce (Chapter 5). This posed the question of what do widowed or divorced male falcons do after they had lost partners?

(1) *Vigilant behaviour*

I found that vigilant males nested earlier in the breeding season than males with less-vigilant males (Chapter 5). This finding indicates that vigilant males can effectively perform mate-guarding and achieve breeding opportunities. Vigilant males are generally persistent. They pursued females and engaged in courtship displays that likely constrained a female's ability to leave the territory and interact with other males (Birkhead, 1987; Wagner et al. 1996). The analysis of the band recovery data of male falcons also showed that falcons that bred earlier in the season had higher breeding success (Chapter 5). Consequently, the vigilant males appeared to be highly advantageous in a population. Some studies documented that larger or older Cooper's hawks nested earlier and had greater reproductive success than younger and smaller males (Rosenfield and Bielefeldt 1999, Rosenfield et al. 2013).

(2) *Territorial versus non-territorial males*

In addition to the persistent behaviour, a non-territorial male may be in a better position to perform the mate-guarding tactic as he does not confine himself to his territory to protect; therefore, it may foster effective mate-guarding. Here, I present my field observations of territorial and non-territorial males to compare their mate-guarding strategies. A territorial male is defined here is an adult male who defends breeding territory, and a non-territorial male is an adult male whose spatial use is not confined. A floater male is a 1–2-year-old falcon that is yet to breed.

Strategy of territorial males

Tactics of territorial males to attract females begin with displaying twitch-fly (while flying in circles, falcons occasionally twists their body from one side to another quickly like twitching, with short wing-beats). A male usually perform twitch-fly high above over his territory to advertise himself to neighbouring females, probably to attract their attention. This behaviour was seen at the beginning of the breeding season by most tagged males, especially those that lost their partners by death or divorce. This contrasts with males that had retained their partners, generally performing flight display and courtship display. For example, a tagged territorial male, Jerry (unknown age), who lost his partner in the early winter 2013, frequently performed twitch-fly over his territory during the following pre-breeding season. A tagged female, Quiet (a banded six-year-old), bred in the neighbouring open-patch approximately 2 km west of Jerry's territory (another open-patch). Mature tree stands (ca. 4 km^2) separated their breeding territories. In the late 2013/2014 breeding season, a month after Quiet had lost her partner, Andy, through depredation by a feral cat (Chapter 4), she appeared in Jerry's territory and interacted with him. At that time, she was still providing parental care (food delivery) for her two fledglings (female and male). We did not record Jerry entering Quiet's breeding territory throughout the tracking period; therefore, he most likely attracted Quiet by performing twitch-fly.

Twitch-fly was also displayed for the purpose of attracting attention from the other member of a pair. Most often I observed this behaviour by male falcons when a female was leaving a male's territory or when the female interacted with an extra-pair male near the territorial male. It is possible that this behaviour is an attempt to deter females from leaving from their territories or interacting with another male. Some females also display twitch-fly when they moved to different areas but still remained within males' territories. Most cases males followed females, indicating twitch-fly was also used for pair communication.

Strategy of non-territorial males

Although territorial males have the benefits of securing breeding attempts by holding territories, my observation indicated that the non-territorial males take advantage of being unrestricted to one territory, therefore, they could perform mate-guarding effectively. Here, I present examples of two non-territorial males. In June 2013, I recorded that an unmarked male, Sneaky, appeared in a breeding territory of a pair (Lena and Andy) and performed courtship behaviour to the resident female, Lena. Throughout the 2013 winter, Sneaky remained much closer to Lena than her partner, Andy. By the end of July, Sneaky evicted Andy from the territory and nested with Lena within 40 m from her previous nest location. The fate of Andy was devastating. After he was evicted from his territory by Sneaky, Andy met Quiet about 2 km SW of his previous territory and nested with her in the sequential breeding season (2013/2014). In November 2013, he was depredated by a feral cat, likely during nest defence of two 10-day-old chicks (Chapter 4).

A six-year-old non-territorial male, Green (banded), moved into Quiet's breeding territory immediately (< one week) after Andy had died, and performed courtship displays to Quiet. Quiet simultaneously interacted with Jerry in his territory over a block of mature tree stands (described in the above section). I observed that Quiet would receive food independently from both Green and Jerry by courtship feeding and then deliver it to her fledglings (CH. unpublished data). Quiet's fledglings constantly begged for food from Green, yet I did not observe him directly feeding them at any time.

Over the 2014 winter, the mature stands, which were located between the breeding territories of Quiet and Jerry, were entirely harvested. This transformed two small to medium-sized open patches (ca. 2 km^2) into one large open-patch (> 6 km^2). The reduction in habitat heterogeneity resulted in a limiting of the number of falcons using a given area (Chapter 3) and reduced nest site suitability (Chapter 5). Without a barrier, Green gradually moved into Jerry's territory. Quiet also interacted with another male (the 3^{rd} male – unmarked), and all three males interacted with Quiet within Jerry's original territory. Quiet nested with Green in the sequential breeding season (2014/2015). Green apparently performed the mate-guarding tactic effectively by following Quiet around and extensively interacted with her.

It is possible that the lack of spatial restrictions or a combination of the lack of spatial restrictions and a persistent behaviour may enhance the mate-guarding performance by non-territorial males. Further analyses are needed to identify other factors fostering mate-guarding strategies of Kaingaroa male falcons, which include body size, age, and social status (territorial vs non-territorial) of males and temperament of both males and females. A study of EPP in relation to their various social statuses (territorial, non-territorial, and floater) also assist in the understanding of the efficacy of breeding strategies by Kaingaroa male falcons.

(3) *Changes in forest structure*

The example above showed that removal of mature stands from the border of two breeding territories influenced pair-bonding and pair-formation (male and female forming a social bond as a pair by having intensive interactions) by inducing accessibility between neighbouring falcons in the form of a habitat corridor (Taylor et al. 1993). Sometimes removal of mature stands can act in favour of some males (e.g. Green) while in other such as Jerry it can act as a hindrance. Here is another example that changes in forest structure affected pair dynamics: during the 2013 winter, a tagged female, Chatri, interacted with a male, Bal (Fig. 2). Another male, Psyco (radio-tracked), occupied an open patch located in the northwest of Bal's territory over the mature stand. Between the winters of 2013 and 2014, the mature stand was harvested. Chatri gradually increased spatial use from Bal's territory to Psyco's territory, and she interacted with both males concurrently throughout the 2014 non-breeding season. In the next breeding season (2014/2015), Psyco successfully nested with Chatri on her third breeding attempt (the first two nests were interrupted by forestry operations, laying one egg in each nest before deserting). I confirmed that her second breeding attempt was with Bal, but could not confirm the male of the first nesting attempt as she interacted with both males intensively in the same breeding site (see Chapter 5). Indeed, falcons are capable of relocating themselves over blocks of mature stands without the removal of mature stands. However, these observations suggest that removal of mature stands induce social interaction and influence dynamics of pair-formation and pair-bonding.

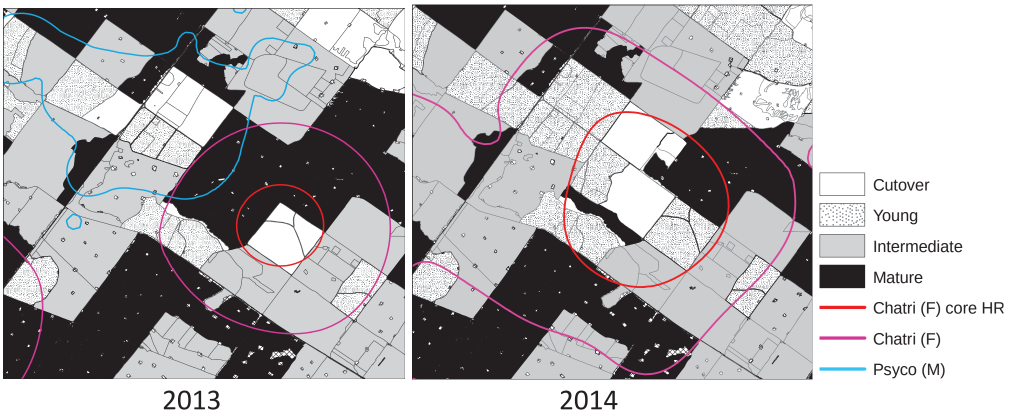

Figure 2. Change of home range use by a female (Chatri) over two winters in 2013 and 2014. Chatri interacted with an unmarked male (Bal) in her core home-range (50% KDE, red circle) in the 2013 winter. After the blocks of mature tree stands located in-between Chatri's core home range (red circle) and a male's (Psyco) home-range (95% KDE) were cleared in the 2014 fall, Chatri expanded her habitat use toward Psyco's range in the 2014 winter. Chatri was radio-tracked in 2013-3014 and Psyco was tracked in the 2013 winter.

I confirmed that use of VHF telemetry allowed me to understand the winter habitat use of adult New Zealand falcons in a plantation forest and it provided far more detailed and accurate data than those obtained by satellite technology (Thomas et al. 2010). This is because VHF telemetry often provided us with the opportunity to confirm exact habitat use by sight. Tracking falcons at local scales also allowed me to observe details of falcon behaviour and inter- and intra-specific interactions. However, to facilitate understanding of juvenile falcons' behaviour, dispersal, survival, and emigration rates, use of satellite telemetry is recommended.

Winter pair interactions in raptors

Unbanded and Quiet 2014

I found that core home ranges of pairs that divorced (divorced pairs) did not overlap, indicating they had minimal interaction during the non-breeding season. In contrast, pairs that retained partners in the sequential breeding season (retained pairs) maintained a greater home-range overlap throughout the non-breeding season (Chapter 5). I also found compelling dissimilarities between retained pairs and newly formed pairs (new pairs) in the degree of interaction and courtship display. Males in new pairs exhibited a greater frequency of courtship display, which includes food pass and copulation throughout the non-breeding season. Newly formed pairs stayed closer for a longer duration per observation period than retained pairs did. In contrast, males in retained pairs did not start performing courtship display until the pre-breeding season. Retained pairs remained within line-of-site of each other and occasionally hunted cooperatively.

Not many studies have followed winter pair interactions to the extent of this study. In general, resident raptors would be expected to have greater pair interaction during the winter period than migratory raptors because migratory pairs are unlikely to travel and winter together (Meyburg & Meyburg 2009), and resident populations likely have sufficient prey throughout the seasons to allow males (territorial and young floaters) to perform courtship feeding to females (Rosenfield et al. 2015). In peregrine falcons (*F. peregrines*), the pattern of pair interaction outside the breeding season may be highly variable (Radcliffe 2010). Lish & Burge (1995) documented pairs of red-tailed hawks (*Buteo jamaicensis*) are frequently observed in the same territories in sequential winters. Cade (1955) documented that American kestrels (*F. sparverius*) displayed courtship behaviour outside the breeding period in a similar fashion to this study (see Chapter 5).

New Zealand forestry and New Zealand falcons

Over the past 7 centuries, more than 60% of the forest in New Zealand has been cut down and converted largely into pasture for grazing livestock (Ewers et al. 2006). This forest clearance has resulted in up to 50% of New Zealand's avifauna being extirpated (Holdaway 1989). Pine plantations currently cover approximately 7% of New Zealand's landmass (MAF 2013). It is clear now that pine plantations can play a role as a surrogate habitat to the native forest for some New Zealand biodiversity (Allen et al., 1995, Ogden et al., 1997; Zurita and Bellocq, 2010) and can offer breeding habitats to New Zealand falcons (Seaton 2007). Nevertheless, there is a national trend of deforestation (the direct human-induced conversion of forested land to non-forested land) of the New Zealand softwood plantation forests.

Between 2014 and 2025, a total of 67,000 ha* of plantation forests is forecasted to be converted primary into dairy farmland (91%) followed by sheep and beef agriculture (6%; Manley 2015), and 67% (44,890 ha) of the total harvesting occurs in the Central North Island. *Note that this number fluctuates based on the changes in the value of carbon (Manley 2015).

New Zealand falcons are unlikely to thrive in a farmland landscape alone as they require woodlands (Seaton et al. 2010, Chapter 2) and nesting features (see Barea 1995 and Fox 1977) that are not available in intensively managed farmland. The New Zealand falcon population was estimated at 3,700 to 4,000 breeding pairs (Fox 1978), and has been predicted to be declining due to on-going habitat loss, predation by introduced species (Kross et al. 2013, Chapter 4), and human persecution and electrocution (Fox and Wynn 2010, Kross 2014). With this nationwide deforestation, it is predicted that further declining of New Zealand falcons over the coming decades will occur. Therefore, an improvement of forestry management to support long-term viability and productivity of New Zealand falcon breeding populations will become increasingly important in the conservation of this threatened species.

1080 poison operation and New Zealand falcons

Twenty-five marked adult falcons were exposed to carrot 1080 poison bait during the winter months (May–August) in 2012–2014, and 21 marked falcons were exposed to cereal 1080 poison bait applied aerially in 2013 and 2014 (Chapter 4). All monitored adult falcons survived over the 1080 poison operation, with the exception of a single radio-tagged male (Kite) that died with an unknown cause.

The risks of secondary poisoning by 1080 to Kaingaroa falcons apply in two forms: through exposure to poisoned animals that have not yet died and from consuming the remains of poisoned animal carcasses. A majority of poisoned mammals display symptoms between 30 minutes and 3 hours (Eason et al. 1997), but these symptoms can take up to 12 hours to two days (Eason et al. 1997, Martin & Twigg 2002). The exposure of poisoned dying animals for prolonged hours or days to falcons is a great concern because prey vulnerability may be a fundamental drive for the hunting behaviour of raptors, especially for young individuals (Kitowski 2003). Although New Zealand falcons are active-pursuit foragers that feed on live prey, they have been documented feeding on carrion (Taylor 1977, Fisher et al. 2015). Poisoned carcasses that remain exposed on open ground can also attract Australasian harriers (*Circus approximans*) who are regular carrion feeders and are common throughout Kaingaroa forest.

The application of 1080 poison in Kaingaroa forest may assist the falcon population by controlling the number of brushtail possums (*Trichosurus vulpecula*, egg and chick eaters) and non-target predators such as stoats (*Mustela ermine*), feral cats (*Felis domesticus*), hedgehogs (*Atelerix albiventris*), and wild pigs (*Sus scrofa*; Seaton 2007). However, more research is required to determine precisely what extent 1080 is benefit to New Zealand falcons in Kaingaroa Forest such as to evaluate numbers of possum and other mammalian predators in the forest using control and treatment sites, and to assess differences between nest depredation rates in control sites and treatment sites.

Carrying capacity of New Zealand falcons in plantation forests

Habitat quality is directly correlated with the carrying capacity of a wildlife population, therefore, improving habitat quality can increase the carrying capacity of a population (Reid et al. 2007). Animals maintain relatively small home ranges when they have sufficient resources but are required to enlarge their space use when resources are limited (Carr & Macdonald 1986). When a threatened species occurs in a limited landscape such as enclosed reserves or managed land in a fragmented landscape, the ability to predict the carrying capacity of the species is fundamental to their conservation (Hayward et al. 2007). For carnivorous species, predator-prey relationships are a common factor that links to the density of the predator population (Van Orsdol et al. 1985, Karanth et al. 2004).

I found a tool to measure habitat quality of the Kaingaora falcons, therefore it could be used to increase Kaingaroa falcon numbers by improving the carrying capacity of the

Kangaroa Forest. For Kaingaroa falcons, their key habitat, the edge-habitat, was associated with their prey accessibility. They used smaller home-ranges when the forest provided the edge-habitats that were concentrated among mature-pine stands through creating open-patches less than 3 km^2 that are distributed closely (< 3 km apart) throughout the pine forest (Chapter 3). With this habitat arrangement, falcons overlapped their home ranges (or used the same area). Falcons nest on the open ground near mature trees (e.g. see Fig 1), and as long as nesting features are available, they use their breeding sites throughout the year. The productivity of Kaingaroa falcons could be increased by having smaller open patches (< 4 km^2) and a greater proportion of the edge-habitats (< 3km apart) throughout the forest. Consequently, Kaingaroa forest could potentially hold greater numbers of New Zealand falcons than it currently does. The results of this study should be integrated into the forestry policies to alter timber harvesting schemes to promote greater proportion of the edge-habitat throughout the forest. In an effort to improve conservation on a large scale, protocols developed and integrated into the Kaingaroa forestry management regimes could be expanded to other pine plantation forests nationwide. Such efforts would certainly enhance the FSC credibility. The results of this study could be applicable to other raptor species worldwide if they require similar habitat qualities to New Zealand falcons.

Future directions

Male chicks of Vicious and Kizzy

The project addressed topics that are new additions to the scientific and species conservation fields. At the same time, I have obtained information on the basic biology and ecology of falcons to gain a broader perspective of the unique characteristics that allow them to adapt to novel and diverse habitats. The results of this study emphasise the importance of all year-round biological and ecological information on a threatened species for conservation management purposes. In addition, understanding of non-breeding season mating behaviour and mating strategy of this non-migratory raptor enhanced overall knowledge for the genus *Falco*.

The nationwide deforestation (over 50,000 ha) of pine plantation forests is forecast within the next decade. A significant impact on the New Zealand falcon is expected, therefore, improvement of falcon habitat qualities is urgently required. Additional studies that delve deeper into the population demography are needed for the conservation of New Zealand falcons. I suggest that future studies should prioritise: (1) estimating the nationwide population of this species for the measurement of the impact of deforestation, and (2) assessing survival of juvenile falcons before and after 1080 operations using detailed monitoring methods (such as satellite/GPS telemetry if the weight of a transmitter is suitable). Furthermore, (3) investigating juvenile behaviour, natal dispersal, and natal philopatry in relation to habitat availability. (4) Continuous monitoring of adult Kaingaroa falcon survival over 1080 poison operations. (5) Assessing changes in the Kaingaroa falcon population size. (6) Identifying nest failure caused by forestry operations using intensive monitoring of breeding pairs. I observed that most nest failures occurred during the early nesting stage, such as egg laying or incubation periods by females deserting their nests due to on-going forest machinery operations near their nests (c. < 500 m). These failures will not be recognised unless potential nest sites are identified for known breeding pairs using the areas during the pre-nesting period (August to November). The current forest protocol is to reschedule operations if an active nest is found in a planned operation-area and when forestry machines have not been moved to the area. An adjustment of the policy is advised to reschedule operations if a breeding pair is sighted in a planned operation-area during the pre-nesting period. Quantification of nest failures would justify changes to current policy, and such adjustments should be applied to other managed forests nationwide. (7) New Zealand falcons are uncommon in Northland of New Zealand (Robertson et al. 2007, Bell and Laurence 2009). Reintroducing of New Zealand falcon to Northland forests and carefully monitoring an established population may well be beneficial to the population growth of this threatened species on the limited landscape.

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