Exploration-Avoidance and an Anthropogenic Toxin (Lead Pb) in a Wild Parrot (Kea: *Nestor notabilis*)

By

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Abstract

The ecological study of personality in animals is a relatively new field of behavioural investigation and of increasing importance to wildlife conservation. Kea (*Nestor notabilis*), hill country parrots endemic to South Island, New Zealand, are a good model for studying personality in an ecological context because they have a neophilic and explorative nature and are accessible for experimentation in the field. The study of personality is relevant to kea conservation if particular personality types (e.g., explorative) cause increased mortality, especially where kea come into contact with anthropogenic dangers. Its relevance may be even greater if, due to kea's social nature, social facilitation spreads that risk to other personality types. In this study I use experimental presentations of novel objects to investigate individual variation in exploration-avoidance behaviour in kea and apply my findings to the risk of lead exposure and poisoning because lead is present as novel objects in kea habitat. Analyses of blood lead levels and reactions to novel objects indicate that sex and age class, but more specifically personality, underlie a kea's reactions to novel objects and lead objects. Kea with explorative personalities have higher blood lead levels than aversive individuals. My results also indicate that social context, i.e., the presence of conspecifics and group size, are influential. Kea are more inclined to investigate novel objects in the presence of conspecifics, indicating that social facilitation plays a role in the exploration of novelty. Significant relationships between dominance category and behavioural response to novel objects indicates that social rank is related to personality, with dominant individuals being more explorative and subordinate individuals less explorative. These results highlight the potentially heavy cost of explorativity where kea and human habitats overlap. Explorative kea may be subject to an increased risk of injury or death and, if they facilitate exploration in aversive kea, increases the risk to those kea as well. Lead is a known cause of death in kea and as such affects kea

survival. Lead has also been shown to have deleterious effects on other species at low levels. Kea live in a highly seasonal and periodically severe environment, the dangers of which are compounded by various anthropogenic hazards including lead exposure. Kea are a long-lived and slow-reproducing species at a high risk of decline from even a small reduction in its survival rate - an imposed reduction in numbers could result in non-recovery.

Chapter 1

Introduction

Personality and the Exploration-Avoidance Trait

The ecological study of personality in non-humans is a relatively new field of behavioural investigation (Réale *et al.* 2007). Personalities are consistent behavioural differences amongst individuals over time or across situations, and include numerous traits (Réale *et al.* 2007). In this context "consistency" does not indicate that trait values cannot change with age or environmental conditions, but that differences between individuals are mostly maintained (Réale *et al.* 2007). Réale *et al.* (2007) treat "personality", "temperament", and "individuality" as synonyms. I prefer "personality" from the available terminology because it represents an immediately recognisable phenomenon in humans, and findings indicate that the phenomenon may be generalised across species (Gosling 2001, Gosling and John 1999, Réale *et al.* 2007). Personality results from a combination of genetic, epigenetic (i.e., developmental) and environmental influences (Buss *et al.* 1987; McDougall *et al.* 2006). A general framework for the ecological study of personality has not yet been developed but Réale *et al.* (2007) offer a supporting theoretical and methodological structure for the ecological study of personality to help integrate it with ecological theory.

Terms commonly used in the study of animal personality include coping style, behavioural syndromes, and behavioural phenotypes, but are not directly synonymous with the term personality. Coping style refers to individual responses to social and non-social challenging or novel situations that are consistent between individuals, regardless of life-history state, sex, or motivational state (Koolhaas *et al.* 1997, 1999; Pfeffer *et al.* 2002; Réale

et al. 2007). Although personality is not necessarily restricted to novel, risky or challenging situations, it appears to be strongly expressed in these particular conditions (Réale *et al.* 2007). Behavioural syndromes are suites of correlated behaviours across situations (Sih *et al.* 2004). The use of the term personality in the current context does not assume a correlation of all traits together in a whole temperament (Réale *et al.* 2007). Behavioural phenotypes are measured individual values for behavioural traits that may be considered as a characteristic of a species that can vary among individuals (Réale *et al.* 2007).

The study of personality as a collection of traits currently lacks the consistent use of terms because similar traits are recognised under different names, or different traits under the same name (Réale *et al.* 2007). I follow Réale *et al.*'s (2007) terminology for personality traits that features 5 recognised categories: exploration-avoidance, shyness-boldness, activity, sociability, and aggressiveness. Réale *et al.* (2007) differentiate between shyness-boldness and exploration-avoidance by defining shyness-boldness as an individual's reaction to any risky situation (e.g., predation) but not new situations. The trait that I focus on in this study is exploration-avoidance that Réale *et al.* (2007) define as an individual's reaction to a new situation, including behaviour towards a new habitat, food, or objects. A new situation may also be considered risky if it includes a new object like a potential predator (Réale *et al.* 2007). Réale (*et al.* 2007) deliberately exclude neophobia and neophilia from their terminology because they consider both as part of exploration. In the context of this study, however, neophobia and neophilia are used in reference to differences at the species level – i.e., kea (*Nestor notabilis*) are recognised as a neophilic species (Gajdon *et al.* 2006; Keller 1975; Kubat 1992).

Differences in personality may affect dispersal (Armitage 1986; Dingemanse *et al.* 2003), dominance (Gómez-Laplaza 2002; Dingemanse and de Goede 2004), mate choice, reproductive success (Dingemanse *et al.* 2004, Both *et al.* 2005; van Oers *et al.* 2006), and

survival (Cavigelli and McClintock 2003). Neophilia and investigative activities are often destructive and may lead to conflict with humans and increased mortality risk due to frequent contact with anthropogenic hazards in some species. The range of explorativity (the level of exploration that an individual consistently exhibits) within the species may have conservation implications. For example, highly explorative birds may be at a greater risk of injury, illness or death due to their encounters with dangerous items or situations such as toxins, traps or predators.

Kea

The kea (*Nestor notabilis*: Psittaciformes) is a large (46 - 50cm) olive-green parrot with a long slender bill and bright orange-red underwing coverts endemic to New Zealand. The closest taxonomic relative to the kea is the kaka (*Nestor meridionalis*), an inhabitant of lowland temperate forests (Diamond and Bond 1999). Kea and kaka are estimated to have emerged during the early Pleistocene (1.8 – 0.78 million years ago), kea in the south and kaka in the north, from an ancestral proto-kaka (Diamond and Bond 1999). Populations of both species fluctuated with the ebb and flow of glacial events. Kea relied primarily on alpine habitat and kaka on forests (Diamond and Bond 1999). Fossil evidence indicates that kea were relatively common in the mid-Pleistocene (781,000 – 126,000 years ago) (Diamond and Bond 1999) and were once resident on North Island (Holdaway and Worthy 1993). Fossil deposits in lowland Canterbury have revealed the remains of similar numbers of kea and kaka (Holdaway and Worthy 1997). This indicates that kea and kaka also once coexisted in Canterbury as far as the east coast.

The kea is noted for its cognitive abilities, neophilia (attraction to new situations), and highly explorative tendencies (Johnston 1999; Keller 1975; Kubat 1992; Stamm 2007). Kea are also highly social and maintain a strict social hierarchy (Diamond and Bond 1999). Kea

are listed as vulnerable and in decline by the World Conservation Union (IUCN), and nationally endangered by the New Zealand Department of Conservation (DOC) (Hitchmough *et al.* 2007), and is a fully protected species (IUCN 2008). The present size of New Zealand's kea population is unknown. The most precise estimates, based on species distribution, indicate that the wild population numbers approximately 3,000 (Diamond and Bond 1999) but a range of 1000 to 5000 is often cited (Anderson 1986). Kea may still appear to be common due to their neophilia and habit of congregating near ski fields and tourist stops (Elliott and Kemp 2004).

Kea are restricted to South Island and are distributed from northwest Nelson, Marlborough and the Seaward and Inland Kaikoura Ranges, to Fiordland and Central Otago Districts. They generally live in montane to alpine habitats (Higgins 1999) from 600 to 3000 m above sea level (a.s.l.) (Forshaw 2006), including southern beech (*Nothofagus* sp.) forest, subalpine scrub, and alpine grassland (Jackson 1960; Wilson 1990), but are also widespread in lowland forest in Westland (O'Donnell and Dilks 1986). Kea often visit lowland sites, especially to the west of the Southern Alps, and are occasionally seen at sea level (Higgins 1999).

Kea forage on more than 100 species of plant as well as insects, carcasses (Brejaart 1988; Campbell 1976; Clarke 1970; Jackson 1960), live animals including Hutton's shearwater (*Puffinus huttoni*) chicks (Cuthbert 2003), mice (*Mus musculus*) (Beggs and Mankelow 2002), sheep (*Ovis aries*) (Diamond and Bond 1999), and human rubbish (Diamond and Bond 1999; Gajdon *et al.* 2006).

Nesting occurs between July and January, with peak activity in July and August (Elliott and Kemp 1999; Jackson 1963) and pairs appear to be monogamous (Elliott and Kemp 1999; Wilson 1990; Wilson and Brejaart 1992). Kea nest on the ground under rock piles or boulders and in holes among tree roots, on rock bluffs, or in hollow logs (Elliott and

Kemp 2004; Jackson 1963). Kea generally nest annually, although on occasional years they will not breed (Elliott and Kemp 1999). If a nest fails, kea will sometimes re-nest and at least 1 female has been observed laying a second clutch in the same season after successfully rearing a first clutch (Elliott and Kemp 2004). A female will lay 2 to 4 eggs with an incubation period of approximately 25 days (Jackson 1963), and a nestling period of 13 weeks (Elliott and Kemp 1999; Jackson 1963; Wilson and Brejaart 1992).

Kea have an extended juvenile period compared to kaka (Diamond and Bond 1999) and are estimated to be dependent on their parents for 5 months (Jackson 1960, 1963; Diamond and Bond 1991; 1999). This period may occasionally be prolonged. In October 2004 a female fledging that was banded in March of that year at Aoraki/Mount Cook National Park (AMCNP) was observed soliciting for food, and being fed by, the dominant adult male (*pers. obs.*). In September 2008 at Treble Cone ski field several family groups of older fledglings and adult kea were present and the fledglings were observed being fed by the adults (K. McInnes *pers. comm.*). These observations suggest a 6-month dependent period, based on the latest observation of fledging in March (Elliott and Kemp 2004). Stamm (2007) also observed 2 captive young kea being fed at 39 and 40 weeks. One was fed by his father and the other by an adult male that took on a paternal role when the young kea was released into his group after removal from her parents' aviary. Stamm (2007) indicates that this reveals a slow, step-wise progression to independence until the age of 40 weeks or more, rather than 13 to 19 weeks. From the time of independence from their parents, young kea live in social flocks until they form breeding pairs at the age of 4 to 5 years (Jackson 1960, 1963; Temple 1996). Males begin breeding at 4 to 5 years and females as early as 3 years (Diamond and Bond 1999).

The Relevance of Novelty and Personality to Kea Ecology

An ability to learn about novel food and indicators of food is useful to many species (Griffin 2001). Griffin (2001) cited the example of red-necked phalaropes (*Phalaropus lobatus*) whose nests were marked with nearby stakes (Reynolds 1985). At least 1 sandhill crane (*Grus canadensis*) learned to associate the stakes with the presence of nests (Griffin 2001; Reynolds 1985). Reynolds (1985) observed the crane intensively searching only near nest markers. Although nest predation was not observed directly, eggs disappeared from nests where there were perforations in the ground similar to those made by the probing bill of a crane (Reynolds 1985). Sandhill cranes are opportunistic foragers known to prey on the eggs and chicks of at least 4 other avian species, in addition to a large variety of plants and invertebrates (Reynolds 1985). Reynolds (1985) pointed out that the crane he observed ignored other markers such as flagging tape and coloured stakes marking capture locations for other species. He discounted the possibility that the crane was using habitat cues and tracks from the researchers due to the varied nature of nest sites and because most nests were checked remotely (Reynolds 1985). Griffin (2001) cites this study as an example of the versatility of birds in learning what to look for when foraging and the use of novel search images. Carrion crows (*Corvus corone*) have also learned to locate and prey upon nests using brightly marked nest stakes, even when markers were placed 10 and 20 m away (Picozzi 1975). A study of common ravens (*Corvus corax*) suggests similar conclusions (Autenrieth 1981). Yahner and Wright (1985) concluded that the use of hair-catchers, placed at nests to determine the identity of mammalian predators, and flagging near artificial nest sites in a ruffed grouse (*Bonasa umbellus)* management area acted as cues to American crows (*Corvus brachyrhynchos*) allowing them to rapidly associate these markers with nest sites and develop a search image for them.

Kea predation of nests or burrows has been observed for at least 3 avian species including Tokoeka brown kiwi (*Apteryx australis*) (J. Tansell *pers. comm.*), whio

(*Hymenolaimus malacorhynchos*) (McMurtrie *et al.* 2004), and Hutton's shearwater (*Puffinus huttoni*) (Cuthbert 2003). Kea prey on the eggs of all 3 species and also the chicks of Hutton's shearwaters. Observers concluded that a kea located a particular whio nest after locating a camera and video unit set up to monitor the nest (McMurtrie *et al.* 2004). A kea was recorded on videotape depredating the nest (McMurtrie *et al.* 2004). Robertson and Colbourne (2003) recommend that brightly coloured identification tags not be placed near kiwi burrows to prevent leading predators to them, including kea. Cuthbert (2001) points out that one of the disadvantages of using inspection hatch burrows to monitor Hutton's shearwaters is that some of the burrows are likely to be dug up by kea. He recommends siting the burrows in areas of the colony with hard compact earth and ensuring the hatches are secure and/or covered with large rocks to reduce this problem (Cuthbert 2001). His comment indicates that kea learn to associate the hatches with a food source.

Kea Personality

In addition to being neophilic, kea are a highly explorative species (Keller 1975; Kubat 1992; Stamm 2007; Temple 1996). This makes kea ideal for studying the exploration-avoidance trait. Kea's highly neophilic and explorative nature has enabled it to survive in the hostile alpine habitat of New Zealand since the early Pleistocene, despite hurdles ranging from ice ages (Diamond and Bond 1999) to government bounties. In the novel circumstances that kea face, such as extensive habitat modification brought about by hill country sheep farming, the establishment of human habitation in hill country areas, and the introduction of browsing mammals, kea have shown a propensity for innovation. These innovations are rapid behavioural changes to exploit novel food sources including sheep and rubbish bins with hinged lids (Gajdon *et al.* 2006). These examples share a common feature. In both cases it was particular individuals that were inclined to investigate and exploit these resources initially. It

was older males that were observed to attack sheep (Marriner 1908; Temple 1996) and only some males were able to successfully open rubbish bins with hinged lids (Gajdon *et al.* 2006).

There have been major changes in available food sources for kea. The arrival of humans in New Zealand has had a considerable impact overall on the endemic fauna and resulted in the extinction of 32% of its landbird fauna (Atkinson and Cameron 1993). Prior to the arrival of humans, Procellariid seabirds (petrels, shearwaters, fulmars, and prions) occupied colonies on the New Zealand mainland from lowland to alpine areas (Worthy and Holdaway 2002). Hutton's shearwaters (*Puffinus huttoni*) currently breed only in a remote alpine area at 1200 to 1800 m a.s.l. in the Seaward Kaikoura Range on the northeast coast of South Island (Cuthbert and Davis 2002). Kea may have preyed on Hutton's Shearwaters in lowland forest where the shearwaters were formerly abundant (Holdaway and Worthy 1997). It appears highly likely that kea included seabirds in their diet where they were sympatric. Moa (*Dinornis* spp.) pelves also have been found bearing evidence of predation by Haast's eagle (*Harpagornis moorei*) and damage consistent with consumption of internal organs (i.e., kidneys) by either eagles, kea, or both (Holdaway and Worthy 1997). One deposit where moa pelves were discovered included both kea and eagle remains (Holdaway and Worthy 1997). The evidence suggests that kea may have regularly scavenged moa carcasses and attended Haast's eagle kills (Holdaway and Worthy 1997). The damage is consistent with the method of attack attributed to modern kea attacking sheep in which the bird focuses on the hind-quarters and the fat surrounding the kidney (Holdaway and Worthy 1997). Sheep may therefore have replaced moa in the diet of some kea (Holdaway and Worthy 1997).

Exploration-Avoidance and Conservation

Personality studies are becoming increasingly important to the conservation of wild populations (Dall *et al.* 2004; Sih *et al.* 2004; McDougall *et al.* 2006). Kea are currently

classified as an endangered species. The exploration-avoidance trait may have an effect on kea survival and so its study may aid in their conservation. Dall *et al.* (2004) indicate that environmental change from anthropogenic influences is expected to be a key factor in determining the future of many species. A primary issue in conservation biology, therefore, is the ability of species to respond to change and the various personality types that determine an individual's ability to survive (Dall *et al.* 2004). For example, bold and neophilic individuals may be able to locate new resources if a traditional resource fails, or aggressive individuals may better compete for resources when they are limited, thereby permitting local populations to survive through anthropogenic challenges (Dall *et al.* 2004). Sih *et al.* (2004) point out that a species should be able to cope with a new environment more effectively if most individuals are able to rapidly adapt their behaviour. They cite the example that more flexible, less neophobic species appear to respond more favourably to novel environments (Sih *et al.* 2004; Sol and Lefebvre 2000; Sol *et al.* 2002). They go further to explain that if the majority of individuals in a species are not the appropriate behavioural type for coping with an environmental change the species can still persist if it has large inter-individual variation in behaviour, so that at least some individuals respond appropriately (Bolnick *et al.* 2003; Sih *et al.* 2004).

These examples are especially relevant to kea because they too are a behaviourally flexible, neophilic, and explorative species (Diamond and Bond 1999; Johnston 1999; Kubat 1992; Stamm 2007). Kea readily show their ability to exploit new food resources. Their feeding innovations include the exploitation of mammal carcasses, live sheep, rubbish dumps, rubbish bins, and hand-outs from humans (Peat 1995). Several studies indicate that innovative tendencies may be consistent individual traits (Laland and Reader 1999; Pfeffer *et al.* 2002; Reader 2007). Innovation and exploration, however, also put kea at risk. For example, they are persecuted for being perceived as pests on hill country sheep farms or become ill and die

from exposure to anthropogenic toxins. The key to the persistence of kea populations might be whether kea's adaptability and explorativity, when faced with continued anthropogenic change, continues to enable their survival, or ultimately decreases it.

History of Human Impact on Distribution

Humans became a feature of the New Zealand landscape after approximately 1280 AD when the ancestors of the Māori arrived (Wilmshurst *et al.* 2008). Kea feature in Māori lore as one of the birds brought down to earth as a captive by Tāne Matua, Tāne the Parent, after his fight with the Whanau Puhi, the "Wind Children", in the heavens (Riley 2001). Kea also took part in the battle between sea and land birds, and it was the kea's form that Maui took during some of his adventures (Riley 2001). Kea feature in a Waitaha Māori legend as kaitiaki of members of that tribe while they were on a path through Browning Pass in search of Greenstone (Temple 1996). Kea were not often eaten by Māori as they found them too tough and lean, and they exuded a strange smell when cooked (Riley 2001). They are reported to have caught the bird in the alpine regions of North Island, where it is now extinct, by spreading a white garment on the ground (Riley 2001). On South Island deliberate and accidental burning by Māori destroyed much of the dry eastern beech forests by the 16th century (Peat 1995; Temple 1996). Pastoral farming by Europeans in the hill country last century further eroded kea habitat by burning large tracts of subalpine shrublands and tussock grasslands to promote pasture growth (Peat 1995). Between the arrival of Polynesians and 1840 forest cover was reduced from 78% to 53% of New Zealand's land area and European settlers further decreased forest cover to 23% (Atkinson and Cameron 1993). The impact of this burning has been intensified by the introduction and spread of browsing mammals including red deer (*Cervus elaphus*), chamois (*Rupicapra rupicapra*), tahr (*Hemitragus jemlahicus*), hares (*Lepus europaeus*), rabbits (*Oryctolagus cuniculus*), goats (*Capra hircus*), and possums

(*Trichosurus vulpecula*) into the mountain interior of South Island that compete with kea for food (Peat 1995; Temple 1996). According to Buller (*in* Turbott 1967) the first recorded specimens of kea were obtained in 1856. Until the early 1860s the kea was considered to be a rare species. Buller relates that James Hector then found it "everywhere" in the mountains in Otago during a topographical survey (Buller in Turbott 1967). Observers in the late 19th century estimated that the kea population was increasing greatly in numbers but it is more probable that the increase in the number of kea records was due to an increase in the number of observers in kea habitat, particularly alpine areas (Holdaway and Worthy 1993; Marriner 1908). Kea are now uncommon to rare outside of government protected areas such as national parks and, although they were common in the mountainous regions of Otago and south Canterbury in the late 1800s, they are virtually absent there now (Diamond and Bond 1999). The distribution of kea roughly corresponds to that of southern beech forests, indicating a strong reliance of kea on beech forest habitat (Diamond and Bond 1999; Wilson 1990).

Historic Human-Kea Conflict

Kea have had a history of conflict with humans since European farmers established themselves in the hill country of South Island. Upon the introduction of hill country sheep farms, kea habitat underwent a widespread and rapid change. Intensive settlement in the hill country began in the 1840s and tenants typically burned the native vegetation in order to graze their sheep in the spring (Diamond and Bond 1999). Large areas of native shrub and grassland were burned (Diamond and Bond 1999; Peat 1995). Kea quickly began frequenting the sheep farms where there was an availability of sheep carcasses and offal (Diamond and Bond 1999). Buller described the kea as an "absolute pest" in the central and southern districts (Buller in Turbott 1967) because a new sheep 'disease' was discovered in 1867: sores on the loins of sheep, which would soon turn out to be inflicted by kea (Temple 1996). The wounds inflicted

by kea on sheep are prone to infection leading to blood poisoning unless the sheep are inoculated beforehand (Diamond and Bond, 1999). Kea were soon blamed for a large number of sheep deaths and the government subsequently placed a bounty on kea (Temple 1996). An estimated 150,000 kea were killed between 1870 and 1970 after which the bounty scheme was finally withdrawn and kea protected except on properties where they caused damage (Peat 1995). In 1986 kea were given full legal protection (Peat 1995).

Reports of kea's sheep-killing capacities were often exaggerated (Diamond and Bond 1999; Jackson 1962a) and it has been found that attacks on sheep are usually led by an older male 'rogue' individual to the benefit of the other kea (Temple 1996). Kea are considered to be opportunists and include scavenging behaviour in their feeding repertoire (Diamond and Bond 1999). In a behaviourally adaptable bird such as the kea it is not surprising that they would have learned how to exploit vulnerable individuals in a flock of sheep, especially since their paths often crossed in the hill country (Diamond and Bond, 1999) and because kea would have encountered sheep carcasses (Diamond and Bond 1999; Temple 1996). Total kea numbers are now greatly reduced due to the kea's widespread persecution as a sheep killer (Forshaw 2006). Population modelling indicates that since the arrival of humans and introduced predators in New Zealand kea have suffered substantially due to the drastic effects of hunting and predation on kea populations which are now considerably smaller, more isolated, and far more vulnerable to extinction than they once were (Elliott and Kemp 2004).

Current Threats

Kea still face conflict with humans wherever kea and human habitats overlap such as at tourist stops, ski fields, alpine and resort villages, on farms, around fishing vessels, and at ski fields (Diamond and Bond 1999; Peat 1995; Temple 1996; *pers. obs.*). Kea are attracted to anthropogenic sources of food such as areas where they are regularly given hand-outs,

unsecured rubbish collection points, and dumps (Diamond and Bond 1999; Gajdon *et al.* 2006; Jackson 1969; Peat 1995; Temple 1996). An unknown number of kea are still illegally killed (Elliott and Kemp 2004; K. McInnes *pers. comm.*).

Kea are also subject to a large number of anthropogenic hazards. In areas where there are unsecured sources of rubbish there are foods that can make them ill (Peat 1995). During foraging or investigations kea often chew foreign objects and ingest parts of them (Peat 1995). Closed-cell foam from padding on ski racks and soft rubber parts from cars are favourites of the kea (Johnston 1999) and chewing these items can result in impactions of the crop and intestines and death (Jarrett 1998; Peat 1995). Kea may also become entangled in objects that are made of synthetic materials, metal, rubber, or cardboard (Peat 1995; *pers. obs.*). Many toxins are also available to kea. At rubbish dumps, household cleaning agents and other toxic chemicals such as pesticides are available (Jarrett 1998; Peat 1995). Reported causes of death include lead toxicity, cyanide poisoning (McLelland *et al.* in press), and methylxanthine toxicity (Gartrell and Reid 2007). Recent monitoring by Department of Conservation (DOC) on the effects of 1080 (sodium monofluoroacetate) on wild kea revealed the death of 7 of 17 (41%) radio-tracked kea in the area between Fox and Franz Josef Glaciers on the West Coast. Twelve kea radio-tracked in more remote areas of the West Coast survived exposure to 1080 (Kemp and van Klink in prep.), which is applied aerially to control possums. Deleterious effects of toxins such as disorientation put them at risk of vehicle impacts (Peat 1995; Jarrett 1998). Buildings and boardwalks also present hazards to kea (Peat 1995; Temple 1996), especially in the form of lead (Pb) building materials (Higgins 1999; Jarrett 1997, 1998; McLelland *et al.* in press). Kea also risk entrapment or injury from items such as live cat traps (*pers. obs.*) and kill traps for pests (J. Kemp *pers. comm.*).

Kea also risk injury or death by misadventure, including vehicle impacts from cars and trains (Jarrett 1998, Peat 1995). Mostly young kea have been affected. Young fledglings often

appear to have poor road sense (*pers. obs.*). Other causes of death include drowning in containers such as water tanks and barrels (Elliott and Kemp 1999; Jackson 1969; J. Kemp *pers. comm.*; Wigley 1979), electrocution (Jackson 1969), window strike (*pers. obs.*), possum traps (J. Kemp *pers. comm.*), and entrapment in buildings (*pers. obs.*). This list is not exhaustive but describes a range of the problems that kea's neophilic and explorative tendencies can cause them in areas where their habitat overlaps that of humans.

A major anthropogenic threat to kea are the introduced mammalian competitors in the form of browsers, mentioned above, and predators. Stoats (*Mustela ermina*) are nest predators of kea (Elliott and Kemp 1999, 2004) and possums (*Trichosurus vulpecula*), although they have not yet been observed preying on kea nests, are known nest predators of kaka and are considered likely nest predators of kea (Elliott and Kemp 2004). A study of kea nests showed that approximately 40% of nests failed and that predators probably caused most of the failures (Kemp and Elliott in prep.). Cats may also prey on kea. In 2008 a fledgling male banded and radio-tracked at AMCNP as part of as study by the Kea Research Project (University of Vienna) was found dead under vegetation and necropsy indicated predation by a cat (*Felis catus*) (B. Gartrell *pers. comm.*). Cats are trapped in parts of AMCNP and cat scat has been observed in the area where the bird was found (*pers. obs.*).

Lead as a Special Threat

Although lead toxicosis has been established as the cause of death for a number of wild kea during the past 15 years, lead exposure was recently discovered to be much more widespread in wild kea than previously thought (McLelland *et al.* in press). Lead naturally occurs in the environment but at low levels compared to anthropogenic sources (Pattee and Pain 2003). Sources of lead in kea habitat include lead based paint, galvanised metal, lead roof and

window flashings, lead-bearing batteries (Jarrett 1997), lead shot (R. Norman unpub. necropsy report), and lead head nails (Higgins 1999).

Lead is known to be one of the most toxic metals as it has been shown to have broad physiological effects that disrupt numerous processes necessary for normal function (Pattee and Pain 2003). Lead is bioaccumulative and relatively small doses can seriously affect health (Goyer 1991). Lead adversely affects the renal, gastrointestinal, reproductive, central and peripheral nervous systems, and the biosynthesis of haeme (Verity 1997). Lead has also been found to have teratogenic effects (i.e., they interfere with normal embryonic development resulting in abnormalities) on birds and bird embryos are sensitive even to relatively low doses of lead (Kertész *et al.* 2006).

Lead toxicity affects a wide range of avian species and is the most common cause of metal poisoning in waterfowl (Platt 2006). It is one of the most commonly recognised toxicities of free-ranging birds, is a common cause of neurological abnormalities, and can be fatal (Platt 2006). Neurological and gastrointestinal clinical signs are usually observed and lead can have severe effects on avian kidneys (Platt 2006). Lead toxicosis may be acute or chronic with clinical signs dependant on the amount and surface area of the lead ingested. Clinical signs in birds include behavioural changes, lethargy, anorexia, vomiting, diarrhoea, ataxia, limb paresis (nerve-related weakness) or paralysis, seizures, anaemia and emaciation (Platt 2006). Death may occur within 48 hours of the first appearance of clinical signs (Platt 2006). Psittacines (parrots and their relatives) in particular fall victim to inadvertent acute lead intoxication because of their curious nature and inclination to chew any object they may encounter (Gelis 2006).

The effects of lead on avian taxa such as waterfowl, shorebirds, and raptors in the wild have been well studied. Lead toxicosis is well known in captive psittacines (Dumonceaux and Harrison 1994) but very little study has been conducted on wild parrots. In 2006 and 2007 an

estimated 5000 + birds including several psittacine species died in the area of Esperance in Western Australia following anthropogenic release of lead into the environment (Golder Associates 2008). These included white-tailed black cockatoos (*Calyptorhynchus baudinii*) and purple-crowned lorikeets (*Glossopsitta porphyrocephala*). Although the sample size of birds submitted for necropsy was small (n = 11), evidence indicated the birds died from lead poisoning (Golder Associates 2008). Two separate bird death events were reported, 1 in December 2006 and 1 in January 2007, and lorikeets comprised approximately 163 of 319 (51%) of dead birds reported (Golder Associates 2008). The lead was released into the environment in the form of airborne lead carbonate ore concentrate from mined lead being handled at Esperance Port (Gulson 2008; Gulson *et al.* 2008). Lead carbonate is a highly toxic form of lead (Gulson *et al.* 2008). Purple-crowned lorikeets are nomadic and largely dependent on flowering eucalypts (Forshaw 1981) and it was concluded that the lead-affected lorikeets probably absorbed lead through a combination of inhalation, ingestion, and preening (Golder Associates 2008).

Jarrett (1998) examined blood lead concentrations in wild kea at Arthur's Pass and found that younger birds were much more likely to have elevated blood lead levels than older birds. Although the sample size of birds in Jarrett's study was small (n = 11) and biased towards birds foraging at a rubbish dump, it may have been representative of birds frequenting areas of human habitation. The rubbish dump, now closed, was located near Arthur's Pass Village and was a probable source of lead roofing materials. The source of lead in the kea tested in Jarrett's study was not identified and it could not be concluded that the lead came from the rubbish dump (Jarrett 1997).

Lead roofing materials are also still common throughout many areas where kea live (*pers. obs.*). Jarrett's findings are also consistent with those of a current Department of Conservation survey (McInnes *et al.* in prep.) where kea living in areas near human habitation

have shown elevated blood lead concentrations. Lead has been used as a building material (e.g., in the form of lead head nails) in New Zealand since the late 19th century (Coutts 1977) and therefore would have been introduced to the kea's environment with the establishment of hill country mountain huts, villages, and farms. Jackson (1969) reported causes of death in kea collected in the Arthur's Pass region over 10 years and his report included clinical and pathological results consistent with lead toxicosis. Although neither tissue nor blood lead concentrations were evaluated in his study, several accounts of kea behaviour (Jackson 1962b, 1969) are consistent with the clinical signs of lead toxicosis. Several of Jackson's accounts (1962b, 1969) of particular kea behaviours, which he attributed to "social regulation" (1969), in light of current knowledge about the effects of lead toxicity appear to indicate the effects of chronic lead exposure rather than normal kea behaviour. He described grossly underweight kea at the bottom of the social hierarchy, amongst which a "haemolytic anaemia" developed (Jackson 1969). He also described 2 kea that were "starving" and "very light" at the time of banding and died within 1 week (Jackson 1969). They showed slow reactions and unwariness, and a post mortem examination of one of the birds revealed stones and rotten wood in the stomach, indicating that it had not been eating properly (Jackson 1969). Both birds were caught while feeding in a drum of rubbish and Jackson noted that they ignored the slight sounds of a cautious approach and the flushing of other nearby kea (Jackson 1969). In my own experience, any kea foraging in this context (e.g., in a rubbish bin) is highly wary, alert, and frequently scans the environment, especially when humans are present in the area. When approached, even cautiously, they will abandon their compromising position well before the approaching person is close enough to catch them. Jackson noted that some kea became "psychotic", a factor that he attributed as an inability to cope with the strain of constant squabbles for position in the social hierarchy (Jackson 1962b). He indicated that these kea

rapidly lost condition from anaemia consequent on the psychosis and "dropped aside" (Jackson 1962b).

The behaviours described by Jackson match several clinical signs reported for birds diagnosed with lead toxicity including behavioural changes, anorexia, anaemia and emaciation (Platt 2006). In my experience the behaviours described by Jackson are highly abnormal for wild kea and indicate a gross deterioration of health. In January 2007 I discovered an unbanded juvenile female displaying clinical signs of lead toxicity. She was in Aoraki/Mt Cook Village late in the morning (approx. 10:00 AM) on a hot, clear day, whereas all kea normally retreat to the shaded forests on the west side of the valley away from the village when the sun reaches the valley floor. Kea have an unusually high metabolic rate and maintain a body temperature of nearly 40ºC (Diamond and Bond 1999). Their thick layer of down feathers (*pers. obs.*) and shading behaviour in hot weather would indicate that they are not tolerant of staying in direct sunlight for very long during hot days. She also repeatedly made loud animated vocalisations, alighted on the ground, where she displayed ataxia to the degree that she was unable to fly, and I was quickly able to catch her by hand. When I first approached her she did not retreat and her head and eye movements were also ataxic. Her behaviours were out of context, i.e., she was in the wrong place at the wrong time of day and in the wrong conditions. Both the ataxia and the ease with which she was captured were unusual. She was sent to a wildlife veterinarian on the same day but died overnight and the cause of death was diagnosed as lead toxicity (J. McLelland and B. Gartrell unpub. necropsy report). Since the kea that Jackson studied at Arthur's Pass had access to an open dump where various toxins would have been available (Jarrett 1997) and to additional sources of lead from buildings, he may not have realised that the behaviours he was observing were atypical of wild kea. Abnormal behaviour has been observed in several kea with lead toxicosis prior to death. One juvenile male was observed showing signs of illness and was removed from the

room of a building he was found in prior to death from lead toxicosis (R. Norman unpub. necropsy report). An adult male at AMCNP was also observed showing signs of illness, including vomiting, the day before he was found dead from lead toxicosis.

Lead exposure to free-ranging New Zealand parrots is not entirely limited to kea. Several kaka from Karori Wildlife Sanctuary in Wellington have also been diagnosed with lead toxicosis (K. McInnes *pers. comm.*). Presumably the kaka ingested lead from chewing lead head nails on the roofs of houses, as kaka are often observed in suburban areas near the sanctuary and on roofs and lead head nails are present on buildings throughout the city (*pers. obs.*). An adult male kaka from Stewart Island also died from lead toxicosis (B. Gartrell unpub. post mortem report) and a kaka from Kapiti Island was diagnosed with lead toxicosis during treatment for a broken leg (B. Gartrell unpub. patient history report).

Research Questions and Hypotheses

The ecological study of personality in animals is a relatively new field of behavioural investigation (Réale *et al.* 2007) and of increasing importance to wildlife conservation (Dall *et al.* 2004; Sih *et al.* 2004; McDougall *et al.* 2006). Kea are a good model for studying personality in an ecological context because of their neophilic and explorative nature and they are accessible for experimentation in the field. The study of personality may also be relevant to kea conservation if particular personality types (e.g., explorative) cause increased mortality, especially where kea come into contact with anthropogenic dangers. Its relevance may be even greater if, due to kea's social nature, social facilitation spreads that risk to other personality types. Lead has been a known threat to kea for the past 15 years but only recently has it been discovered to be a widespread problem that may affect all kea living in areas with anthropogenic sources of lead.

In this study I use experimental presentations of novel objects to investigate individual variation in exploration-avoidance behaviour in kea and apply my findings to the problem of lead because lead is present as novel objects in kea habitat. When presenting kea with novel objects I expected individuals to show a consistent tendency to be explorative or aversive. I predicted age and sex to influence kea's response to novelty but beyond that I also wanted to know the effect of personality on that response. Due to kea's social nature I also predicted social context to have some influence on their reactions such that aversive individuals might be drawn into exploration of a novel object by the activities of conspecifics. I wanted to see whether their reactions were related to social rank, i.e., if dominant birds were more explorative and submissive birds aversive. I also wished to discover if kea's blood lead concentrations could be predicted by the same predictors that explain their behavioural reactions to novel objects. If this is the case it could mean that kea approach lead sources in the same way that they approach novel objects and that different personality types could be more prone to the detrimental effects of lead exposure.

Chapter 2

Methods

Study Areas

The study was conducted in Aoraki/Mount Cook (43º44'0"S, 170º6'0"E) and Mount Aspiring (44º23'0"S, 168º44'0"E) National Parks in South Island, New Zealand.

Aoraki/Mount Cook National Park (AMCNP) has New Zealand's highest peak, Aoraki/Mount Cook, at 3754 m a.s.l. The park is east of South Island's main divide and comprises deep glacial valleys between geologically young mountain ranges. Ice and snow are permanent in the nival zone above the 2150 m snowline. Glaciers descend from the ranges and are bordered by steep moraine walls as they reach the valley floors. At the glacier termini are lakes that empty into rivers draining into Lake Pukaki and Lake Tekapo in the Mackenzie Basin. The study sites were in the lower Hooker Valley on the southeast side of Aoraki/Mt Cook. Vegetation communities in these valleys include montane short grassland with matagouri (*Discaria toumatou*) on the valley floor (730 m), giving way to totara forest dominated by Hall's totara (*Podocarpus hallii*) and broadleaf (*Griselinia littoralis*) on the valley sides, and remnants of silver beech woodland (*Nothofagus menziesii*). These forests are interspersed with shrubland composed of *Dracophyllum* spp., snow totara (*Podocarpus nivalis*), three finger (*Pseudopanax colensoi* var. *ternatus*), tree daisies (e.g., *Olearia* spp.), *Hebe* spp., and mountain ribbonwood (*Hoheria lyallii*). Alpine grasslands (*Chionochloa* spp.) are found above the treeline, and include herbs such as *Celmisia* spp. On alpine rock and on nival rock and debris above the snowline are found flowering plants such as *Ranunculus* spp., mosses, and lichens. Mobile screes, shingle riverbeds, subalpine and montane rock intermittently cut through the flora. In the Lower Hooker Valley near the study sites is

Aoraki/Mt Cook Village, housing approximately 300 residents in the summer months, and receiving approximately 4.0 m annual precipitation. A number of huts and outbuildings are situated throughout AMCNP, including Hooker Valley and its surrounding ranges. This part of AMCNP was chosen for its accessibility and because large numbers of kea could reliably be found there during the summer months (Figure 1).

Mount Aspiring National Park (MANP) is also located near South Island's main divide, southwest of AMCNP. Mount Aspiring is the tallest peak in the park at 3027 m a.s.l. Like AMCNP, MANP is in a heavily glaciated mountainous region with deep glacial valleys and sharp peaks. The snowline here occurs at lower altitude than in AMCNP at approximately 2000 m, and most alpine areas of the park have an annual precipitation exceeding 5.0 m per annum. The study sites were located on the Rob Roy Track (approx. 400 – 750 m a.s.l.). Vegetation communities along the track ranged from mixed mountain and silver beech forest (*Nothofagus solandri* var. *cliffortoides* and *Nothofagus menziesii* respectively), to the subalpine meadows of Rob Roy Valley, overlooked by the sheer schist valley walls topped by the Rob Roy Glacier. The meadows surrounding the track's terminus were at the edge of the mountain beech forest and dominated by invasive tussock hawkweed (*Hieracium lepidulum*), and include natives such as *Olearia* spp., *Coprosma* spp., small *Nothofagus* spp., speargrasses (*Aciphylla* spp.), and *Podocarpus nivalis*. The track follows Rob Roy Stream, a tributary of the West Branch of the Matukituki River (400 m a.s.l.). Unlike the lower Hooker Valley in AMCNP, the West Matukituki Valley and Rob Roy Valley do not feature any permanent settlements, only occasional huts, shelters, and outbuildings on the access road and remote walking tracks. This part of MANP was chosen for its accessibility, reliable numbers of kea in the summer, and because I expected the local kea population to have a lower level of lead exposure than the kea of AMCNP (Figure 1).
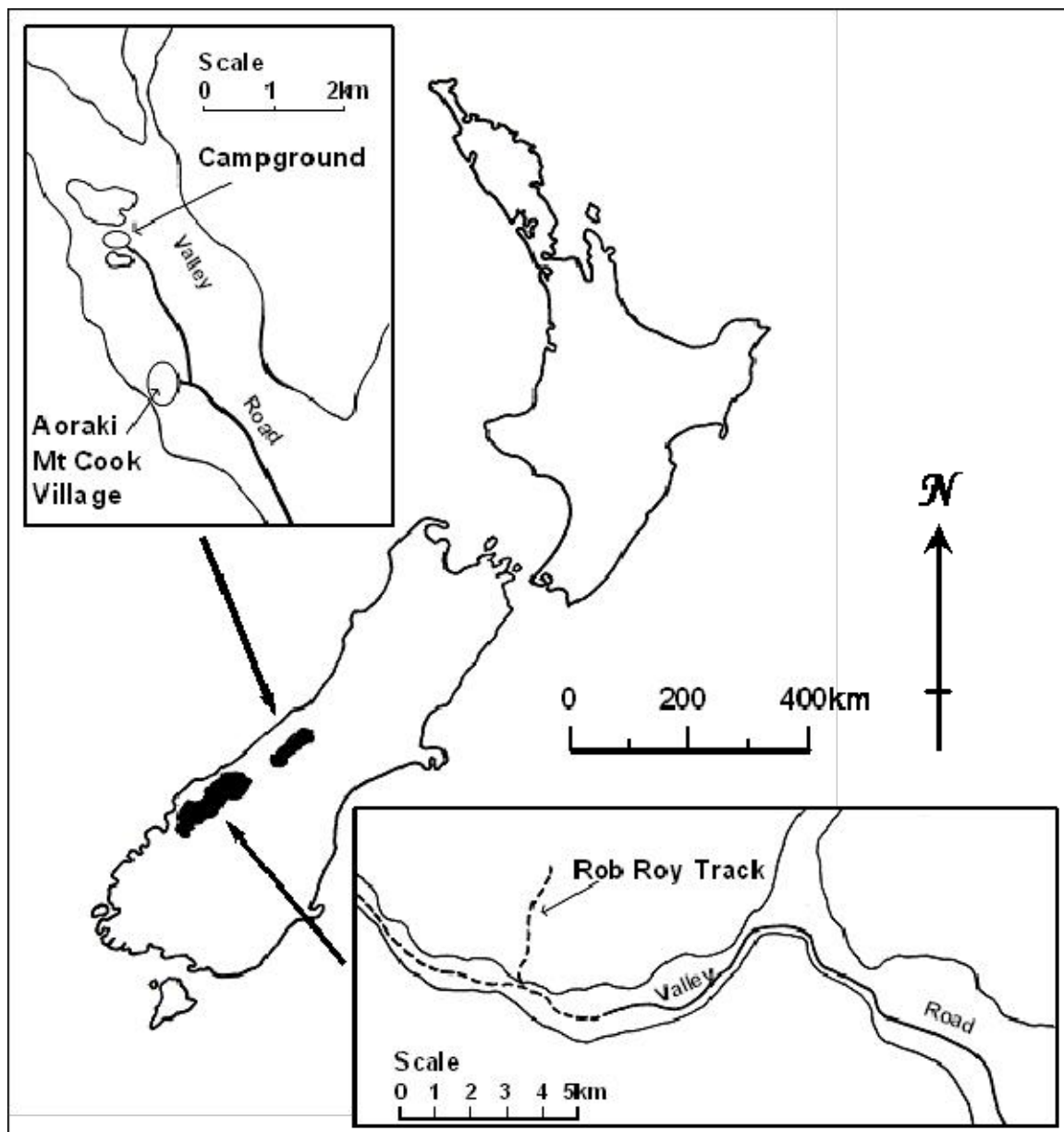
Figure 1. Map of New Zealand with study locations. The extent of national parks are indicated in black: Mount Aspiring National Park on the left, Aoraki/Mt Cook National Park on the right.

Subjects and Sampling

Every unbanded bird that I captured was fitted with a uniquely numbered metal leg band on 1 tarsometatarsus and 2 coloured darvic plastic bands on the other tarsometatarsus for remote visual identification. Colour band combinations were unique within each study area and fitted to the left leg in AMCNP and the right leg in MANP. Bill length and width were measured for all birds captured from April 2006 and weights also measured for birds caught from November 2006 onwards. A clinical examination was also conducted and a sample of blood obtained from the ulna vein for most birds or from the median metatarsal vein in several birds. As part of clinical examination the body condition of individual kea was determined via palpation of the pectoral muscles (Doneley *et al.* 2006). Body condition was scored on a 5-point scale to 0.5 number gradations, where 1 is emaciated and 5 is grossly obese (McLelland *et al.* in press) (Figure 2). Sex and age class of the birds was established (Bond *et al.* 1991, Diamond and Bond 1999) using bill length and weight for sex determination and body and plumage colouration for age classification. Blood sampling and clinical examinations of birds captured in 2006 were conducted by Jenny McLelland (JM). Birds captured in 2007 and 2008 were sampled and examined by the author.

At AMCNP 44 kea were captured and fitted with leg bands between 19 April 2006 and 19 February 2008. Fieldwork was conducted each year between November and May. Five female and 23 male fledglings, 14 juvenile males, and 2 sub-adult males were captured. Fledglings are in the summer of their emergence from the nest, juveniles are in their second summer, sub-adults are in their 3rd or 4th summer,
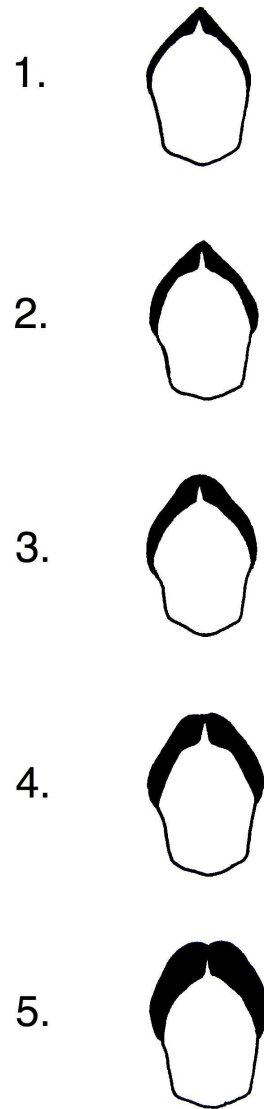
Figure 2. Body condition score classes showing the cross-section of a bird's body approximately half way along the breast muscles. Breast muscle is indicated in black. (After Griffin 2002, BTO Swallow Roost Project field manual.)

and adults are 4 + years of age (Diamond and Bond 1999). Other kea banded by researchers in previous seasons were occasionally seen and 3 participated in experiments. These birds were usually difficult to identify because several had lost their plastic bands and I was not able to confirm their metal band numbers. Only 2 were captured and had their blood sampled for lead testing. Three kea banded as part of a simultaneous project, the Kea Research Project at the University of Vienna, were observed in 2008 and one of them, a fledgling male, participated in experiments. Experiments were conducted from 6 December 2006 onwards. Banded kea that participated in experiments at AMCNP included 1 female and 2 male adults, 1 male juvenile, 5 female and 14 male fledglings.

At MANP 20 kea were captured and banded between 5 December 2007 and 14 February 2008 including 1 female and 5 male fledglings, 1 female and 3 male juveniles, 5 male sub-adults, and 2 female and 3 male adults. One female and 1 male juvenile, 3 male sub-adults, 1 female and 1 male adult participated in experiments at MANP. An unknown number of unbanded kea at both sites were observed and some participated in experiments.

Blood Sampling and Analysis

Blood lead levels were analysed for 41 of the 44 kea banded at AMCNP between 19 April 2006 and 19 February 2008. Four female and 21 male fledglings, 14 male juveniles, 1 previously banded female and 2 male sub-adults, and 1 previously banded adult male were captured and blood sampled. Six additional kea were banded as part of a simultaneous project, the Kea Research Project at the University of Vienna, and blood samples from 3 of them submitted to New Zealand Wildlife Health Centre (NZWHC) at Massey University. Three of these kea were observed as part of this study in 2008 and one of them, a fledgling male, participated in experiments. Blood samples from 19 of the 20 kea banded between 5 December 2007 and 14 February 2008 at MANP were analysed for lead levels.

Kea were blood sampled from the left or right ulna vein. Of the birds sampled in 2006, several were sampled from the median metatarsal vein. Blood was put in 0.4 ml lithium heparin microtainers (Benton Dickenson Vacutainer Systems, Preanalytical Solutions, Franklin Lakes, NJ 07417). Blood lead was analysed in the field by Jenny McLelland (JM), Kate McInnes (KM) of the Department of Conservation (DOC), or submitted to the NZWHC at Massey University for analysis.

Blood sampling and clinical examinations were conducted by JM (2006), KM (MANP), or the author (2007 and 2008, AMCNP). Several birds were recaptured and sampled deliberately in order to obtain a serial blood lead level. Blood samples were analysed for lead content with a portable lead analyser (LeadCare®; ESA Inc., Chelmsford, Massachusetts, 01824, USA). All blood lead analyses for this study were carried out on the same analyser. Blood was prepared according to the analyser instructions. The heparinised sample was mixed with the supplied treatment reagent within the manufacturer's recommended time frame, and either analysed in the field or refrigerated and sent for analysis to the NZWHC at Massey University packed in ice. The analyser uses anodic stripping voltammetry (ASV) to measure the amount of lead in a sample, as described in Wang (2000), and has a detection range of 0.0 µg/dl – 65.0 µg/dl and an analytical reporting range of 1.4 µg/dl – 65.0 µg/dl (Anonymous 2005). Levels greater than 65.0 µg/dl are designated as "HI", i.e., beyond the upper detection limit of the analyser. Where the upper limit of the analyser was reached, a 1:10 dilution with saline was used to provide a quantitative measure.

Behavioural Observations

Data were obtained during 517 hours of observation conducted during 3 field seasons. Data were collected at AMCNP from 19 to 25 April 2006, 27 November 2006 to 19 May 2007, and 27 January to 19 February 2008. Data were collected at MANP from 5 to 14 December 2007

and 11 to 14 February 2008. Data were collected using instantaneous scan sampling and focal-individual sampling. All-occurrence sampling was used during experimental novel object presentations.

Observation sessions coincided as closely as possible with peak kea activity periods at dawn and dusk when the birds are also most accessible for study. The number of sessions conducted per day was dependent on the accessibility of kea but was generally restricted to 1 in the morning and 1 in the evening. Kea are usually more active at the AMCNP study sites in the morning. Morning observation periods were begun when daylight allowed remote identification of band colours and ended when the kea dispersed. Daytime and evening sessions began upon arrival of kea at the study site and ended either when the kea dispersed or poor light no longer allowed remote identification of band colours. Sampling during the middle of the day was only carried out in MANP. Kea were not accessible during the day at AMCNP. During each observation period the presence of banded and unbanded birds was noted. Group size varied from 1 to 20 birds per observation session ($\overline{X} \pm$ SD, 4.49 ± 3.87). Instantaneous scan samples were taken approximately every 10 minutes, unless a novel object presentation, focal individual sample, or capture were underway.

The activity of all visible individuals and the individuals within 1 body length of each other were recorded during instantaneous scan samples. Focal animal sampling was conducted on a randomly chosen individual unless rarely seen birds or those not previously sampled were present, in which case they were prioritised. Behaviour of the focal individual was recorded at 1 minute intervals unless it was engaged in social behaviour, in which case the behaviours of the focal individual and other individuals involved were sampled continuously. Focal animal samples were 10 minutes in duration. If a focal animal sample was terminated prematurely because the bird left the study area it was used if at least 7 minutes in length. All observations were recorded directly onto a dictaphone (Sony Microcassette-corder

M-455) and transcribed. The majority of birds sampled were fledgling males. Juveniles, sub-adults, adults, and females of all age classes were encountered less frequently at AMCNP (Table 1).

Social Rank

Social hierarchy in kea is determinable by noting instances of displacement. A displacement is where a bird moves away from an approaching individual (Diamond and Bond 1999). Dominance hierarchies were constructed from the numbers of observed displacements where more dominant animals displace other individuals more often (Martin and Bateson 2007). Not all banded kea within each site and season were observed interacting with each other. Because the observed numbers of kea varied between site and season kea were divided into categories 1 to 5 according to rank to allow comparison between sites and seasons. Kea in the highest 1/5 of the hierarchy, i.e., those that most commonly displaced other kea, were placed in category 1, kea in the 2nd 1/5 in category 2, kea of the 3rd 1/5 in category 3, kea of the 4th 1/5 in category 4, and kea of the lowest 1/5 in category 5 to establish an ordinal dominance scale.

Table 1. The maximum number of birds of each age-sex class sampled simultaneously at Aoraki/Mount Cook National Park (AMCNP) and Mount Aspiring National Park (MANP).

Field Site	Field Season	Fledglings		Juveniles		Sub-adults		Adults	
AMCNP		**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**
	2006	0	0	2	10	0	0	0	1
	2006/2007	5	10	2	3	2	6	1	2
	2007/2008	2	7	1	2	0	1	1	3
MANP									
	2007/2008	1	2	2	1	1	3	1	2

F = Female, M = Male. Fledglings = kea in the summer of their emergence from the nest; juveniles = kea in their second summer; sub-adults = kea in their 3rd or 4th summer; adults = kea that are 4 + years of age.

Novel Object Presentations

Novel object presentations were conducted by presenting kea with 1 of 19 toys in the size range of 100 - 310 mm ($\overline{X}$ = 186.3). Most of the objects were toys commercially available for domestic dogs and chosen for their robustness. A kea was randomly selected for each trial from the banded individuals present, unless an untested bird was present in which case that individual was prioritised. Similarly, kea observed infrequently were prioritised for the experiments. Novel objects were randomly chosen for presentation to focal individuals from a randomly allocated subset of objects taken to the field site for each observation period. Objects previously presented to and contacted by the focal individual were removed from the subsequent sample set for that bird. Some birds contacted the same novel object in more than 1 trial because they were present during presentations to other focal birds and group compositions were not controlled. Only the first trial with the same novel object per bird was included in the analysis of contact data. In the analysis of latency to contact data only the first trial in which the individual was presented with the novel object was included. The number of novel objects presented to each individual differed due to the variation in group composition between observation sessions and because kea participation in experiments was voluntary. Individual kea were presented with novel objects whenever kea were accessible. Generally novel object presentations were avoided when a group of kea were actively foraging because they tended to ignore the novel objects in these instances.

Before each trial began I held the novel object out in front of me until I observed the bird orientate towards the toy. I then placed the novel object on the ground (t_o) and started the stopwatch as I moved away to a distance of at least 1 m. The kea were tolerant of human presence and readily participated in experiments when I was within close range, enabling me to retreat only a short distance in order to observe them. The test area comprised a circular area of approximately 2 m radius from the novel object. During trials I recorded the numbers

and identities of kea present in the test area. For each focal individual I recorded whether or not the bird made contact with the novel object and, if it did, latency to contact in seconds with a stopwatch. I made an all occurrence record of the behaviour of the focal kea towards the novel object and other objects. Instances of contact, latency to contact, and behavioural diversity were also recorded for non-focal birds. Latency data were rounded to the nearest second. Based on my observations and the literature (Diamond and Bond 1991, 1999; Gajdon and Voelkl 2002; Jackson 1963; Johnston 1999; Keller 1974, 1975; Potts 1969; Zeigler 1975) I identified 35 behaviours as useful for measuring object-related behavioural diversity (Table 2). Tests were generally stopped after no kea had contacted the toy for 2 minutes or when all kea departed the surrounding visible area. Data were also collected for birds that were exposed to the same novel object multiple times. Not all kea that participated in novel object trials had their blood sampled and so the blood lead data set was smaller (137 trials for 23 birds) than the novelty response data set (183 trials for 31 birds). Contact, latency to contact, and behavioural diversity were compared using the novelty response data set. In order to compare the lead data against the novelty response variables, only those birds that had known blood lead levels were included in the analysis of novelty response versus lead levels (Table 3). Behavioural diversity data were square root transformed.

Table 2. Ethogram of behaviours associated with novel object presentations in kea (*Nestor notabilis*).

Behaviour to be Measured	Description of Behaviour
Carry	An object is transported, typically by carrying it in the bill while the bird runs or walks away. Often associated with Take.
Cere	The forehead is held to an object so that the cere touches it. This position is maintained for some time.
Chew	Once an object has been grasped in the bill, it is held in place with the maxilla and repeatedly pressed with the mandible.
Drag	An object is held in the bill and dragged along the ground as the bird walks backwards.
Drop	Releasing a lifted object from the bill or the foot so that it is subjected to gravity.
Flick	With an object grasped in the bill, the kea jerks its head vertically so that the object is lifted into the air, but not released as in Toss Up. This may be done repeatedly while the bird is stationary or Carrying the object.
Grasp with Bill	A large or anchored object is grasped with the bill (often associated with Pull or Pry).
Hold with Bill	An object is held in the bill without manipulation while the bird is stationary.
Hold with Foot	A large object is grasped with the foot and held upright while resting on the substrate and is manipulated with the bill.
Hold Down with Foot	An object is held against the substrate with a foot while the bird manipulates it with the bill.
Invert Object	Once a kea has grasped an object in its bill, it exerts force on it by Pulling until it is turned on its opposite side and then released.
Jump On	A kea jumps forward toward an object and lands on it with both feet, sometimes accompanied by wing flapping.
Lever	The tip of the maxilla is inserted into a hole or crevice, then pulled and twisted. The force is exerted mainly with the head and neck. The tip of the mandible may be used as a fulcrum, or the bird may pry against the curved upper surface of the maxilla or twist the maxilla laterally.

Table 2 continued.

Behaviour to be Measured	Description of Behaviour
Lick	A kea repeatedly touches an object with its tongue as it holds an object between maxilla and mandible. As opposed to Moving the Bill, the maxilla and mandible remain still.
Lying on Back	A kea rolls onto its back or side with wings closed and feet extended, sometimes making wrestling movements. This is accompanied by manipulation of an object with bill or feet.
Manoeuvre Object	The bird directs a moving object around an obstacle while Pushing the object with its head.
Move Around Object	A kea moves around a stationary object with the bill or a foot in contact with it.
Move Bill	A forceps-like movement of the bill, opposing tips of the mandible and maxilla, often accompanied by in-and-out movements of the tongue.
Pick Up	An object is seized with the bill and lifted.
Probe	The maxilla is inserted vertically into any crevices or grooves in an object and may also be dragged along a groove.
Pull	Once an object is grasped in the bill, the kea exerts leverage through the back and legs, pulling toward itself. Both feet are planted on the ground, with the hallux flexed and serving as a fulcrum, with the result that an object is pulled towards the bird.
Push with Head	A kea lowers its head and presses its forehead against an object, and either: – the kea raises its head and the object moves. This may be done repeatedly by moving quickly after the object. – the kea pushes the object with its head and the object rolls from one side to the other.
Push with Foot	The kea extends its leg and presses its foot against an object.
Rummage	An object is picked up with the bill and let go with a quick lateral movement of the head, so that the item is flung for some distance.
Run and Toss	Grasping an object in its bill, a kea moves quickly in a lateral direction and jerks its head sideways, releasing the toy and throwing it some distance.

Table 2 continued.

Behaviour to be Measured	Description of Behaviour
Scrape	An object is held in position with the maxilla while the mandible is scraped over the surface of the object. Often accompanied by Hold Down with Foot.
Scratch	The tip of the maxilla is moved over the surface of an object, the tongue may also come into contact with the object.
Squeeze	A kea extends its head and briefly presses part of a stationary object between its maxilla and mandible once, then releases the object and retracts its head from it.
Stand on Object	A kea steps onto an unstable object that is on the ground, and maintains its balance with both feet on top of it, usually for a few moments.
Swing Object	Once a kea has Picked Up an object in its bill, it stands stationary and repeatedly moves the object from side to side suspended in the air.
Take Object from	A kea seizes, or attempts to seize, an object with its bill that is currently being held by another bird. This is often followed by Carry.
Toss Up	While an object is held in the bill, the head is jerked vertically, tossing the object into the air. The behaviour may be accompanied by a Hop or Wing Flap just before the object is released and may be repeated for several min at a time. Toss Up often follows directly after Pick Up in a quick series of motions.
Touch with Bill	An object is briefly touched with the tip of the maxilla.
Touch with Foot	The kea lifts and extends a leg towards an object, and briefly touches it with part of the foot.
Wrestle Object	Grasping an object with its bill, a kea pulls vigorously at it in a repeated back-and-forth or side-to-side motion. The object moves but remains in contact with the ground.

Table 3. Composition of study populations of kea (*Nestor notabilis*) at Aoraki/Mount Cook National Park (AMCNP) and Mount Aspiring National Park (MANP).

Kea ID	Site	Blood Lead Analysis	Age	Sex	Number of Trials	% Trials with conspecifics present
KA	AMCNP	Yes	J	M	0	N/A
KB	AMCNP	Yes	J	M	0	N/A
KC	AMCNP	Yes	J	M	0	N/A
KD	AMCNP	Yes	J	M	0	N/A
KE	AMCNP	Yes	J	M	0	N/A
KF	AMCNP	Yes	J	M	0	N/A
KJ	AMCNP	Yes	J	M	0	N/A
KL	AMCNP	Yes	J	M	0	N/A
KM	AMCNP	Yes	J	M	0	N/A
KN	AMCNP	Yes	J	M	0	N/A
KO	AMCNP	Yes	J	M	0	N/A
KP	AMCNP	Yes	J	M	0	N/A
KQ	AMCNP	Yes	S	F	0	N/A
KR	AMCNP	No	A	M	18	0
KS	AMCNP	Yes	A	M	2	50
KT	AMCNP	Yes	S	M	0	N/A
KU	AMCNP	Yes	F	M	7	100
KV	AMCNP	No	F	F	3	100
KW	AMCNP	Yes	F	M	17	59
KX	AMCNP	Yes	F	F	5	100
KY	AMCNP	Yes	F	M	10	80
KZ	AMCNP	Yes	F	F	2	50
LA	AMCNP	Yes	F	M	2	50
LB	AMCNP	Yes	J	M	3	67
LC	AMCNP	Yes	F	M	0	N/A
LD	AMCNP	Yes	F	M	8	63
LE	AMCNP	Yes	J	M	0	N/A
LF	AMCNP	Yes	F	M	2	100
LG	AMCNP	Yes	F	M	0	N/A
LH	AMCNP	Yes	F	M	0	N/A
LI	AMCNP	No	F	M	0	N/A
LJ	AMCNP	Yes	F	M	1	0
LK	AMCNP	Yes	F	M	2	100
LM	AMCNP	No	F	M	7	0
LN	AMCNP	Yes	F	M	0	N/A
LO	AMCNP	Yes	F	M	0	N/A
LP	AMCNP	Yes	S	M	0	N/A

Sex: F = female, M = male. Age: F = fledgling; J = juvenile; S = sub-adult; A = adult. Fledglings = kea in the summer of their emergence from the nest; juveniles = kea in their second summer; sub-adults = kea in their 3rd or 4th summer; adults = kea that are 4 + years of age.

Table 3 continued.

Kea ID	Site	Blood Lead Analysis	Age	Sex	Number of Trials	% Trials with conspecifics present
LQ	AMCNP	Yes	F	M	0	N/A
LR	AMCNP	Yes	F	M	0	N/A
LS	AMCNP	Yes	F	M	0	N/A
LT	AMCNP	Yes	F	M	3	100
LU	AMCNP	No	F	M	0	N/A
LV	AMCNP	Yes	F	M	7	86
LW	AMCNP	No	F	M	10	40
LX	AMCNP	Yes	F	M	3	100
LY	AMCNP	Yes	F	M	0	N/A
LZ	AMCNP	Yes	F	M	7	71
MA	AMCNP	Yes	F	M	8	63
MB	AMCNP	Yes	F	F	4	100
MC	AMCNP	Yes	F	F	7	29
MD	MANP	Yes	A	M	15	0
ME	MANP	Yes	J	M	7	14
MF	MANP	Yes	S	M	15	0
MG	MANP	Yes	J	M	0	N/A
MH	MANP	Yes	A	M	0	N/A
MI	MANP	Yes	S	M	0	N/A
MJ	MANP	Yes	A	F	0	N/A
MK	MANP	Yes	F	F	0	N/A
ML	MANP	Yes	F	F	0	N/A
MM	MANP	Yes	F	M	0	N/A
MN	MANP	Yes	A	M	0	N/A
MO	MANP	Yes	F	M	0	N/A
MP	MANP	Yes	J	M	0	N/A
MQ	MANP	Yes	J	F	3	100
MR	MANP	Yes	S	M	1	100
MS	MANP	Yes	F	M	0	N/A
MT	MANP	Yes	S	M	2	50
MU	MANP	Yes	F	M	0	N/A
MV	MANP	No	A	M	1	100
MW	MANP	Yes	S	M	0	N/A

Sex: F = female, M = male. Age: F = fledgling; J = juvenile; S = sub-adult; A = adult. Fledglings = kea in the summer of their emergence from the nest; juveniles = kea in their second summer; sub-adults = kea in their 3rd or 4th summer; adults = kea that are 4 + years of age.

To examine the range of explorativity between individuals I used contact and latency to contact data. To exclude potential effects of age and sex only fledgling males from AMCNP were scored. Individuals did not always contact the novel objects during the test period and so I used latency categories of 1 to 5 instead of exact latency times (Stöwe and Kotrschal 2007). I used a latency category 1 for latencies 1 to 45 s; 2 for latencies 46 to 90 s; 3 for latencies 91 to 135 s; 4 for latencies 136 to 180; and 5 for latencies >180 s. The greatest latency observed was 180 s so trials in category 5 were those in which no contact was made with the novel object. I calculated the mean latency for each bird and used it as a score for explorativity. Only kea that participated in 2 or more trials were scored. Kea with mean latency categories between 1.0 and 3.0 were categorised as explorative, with a score of 1.0 considered as highly explorative and a score of 3.0 scarcely explorative. Scores between 3.1 and 5.0 were categorised as aversive, with 5.0 considered highly aversive and 3.1 scarcely aversive.

Statistical Analyses

I employed an information-theoretic approach to testing hypotheses about the relationships between a kea's behavioural responses to novel objects, their biological character, social context, and blood lead levels (Johnson and Omland 2004). First I considered site (national park) as the base model because I knew there to be site differences in kea blood lead concentrations but was primarily interested in whether biological character or social context contributed significantly to explaining a kea's behaviour towards a novel object and by inference lead. In compiling my candidate models I began with the hypothesis that an individual kea's biological character, defined here by age and sex, influences its response to novelty and so predicts blood lead levels. Novelty response is here defined by whether or not kea made contact, the latency to contact, and behavioural diversity when interacting with a

novel object. Secondly I considered whether social context, defined by the presence or absence of conspecifics and the number of kea present in the test area (group size), performed better than the starting model. I then considered whether biological character and social context combined performed better than the 2 models separately. These hypotheses are numbered in sequence and listed as candidate models (e.g., Table 4).

I conducted all procedures using R version 2.6.2 (The R Foundation for Statistical Computing, Vienna, Austria) to generate likelihood ratios and calculate the Akaike Information Criterion (AIC) for each linear regression model in the way described by Burnham and Anderson (2002). Contact data are binary and so a logistic regression was used to construct the models. I judged the relative power of candidate models by comparing their AIC and ratios of Akaike weights (w_i). Models with lowest AIC have the most support from the data. Relative support between candidate models was the difference between each model's AIC and the minimum value (AIC_{min}) from all models (ΔAIC). I considered models with $\Delta AIC \leq 2$ to have substantial support from the data, those where $2 \leq \Delta AIC \leq 4$ to have moderate support, those where $4 \leq \Delta AIC \leq 7$ to have minimal support, and models with $\Delta AIC > 10$ to have no support (Burnham and Anderson 2001).

Data are presented as percentage frequency graphs because of the unequal distribution of trials between individuals (e.g., Figure 3). The changes in response for birds that were repeatedly exposed to the same novel object were also examined using linear regression.

Chapter 3

Results

Response to Novel Objects

A kea's biological character provided the greatest inference (i.e., lowest AIC) for contact (w_i = 0.838, Table 4a) and latency to contact (w_i = 0.609, Table 4b), and substantial support (i.e., ΔAIC < 2) for behavioural diversity (w_i = 0.350, Table 4c) in response to a novel object. Biological character and social context together provided the greatest inference for behavioural diversity (w_i = 0.650), substantial support (i.e., ΔAIC < 2) for latency to contact (w_i = 0.390), and moderate support (i.e., $2 \leq \Delta$AIC ≤ 4) for contact (w_i = 0.161) with a novel object. There was no support for the role of social context or site (i.e., ΔAIC > 10, low w_i values) in the response to a novel object. Social context provided less support than site for both contact and behavioural diversity.

The rate of contact at MANP was significantly higher than AMCNP (Figure 3) (χ^2 = 11.82, df = 1, P < 0.001), for males versus females (Figure 4) (χ^2 = 15.51, df = 1, P < 0.001), and for birds in the absence of conspecifics (Figure 5) (χ^2 = 4.83., df = 1, P = 0.028). Contact varied significantly with group size, and was highest with 4 kea present (Figure 6) (χ^2 = 15.06, df = 7, P = 0.035). Contact was significantly higher for non-fledglings (Figure 7) (χ^2 = 13.57, df = 3, P = 0.0036). Latency to contact was significantly lower at MANP than AMCNP (Figure 8) (Welch two sample t-test: t = 4.201, df = 100.34, P < 0.001), for males versus females (Figure 9) (Welch two sample t-test: t = 4.033, df = 40.40, P < 0.001), and for birds in the

Table 4: Ranked information theoretic models for contact (a), latency to contact (b), and behavioural diversity (c) in the novelty response data set. *Age, sex, and site. **Presence of other kea, number of other kea present, and site. ***Site only. K = number of explanatory variables, n = number of novel object experimental presentations, AIC = Akaike Information Criterion, ΔAIC = Change in AIC value.

(a)

Model	K	n	AIC	ΔAIC	Akaike Weights (w_i)
Biological Character*	3	183	207.993	0	0.8382
Biological Character + Social Context	5	183	211.289	3.297	0.1613
Site***	1	183	223.331	15.338	0.0004
Social Context**	3	183	225.965	17.973	0.0001

(b)

Model	K	n	AIC	ΔAIC	Akaike Weights (w_i)
Biological Character*	3	183	725.349	0	0.6091
Biological Character + Social Context	5	183	726.242	0.892	0.3899
Social Context**	3	183	739.096	13.747	0.0006
Site***	1	183	740.338	14.989	0.0003

(c)

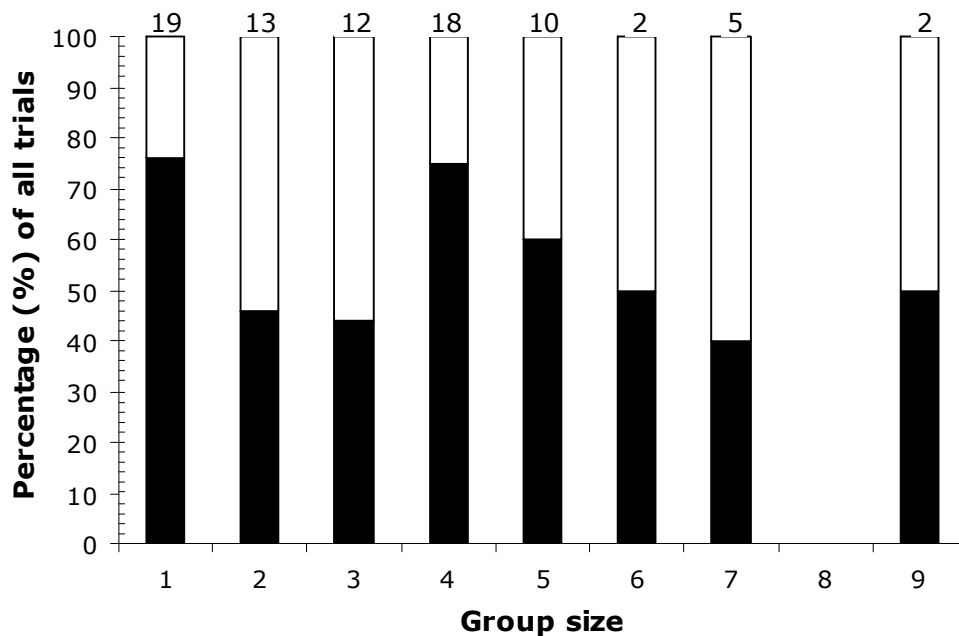| Model	K	n	AIC	ΔAIC	Akaike Weights (w_i)
Biological Character + Social Context	5	183	531.893	0	0.6495
Biological Character*	3	183	533.130	1.237	0.3499
Site***	1	183	547.025	15.131	0.0003
Social Context**	3	183	547.723	15.830	0.0002

Figure 3. Percentage of trials in which contact with a novel object was made at each site. White bars represent no contact, black bars contact. Numbers above bars show the number of kea contributing to each bar.

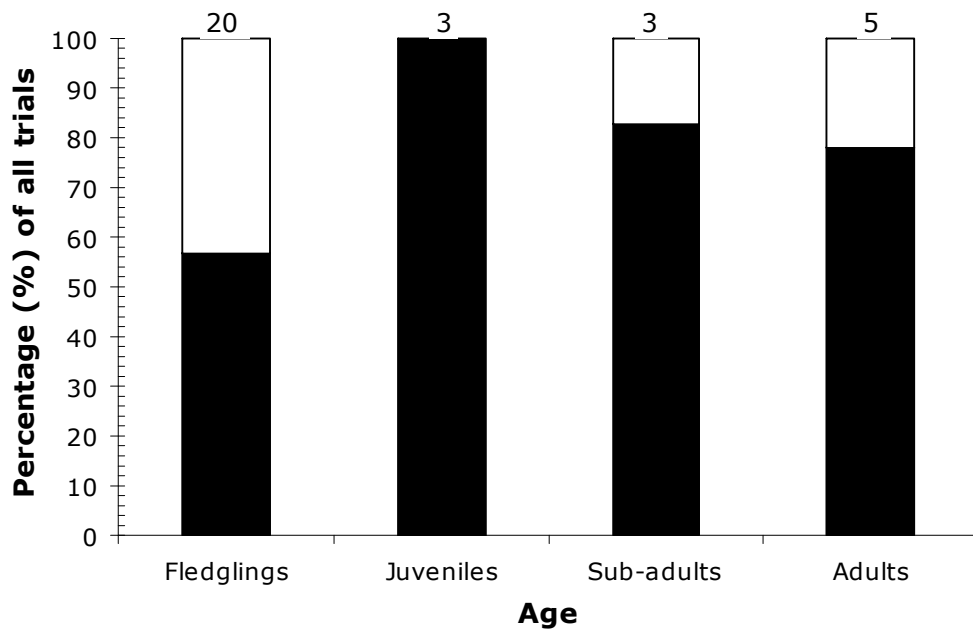Figure 4. Percentage of trials in which contact with a novel object was made by females and males. White bars represent no contact, black bars contact. Numbers above bars show the number of kea contributing to each bar.
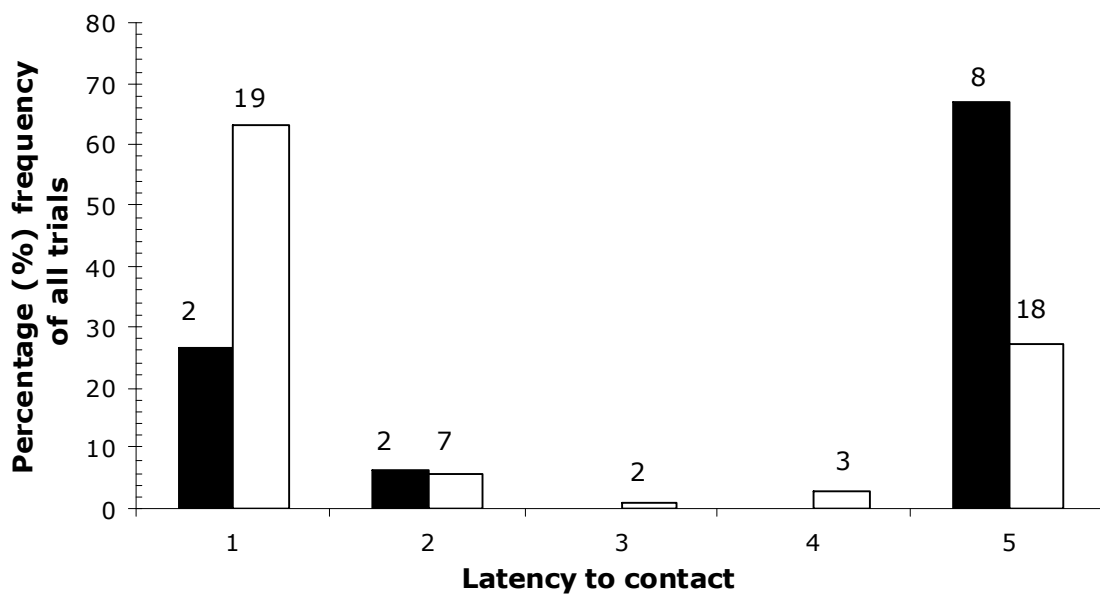
Figure 5. Percentage of trials in which contact with a novel object was made in the presence or absence of conspecifics. White bars represent no contact, black bars contact. Numbers above bars show the number of kea contributing to each bar.

Figure 6. Percentage of trials in which contact with a novel object was made according to group size. White bars represent no contact, black bars contact. Numbers above bars show the number of kea contributing to each bar.

Figure 7. Percentage of trials in which contact with a novel object was made by kea of 4 age groups. White bars represent no contact, black bars contact. Numbers above bars show the number of kea contributing to each bar.

Figure 8. Contact latencies measured during novel object experiments for kea at each site. Black bars represent birds from Aoraki/Mount Cook National Park; white bars represent birds from Mount Aspiring National Park. 1 = 1 - 45 s; 2 = 46 - 90 s; 3 = 91 - 135 s; 4 = 136 - 180 s, 5 = 181+ s (no contact made). Numbers above bars show the number of kea contributing to each bar.

Figure 9. Contact latencies measured during novel object experiments for female and male kea. Black bars represent females, white bars males. 1 = 1 - 45 s; 2 = 46 - 90 s; 3 = 91 - 135 s; 4 = 136 - 180 s, 5 = 181+ s (no contact made). Numbers above bars show the number of kea contributing to each bar.

absence of conspecifics (Figure 10) (Welch two sample t-test: $t = - 3.35$, $df = 176.06$, $P < 0.001$). Latency was significantly higher for fledglings than other age groups (Figure 11) (Kruskal-Wallis rank sum: $\chi^2 = 12.19$, $df = 3$, $P = 0.0068$). Latency increased significantly with group size (Figure 12) (Kruskal-Wallis rank sum: $\chi^2 = 25.36$, $df = 7$, $P < 0.001$). Behavioural diversity was significantly higher at MANP than AMCNP (Figure 13) (Welch two sample t-test: $t = -4.455$, $df = 81.76$, $P < 0.001$), males versus females (Figure 14) (Welch two sample t-test: $t = -3.627$, $df = 41.26$, $P < 0.001$), and for birds in the absence of conspecifics (Figure 15) (Welch two sample t-test: $t = 3.0985$, $df = 180.536$, $P = 0.0023$). Behavioural diversity decreased significantly with group size (Figure 16) (1-way ANOVA: $F_{1,181} = 5.45$, $P = 0.021$). Behavioural diversity did not vary significantly with age (1-way ANOVA: $F_{1,181} = 2.85$, $P = 0.093$).

Lead and Response to Novel Objects

Biological character provided the greatest inference (i.e., lowest AIC) for contact ($w_i = 0.874$, Table 5a), latency to contact ($w_i = 0.751$, Table 5b), and behavioural diversity ($w_i = 0.783$, Table 5c), but minimal support (i.e., $4 \leq \Delta AIC \leq 7$) for blood lead concentrations in kea ($w_i = 0.091$, Table 5d). Biological character and social context together provided the greatest inference for blood lead concentrations ($w_i = 0.899$), moderate support (i.e., $2 \leq \Delta AIC \leq 4$) for contact ($w_i = 0.122$), latency to contact ($w_i = 0.237$), and behavioural diversity ($w_i = 0.216$). Social context provided only negligible support ($\Delta AIC = 9.033$, low w_i value) for lead and the other variables (i.e., $\Delta AIC > 10$, low w_i values). Social context provided less support than site for all models except when predicting lead levels. Site provided negligible support for
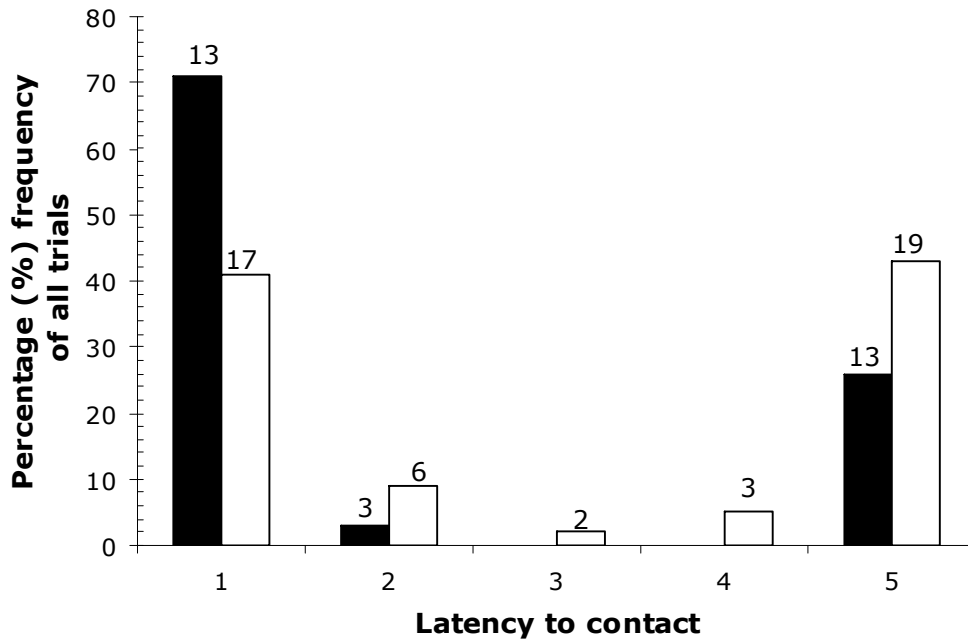
Figure 10. Contact latencies measured during novel object experiments for kea in the presence or absence of conspecifics. Black bars represent absence; white bars presence. Latency categories: 1 = 1 - 45 s; 2 = 46 - 90 s; 3 = 91 - 135 s; 4 = 136 - 180 s, 5 = 181+ s (no contact made). Numbers above bars show the number of kea contributing to each bar.
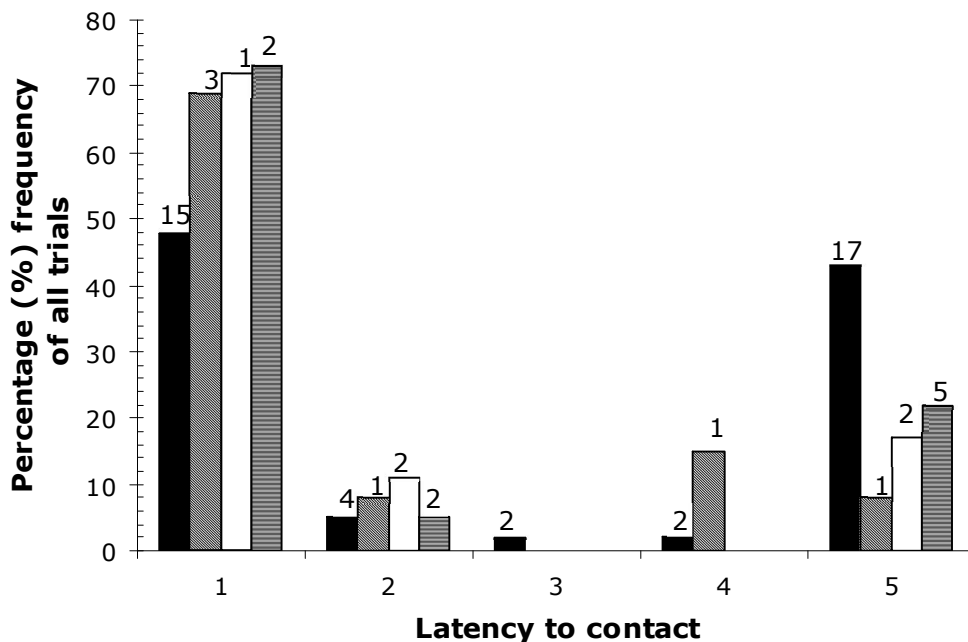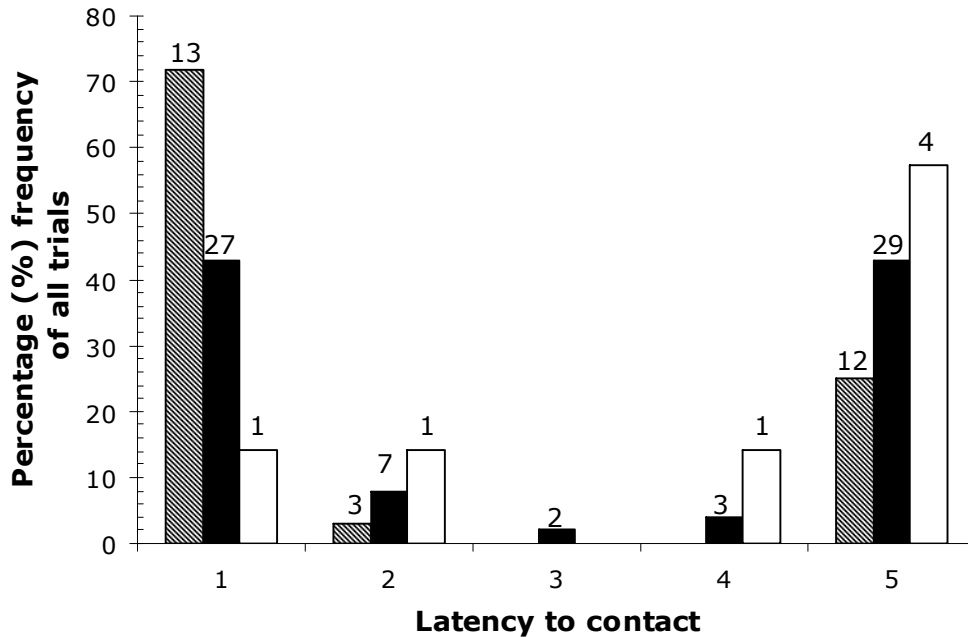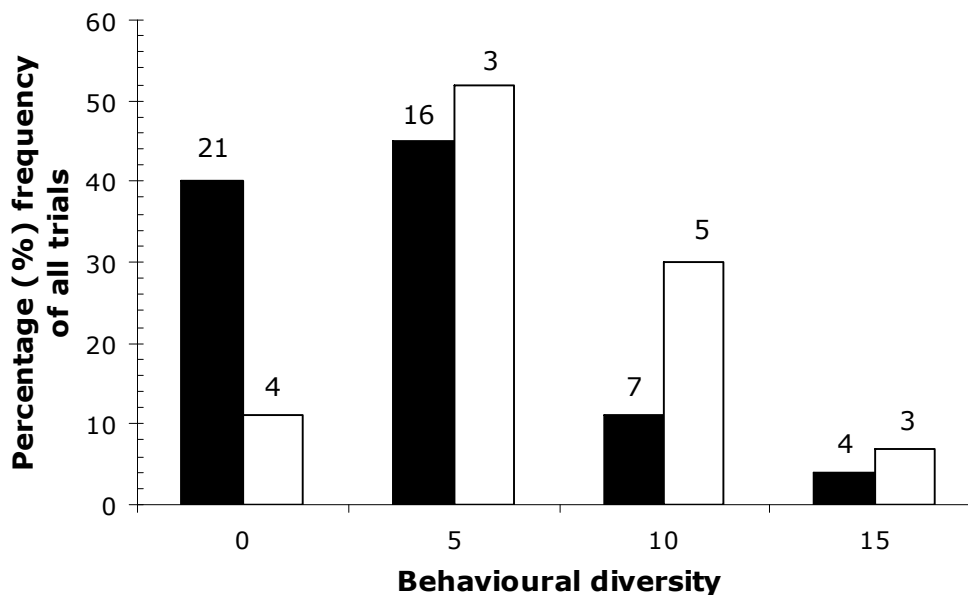

Figure 11. Contact latencies measured during novel object experiments for kea of 4 age groups. Black bars represent fledglings, diagonal lines juveniles, white bars sub-adults, and horizontal lines adults. Latency categories: 1 = 1 - 45 s; 2 = 46 - 90 s; 3 = 91 - 135 s; 4 = 136 - 180 s, 5 = 181+ s (no contact made). Numbers above bars show the number of kea contributing to each bar.

Figure 12. Contact latencies measured during novel object experiments for kea according to group size. Diagonal lines represent 1 kea, black bars 2 – 6 kea, and white bars 7 - 9 kea. Latency categories: 1 = 1 - 45 s; 2 = 46 - 90 s; 3 = 91 - 135 s; 4 = 136 - 180 s, 5 = 181+ s (no contact made). Numbers above bars show the number of kea contributing to each bar.

Figure 13. Behavioural diversity exhibited by kea at Aoraki/Mt Cook and Mount Aspiring National Parks during contact with novel objects. On the x-axis is the grouped number of object-related behaviours per trial: 0 = no behaviours; 5 = 1 - 5 behaviours; 10 = 6 - 10 behaviours; 15 = 11 - 15 behaviours. Black bars represent birds from Aoraki/Mount Cook National Park, white bars represent birds from Mount Aspiring National Park. Numbers above bars show the number of kea contributing to each bar.
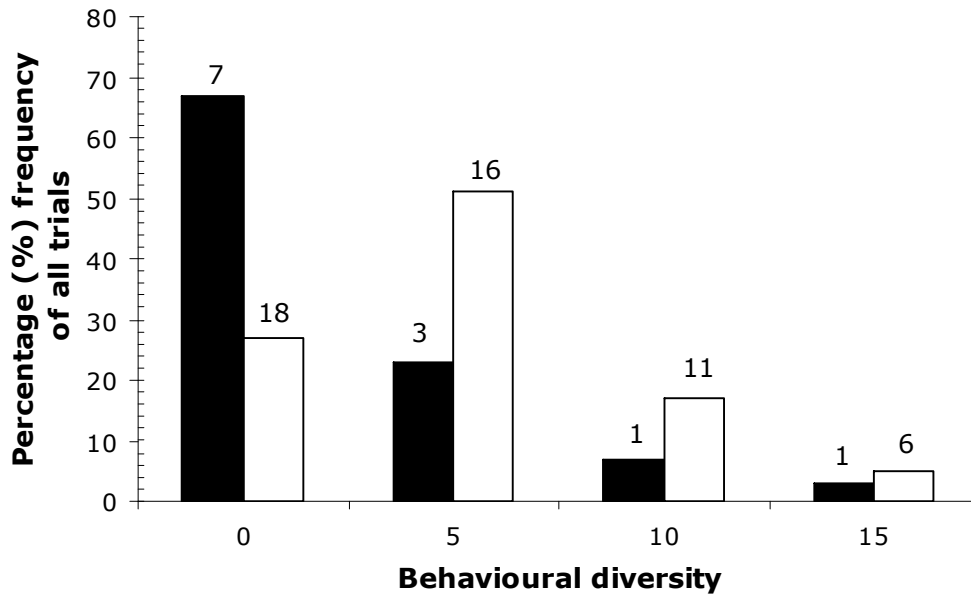
Figure 14. Behavioural diversity exhibited by female and male kea during contact with novel objects. On the x-axis is the grouped number of object-related behaviours per trial: 0 = no behaviours; 5 = 1 - 5 behaviours; 10 = 6 - 10 behaviours; 15 = 11 - 15 behaviours. Black bars represent females, white bars males. Numbers above bars show the number of kea contributing to each bar.
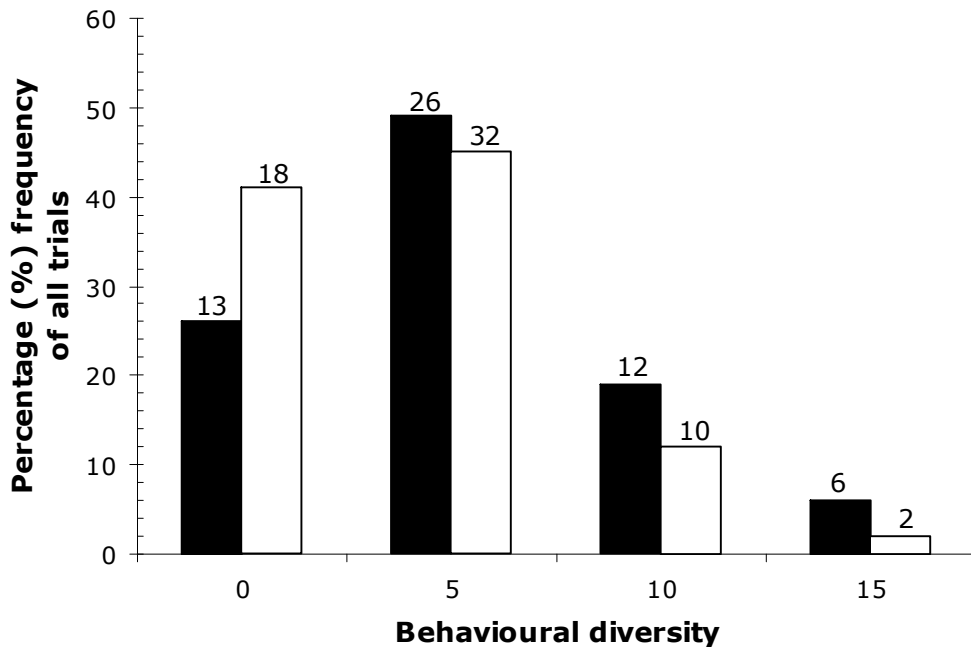

Figure 15. Behavioural diversity exhibited by kea during contact with novel objects in the presence or absence of conspecifics. On the x-axis is the grouped number of object-related behaviours per trial: 0 = no behaviours; 5 = 1 - 5 behaviours; 10 = 6 - 10 behaviours; 15 = 11 - 15 behaviours. Black bars represent the absence of conspecifics, white bars presence. Numbers above bars show the number of kea contributing to each bar.
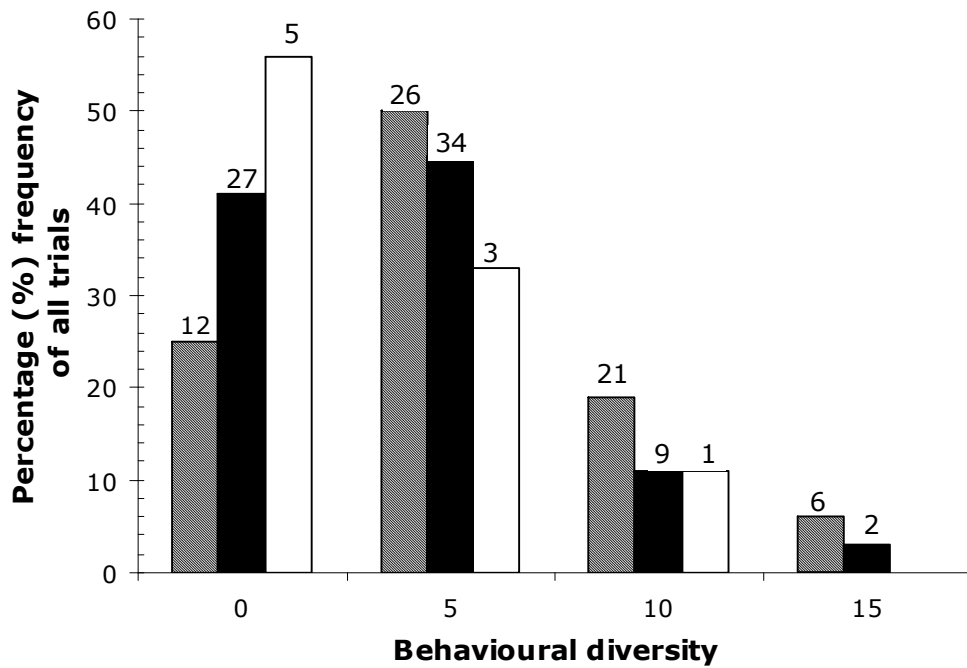
Figure 16. Behavioural diversity exhibited by kea during contact with novel objects according to group size. On the x-axis is the grouped number of object-related behaviours per trial: 0 = no behaviours; 5 = 1 - 5 behaviours; 10 = 6 - 10 behaviours; 15 = 11 - 15 behaviours. Diagonal lines represent group size of 1, black bars group size 2 to 6, white bars 7 to 9. Numbers above bars show the number of kea contributing to each bar.

Table 5: Ranked information theoretic models for contact (a), latency to contact (b), behavioural diversity (c), and blood lead concentrations (µg/dl) in the lead and novelty response data set. *Age, sex, and site. **Presence of other kea, number of other kea present, and site. ***Site only. K = number of explanatory variables, n = number of novel object experimental presentations, AIC = Akaike Information Criterion, ΔAIC = Change in AIC value

(a)

Model	K	n	AIC	ΔAIC	Akaike Weights (w_i)
Biological Character*	3	137	148.155	0	0.8739
Biological Character + Social Context	5	137	152.085	3.93	0.1225
Site***	1	137	159.391	11.236	0.0032
Social Context**	3	137	163.131	14.976	0.0005

(b)

Model	K	n	AIC	ΔAIC	Akaike Weights (w_i)
Biological Character*	3	137	537.560	0	0.7513
Biological Character + Social Context	5	137	539.870	2.310	0.2367
Site***	1	137	546.224	8.664	0.0099
Social Context**	3	137	549.238	11.678	0.0022

(c)

Model	K	n	AIC	ΔAIC	Akaike Weights (w_i)
Biological Character*	3	137	390.944	0	0.7832
Biological Character + Social Context	5	137	393.520	2.576	0.2161
Site***	1	137	405.123	14.179	0.0007
Social Context**	3	137	408.935	17.991	0.0001

(d)

Model	K	n	AIC	ΔAIC	Akaike Weights (w_i)
Biological Character + Social Context	5	137	1042.900	0	0.8985
Biological Character*	3	137	1047.470	4.570	0.0915
Social Context**	3	137	1051.933	9.033	0.0099
Site***	1	137	1059.671	16.771	0.0002

latency to contact (ΔAIC = 8.66, low w_i value) and the other variables (i.e., ΔAIC > 10, low w_i values).

The rate of contact increased significantly with age (χ^2 = 15.17, df = 3, P = 0.0017), was significantly higher at MANP than AMCNP (χ^2 = 14.23, df = 1, P < 0.001) and for males versus females (χ^2 = 11.78, df = 1, P < 0.001). Contact varied significantly with group size, and was highest with 4 kea present (χ^2 = 12.57, df = 7, P = 0.083). Contact did not differ significantly with the presence of conspecifics (χ^2 = 2.72, df = 1, P = 0.099). Latency to contact was significantly lower at MANP than AMCNP (Welch two sample t-test: t = 4.766, df = 116.02, P < 0.001), for males versus females (Welch two sample t-test: t = 3.24, df = 33.56, P = 0.0027), and for kea in the absence of conspecifics (Welch two sample t-test: t = - 2.84, df = 134.49, P = 0.0053). Latency decreased significantly with age (Kruskal-Wallis rank sum: χ^2 = 13.15, df = 3, P = 0.0043) and increased with group size (Kruskal-Wallis rank sum: χ^2 = 20.39, df = 7, P = 0.0048). Behavioural diversity at MANP was significantly higher than at AMCNP (Welch two sample t-test: t = - 4.772, df = 95.87, P < 0.001), for males versus females (Welch two sample t-test: t = - 2.977, df = 34.21, P = 0.0053), and for kea in the absence of conspecifics (Welch two sample t-test: t = 2.59, df = 129.36, P = 0.011). Behavioural diversity decreased significantly for all age groups (1-way ANOVA, $F_{1,135}$ = 8.468, P = 0.0042), and decreased significantly with group size. Blood lead concentrations were significantly lower at MANP than at AMCNP (Figure 17) (Welch two sample t-test: t = 8.79, df = 16.41, P < 0.001), and for non-fledglings versus fledglings (Figure 18) (1-way ANOVA: $F_{1,21}$ = 27.562, P < 0.001). Lead levels did not differ significantly between sexes (Welch two sample t-test: t = - 0.935, df = 34.453. P = 0.3563). Lead levels were significantly higher for kea that participated in trials with conspecifics present than for those in trials where
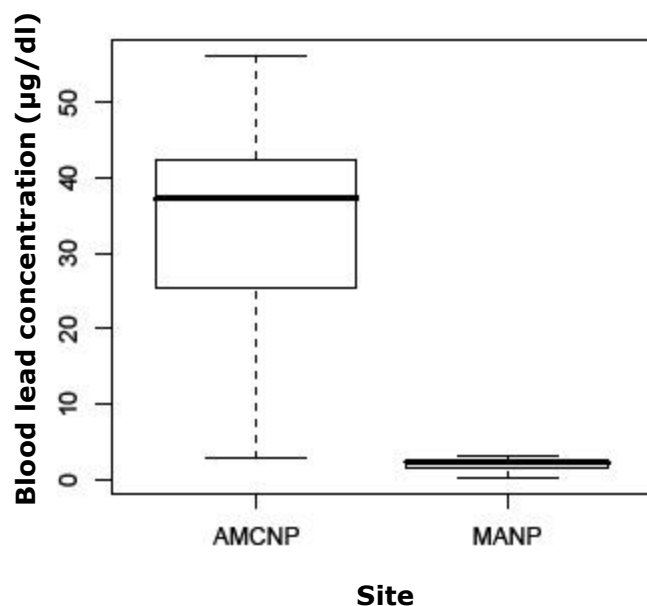
Figure 17. Blood lead concentrations (µg/dl) of kea at Aoraki/Mount Cook and Mount Aspiring National Parks that participated in novel object experiments. *Box plots* show the median and the interquartile range from the 25th to the 75th percentile. *Whiskers* show the 10th and the 90th percentiles.
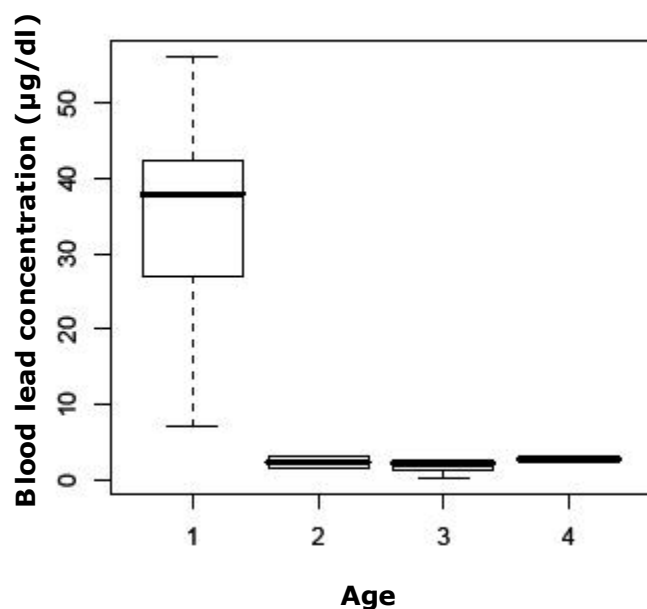

Figure 18. Blood lead concentrations (µg/dl) for the 4 age groups that participated in novel object experiments at Aoraki/Mount Cook and Mount Aspiring National Parks: 1 = fledglings; 2 = juveniles; 3 = sub-adults; 4 = adults. *Box plots* show the median and the interquartile range from the 25th to the 75th percentile. *Whiskers* show the 10th and the 90th percentiles.

none were present (Figure 19) (Welch two sample t-test: $t = -7.588$, $df = 127.09$ $P < 0.001$). Lead levels varied significantly for kea participating in trials with different group sizes, and was highest with 1 conspecific present (Figure 20) (1-way ANOVA: $F_{1,135} = 21.601$, $P < 0.001$).

Multiple Presentations

The relationship between the number of repeated presentations with the same object and contact was not significant (Kruskal-Wallis rank sum: $\chi^2 = 1.91$, $df = 4$, $P = 0.75$). The relationship between latency to contact and number of presentations was also not significant (Kruskal-Wallis rank sum: $\chi^2 = 1.172$, $df = 4$, $P = 0.88$). However, the relationship between the number of repeated presentations and behavioural diversity was significant (Figure 21) (1-way ANOVA: $F_{1, 271} = 4.092$, n = 31, $P = 0.044$).

Lead

All kea sampled for blood lead testing (n = 65) had been exposed to lead (Figure 22) and 45 of 46 (97.8%) kea tested at AMCNP had blood lead concentrations above 5 µg/dl at the time of testing. All MANP kea were below 5 µg/dl. Blood lead concentrations ranged from 2.8 to 343 µg/dl for kea at AMCNP ($\overline{X} \pm$ SD, 43.0 ± 53.1) and 0.3 to 3.1 µg/dl at MANP ($\overline{X} \pm$ SD, 2.0 ± 0.7). Blood lead concentrations from kea at the two sites differed significantly (Welch two sample t-test: $t = 5.039$; $df = 42.03$; $P < 0.001$). One juvenile male from AMCNP was removed from the analyses due to the effect of his extremely elevated blood lead level (343 µg/dl) on the results.

Blood lead concentrations decreased as body condition increased, but not significantly (Figure 23) (1-way ANOVA: $F_{1, 37} = 3.658$, n = 39, $P = 0.064$). Only
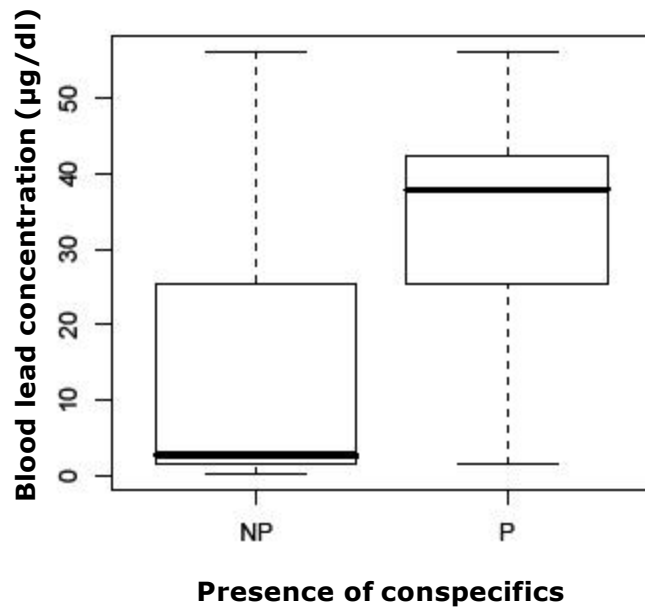
Figure 19. Blood lead concentrations (µg/dl) for kea that participated in novel object experiments in the absence (NP) or presence (P) of conspecifics. *Box plots* show the median and the interquartile range from the 25th to the 75th percentile. *Whiskers* show the 10th and the 90th percentiles.
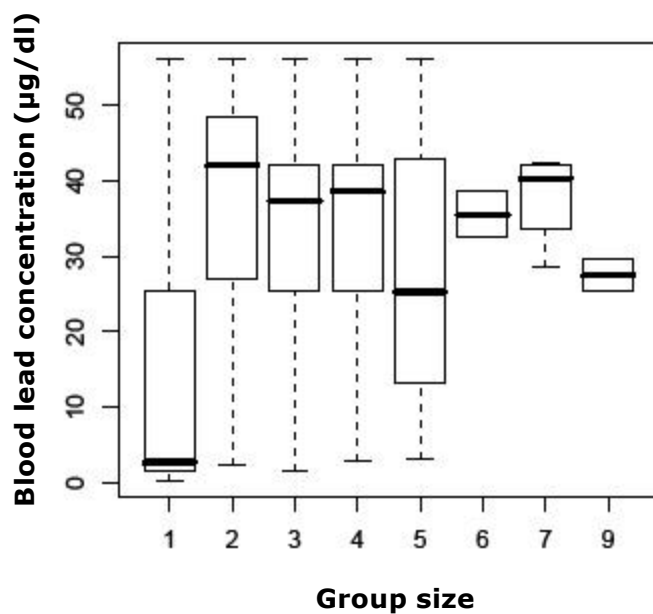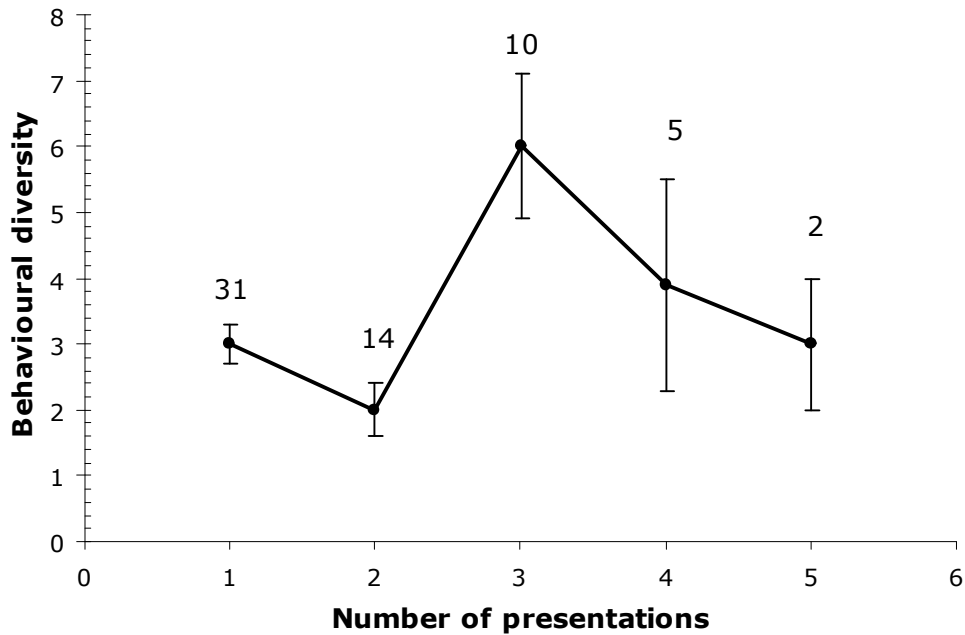

Figure 20. Blood lead concentrations (µg/dl) for kea that participated in novel object experiments with different group sizes. *Box plots* show the median and the interquartile range from the 25th to the 75th percentile. *Whiskers* show the 10th and the 90th percentiles.

Figure 21. Mean behavioural diversity exhibited by kea during contact with novel objects in repeated presentations. On the y-axis is the number of object-related behaviours per trial. Numbers show the number of kea contributing to each data point.
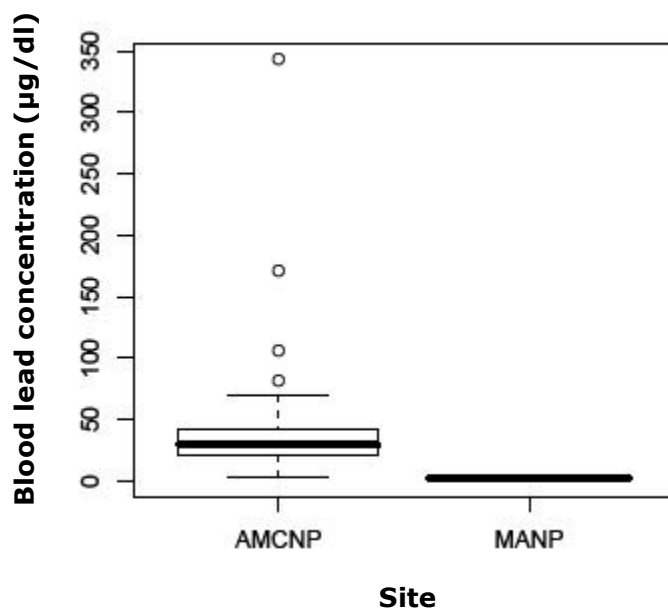

Figure 22. Blood lead concentrations (µg/dl) for kea sampled at Aoraki/Mount Cook and Mount Aspiring National Parks. *Box plots* show the median and the interquartile range from the 25th to the 75th percentile. *Whiskers* show the 10th and the 90th percentiles. *Circles* show outliers.
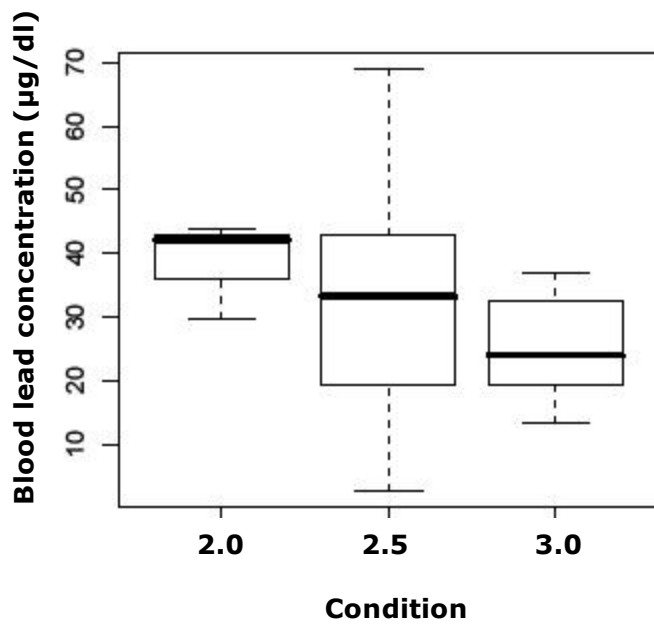
Figure 23. Blood lead concentrations (µg/dl) versus condition for kea at Aoraki/Mount Cook National Park. *Box plots* show the median and the interquartile range from the 25th to the 75th percentile. *Whiskers* show the 10th and the 90th percentiles.

kea from AMCNP were included because the low blood lead concentrations of MANP kea did not provide a broad enough range to reflect any meaningful relationship between lead levels and condition (Figure 22). Four kea were also removed from the analysis as outliers (Figure 22): 2 fledglings and 2 juveniles had blood lead levels in excess of 80 µg/dl. All kea palpated had condition scores between 2 and 3.5.

Lead did not have a significant relationship with contact (logistic regression: n = 23, P = 0.31), or latency to contact (linear regression: $F_{1, 135}$ = 1.768, n = 23, P = 0.19), or behavioural diversity (Figure 24) (linear regression: $F_{1, 135}$ = 1.18, n = 23, P = 0.28).

Explorativity

Fourteen fledgling males from AMCNP were given latency scores. Scores ranged from 1.0 (highly explorative) to 3.7 (medium aversive). Latency scores were significantly related to behavioural diversity (Figure 25) (linear regression: $F_{1, 91}$ = 31.99, n = 14, $P < 0.001$), but not lead (linear regression: $F_{1, 9}$ = 4.139, n = 11, P = 0.072). Sample sizes of birds in other sex-age classes were too small for statistical analysis, but fledgling females (n = 5) and adult males (n = 3) appeared to follow the same trend as demonstrated by the fledgling males (Figure 26). Sample sizes of individuals in the remaining demographics that participated in > 1 trial were too small (n ≤ 2) for an examination of explorativity range.

Dominance

Dominance rank was compared with explorativity for 13 male fledglings of known rank, and the relationship was not significant (linear regression: P = 0.83, $F_{1, 11}$ = 0.051). However, the proportion of contact decreased significantly as dominance
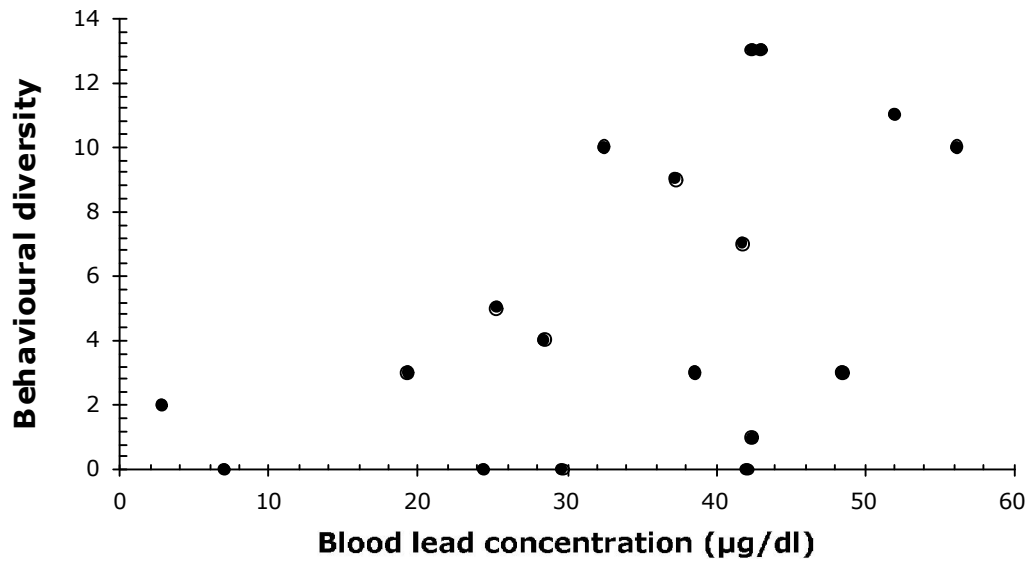
Figure 24. Maximum behavioural diversity versus blood lead concentrations (µg/dl) for individual kea at Aoraki/Mount Cook.
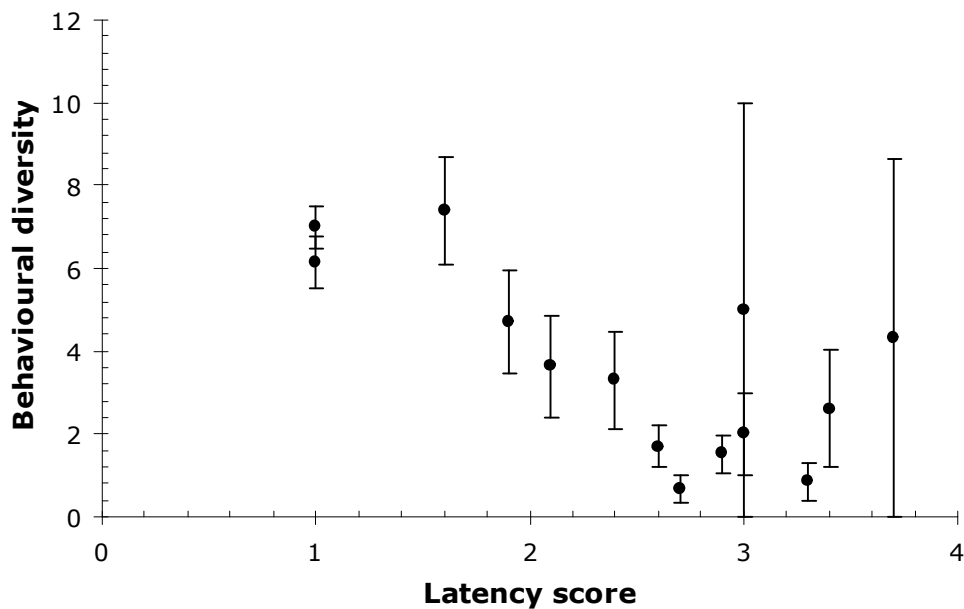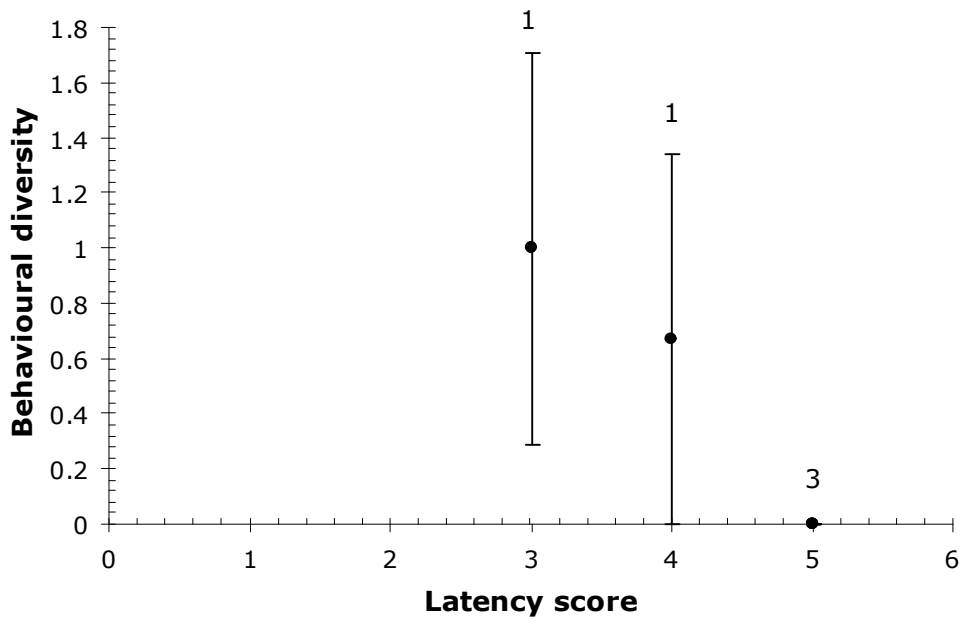

Figure 25. Mean behavioural diversity exhibited by 14 fledgling male kea at Aoraki/Mount Cook during contact with novel objects. On the x-axis is the mean latency score. On the y-axis is the number of object-related behaviours per trial.
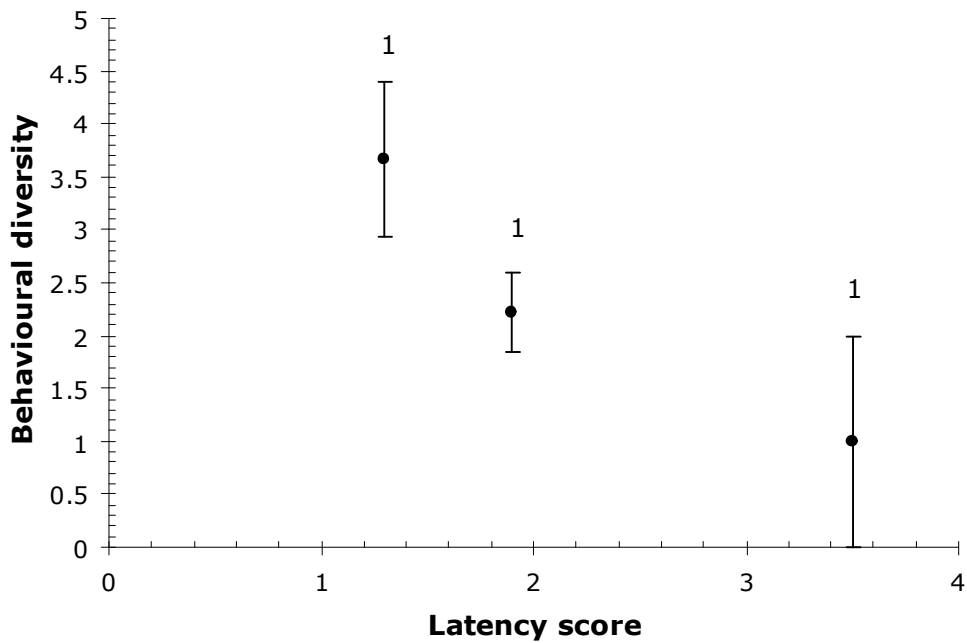
Figure 26. Mean behavioural diversity exhibited by 5 fledgling female kea at Aoraki/Mount Cook National Park (a), and adult males (both sites) during contact with novel objects. On the x-axis is the mean latency score. On the y-axis is the number of object-related behaviours per trial. Numbers show the number of kea contributing to data point.

rank increased (Figure 27) (logistic regression: n = 29, $P < 0.001$). Latency to contact increased significantly with dominance rank (Figure 28) (linear regression: $F_{1,\,173} = 16.7$, n = 29, $P < 0.001$), and behavioural diversity decreased as dominance rank increased (Figure 29) (linear regression: $F_{1,\,173} = 9.466$, n = 29, $P = 0.0024$). The relationship between dominance rank and lead was not significant (linear regression: $F_{1,\,21} = 0.9206$, n = 23, $P = 0.35$). Note that increase in dominance rank in this context equates to a numerical increase, not an increase in status (i.e., a bird of dominance category 1 is in the category of highest status).
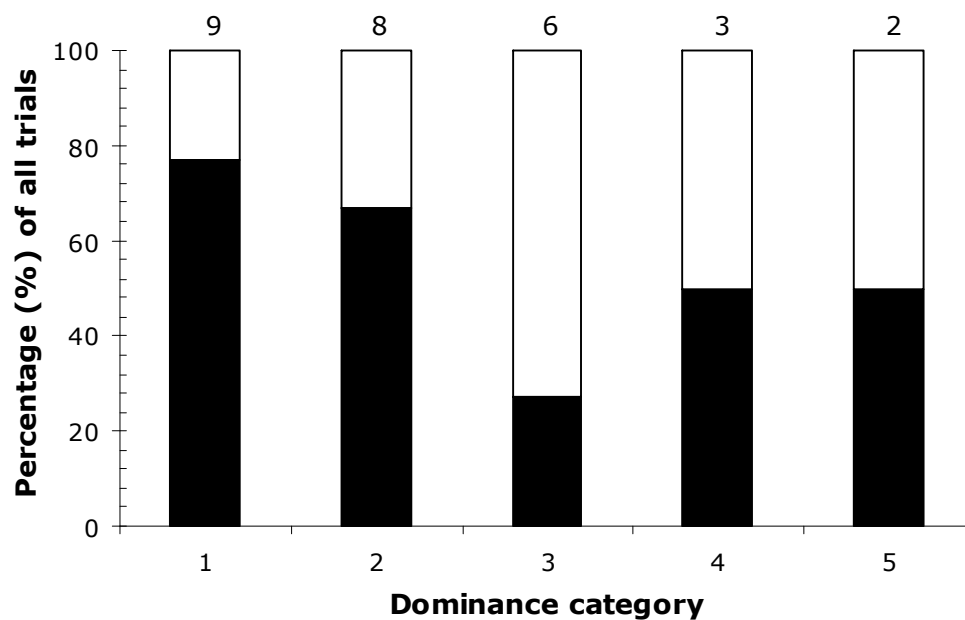
Figure 27. Percentage proportion of trials in which kea of each dominance category made contact with a novel object. White bars represent no contact, black bars contact. Numbers above bars show the number of kea contributing to each bar.
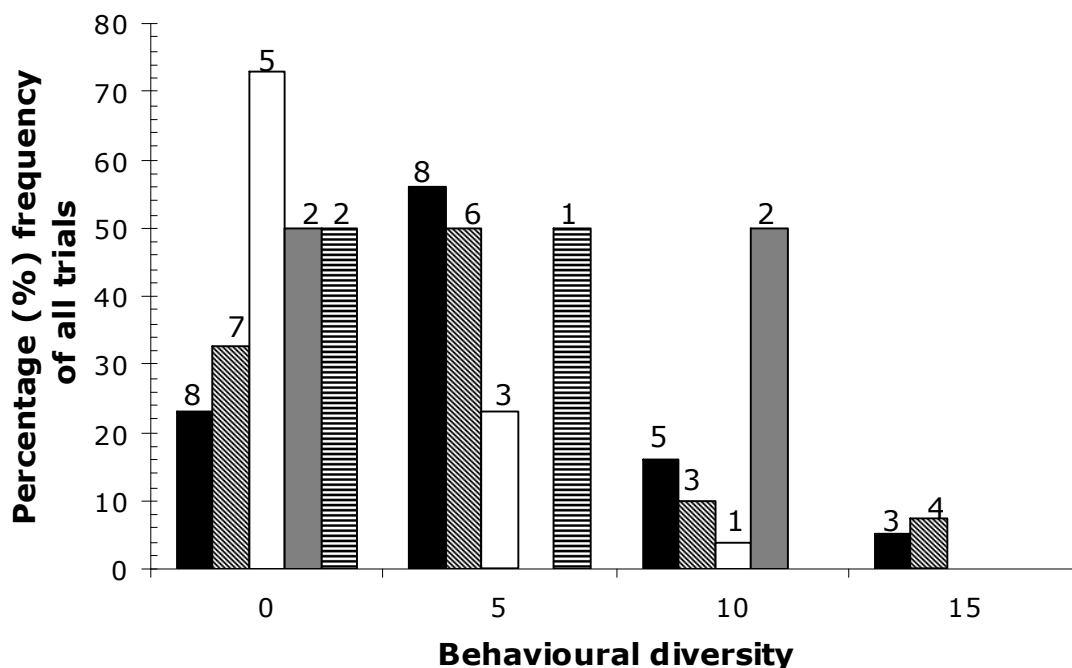

Figure 28. Contact latencies exhibited by kea of dominance categories 1 to 5. On the x-axis are the latency categories: 1 = 1–45 s; 2 = 46 - 90 s; 3 = 91–135 s; 4 = 136-180 s, 5 = 181+ s (no contact made). (Black: dominance category 1; diagonal lines 2; white 3; dark grey 4; horizontal lines 5). Numbers above bars show the number of kea contributing to each bar.

Figure 29. Behavioural diversity exhibited by kea of dominance categories 1 to 5 during contact with novel objects. On the x-axis is the grouped number of object-related behaviours per trial: 0 = no behaviours; 5 = 1 – 5 behaviours; 10 = 6 – 10 behaviours; 15 = 11 – 15 behaviours. Black bars represent dominance category 1; diagonal lines 2; white bars 3; dark grey bars 4; horizontal lines 5). Numbers above bars show the number of kea contributing to each bar.
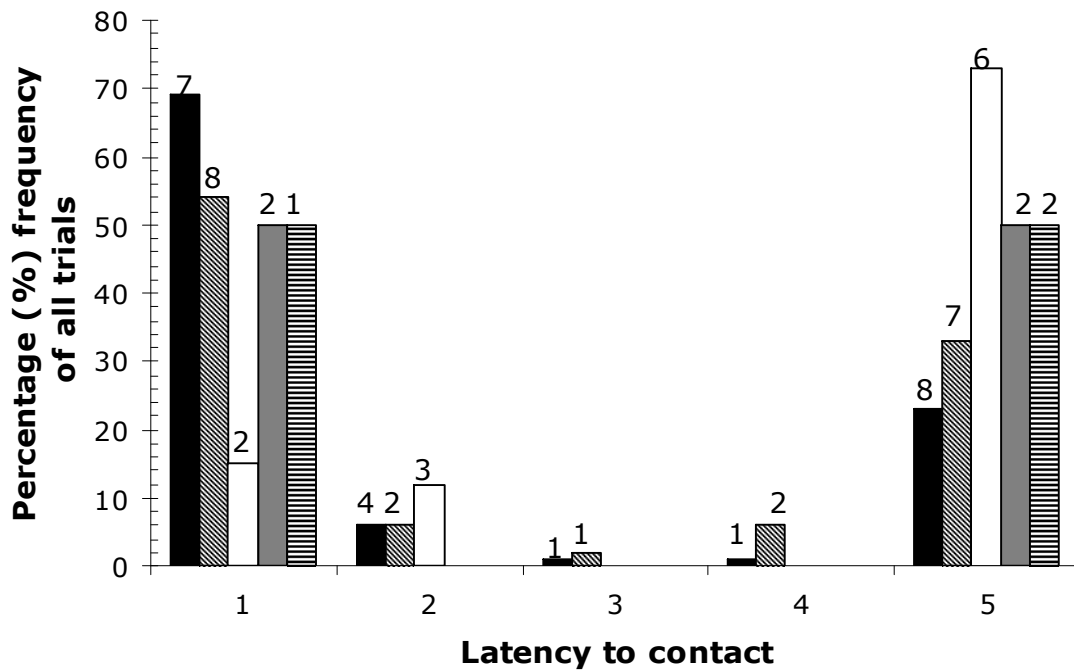
Chapter 4

Discussion

Explorativity

The relationship between the mean latency score of fledgling males at AMCNP and their behavioural diversity was a significant negative relationship, with explorative birds exhibiting a higher behavioural diversity towards novel objects than aversive birds. The same trend was shown for fledgling females and adult males. The results regarding explorativity indicate that, beyond the effects of an individual's age class and sex, personality underlies its reactions to novel objects. The range in explorativity shown by fledgling males at AMCNP and the trends shown by fledgling females and adult males support this hypothesis.

Verbeek *et al.* (1994) found that hand-reared juvenile male great tits (*Parus major*) differed consistently in their reactions to novel objects and that birds which approached novel objects more quickly also visited all artificial trees present in a novel environment more quickly than birds that visited the novel objects more slowly. These behavioural differences also extended to the strength of foraging habits developed during a training period in which food was always offered at the same place (Verbeek *et al.* 1994). After the location of food was changed, the faster birds continued visiting the place where the food was formerly located, but the slower birds tended to change their behaviour and stopped going to the original location (Verbeek 1994).

Dominance

The relationship between dominance category and contact was significantly negative. Subordinate birds were less likely to make contact with the novel object. Latency to contact increased and behavioural diversity decreased significantly as dominance rank increased. In

other words, kea of high social rank (low numerical dominance category) made contact with novel objects faster, more often, and exhibited a higher behavioural diversity towards them than kea of low social rank (high numerical dominance category). Although dominance category was not significantly related to explorativity, the significant relationships between dominance category and behavioural response to novel objects indicate that social rank is likely to be related to personality. Explorativity was based on readiness to make contact and latency to contact, and was significantly related to behavioural diversity. Dominance category had significant relationships with all of these variables. These results indicate that subordinate kea were limited in their interactions with novel objects in this study by dominant ones. In a study of captive kea, dominant birds had priority of access to novel objects and subordinate birds only had limited opportunities to explore them as a result (Kubat 1992). In studies of ravens (Stöwe and Kotrschal 2007) and great tits (Verbeek *et al.* 1996) explorative birds were more often aggressors in displacement interactions than aversive birds. Stöwe and Kotrschal (2007) indicate that the observed differences in the raven's approach latencies during novel object exploration are therefore related to personalities.

Information Theoretic Analyses

Biological character was the hypothesis most supported as an explanation for a kea's contact with and latency to contact novel objects. This result indicates that kea sex and age classes have the greatest influence on contact and latency to contact novel objects. In a study of the responses of captive kea to novel objects, Kubat (1992) also found that sex and age influenced responses to novel objects, with young males being the most explorative. Social context in combination with biological character was the hypothesis most supported as an explanation for a kea's behavioural diversity in response to a novel object (Table 4). Social context alone, however, did not predict a kea's behaviour towards novel objects. This result, along with the

predictive strength of combined biological character and social context, indicates that social context by itself is not an important factor in kea's reactions towards a single novel object, but that the effect of social context on behavioural diversity is important. This may best be explained in terms of social facilitation and is discussed later (see Social Context and Social Facilitation).

The information theoretic models based on the lead data set indicate that lead was not predicted in the same way as the behaviour towards a novel object (Table 5). Lead is most strongly predicted by the combination of biological character and social context, while the behavioural variables are all most strongly predicted by biological character alone (Table 5).

Behavioural diversity appears to be the most important behavioural measure related to blood lead levels. Whether a kea makes contact with a lead object or how quickly it does so are not likely to influence a kea's blood lead level as much as how it behaves towards the lead object when it makes contact with it. How a kea manipulates the lead and its degree of manipulation are most likely to be directly related to its blood lead levels. This is due to the malleable and fragile nature of lead. When a kea manipulates lead pieces of the metal are broken off and ingested. Particular characteristics of lead, such as malleability and taste, are features not shared with the novel objects presented in this study. Lead objects are reported to have a sweet taste and smell attractive to parrots (Lightfoot and Yeager 2008). Malleable objects such as rubber dog toys were included in the experiments but unlike lead objects they resumed their shape after manipulation and provided no taste reward. Signs of damage were apparent on lead head nails and flashings of buildings in Aoraki/Mt Cook Village that were typical of the marks left by chewing parrots (*pers. obs.*). Lead toxicosis has occurred in captive parrots after ingesting significant amounts of lead within the first 24 hours of exposure to lead toys due to the taste and smell and the malleability of this material (Lightfoot and Yeager 2008).

Site did not predict a kea's behaviour towards novel objects nor its blood lead levels, indicating that the two study populations were very similar in their overall behaviour towards novel objects and sources of lead. Despite the significant difference in blood lead levels between sites, biological character and social context together were a much stronger predictor of lead levels, outweighing any site effects.

Social Context and Social Facilitation

The predictive strength of combined biological character and social context indicates that social facilitation influences kea's behavioural diversity in interactions with novel objects. In other words the effect of social context, specifically the activities of conspecifics, on an individual influences its behavioural diversity. The lack of predictive weight of social context by itself indicates that the presence of other kea and group size are inadequate factors in isolation for predicting a kea's behavioural responses to novel objects. It is only in combination with biological character, and more specifically personality, that the effects of social context become apparent. This may be illustrated by the following example. A fledgling female ("MC", Table 3) was presented with novel objects in the absence of conspecifics. She avoided contact with all of the objects, occasionally showing tentative movements towards them but stayed at least 1 m distance. Two fledgling males arrived and all 3 were present for further trials. The fledgling males quickly made contact with the novel objects and manipulated them, and the female began to show a greater readiness to approach the objects. She approached the objects and remained within a much shorter distance than she had when alone, and exhibited play behaviour with pebbles in the test area. When she approached the objects within the distance of a few body lengths she was displaced by the male fledglings. In this situation the presence of the two males, both more explorative and dominant than the female, appeared to increase her readiness to approach the novel objects,

but simultaneously decreased her opportunity to contact the objects. This could be defined as social facilitation. I use the term social facilitation as outlined by Diamond and Bond (1999), which refers to an increased responsiveness to particular objects as a result of another's interaction with them. Therefore it ensures that a kea will pay attention not just to what other kea are doing but also to what they are feeding on or interacting with (Diamond and Bond 1999). Social facilitation appears to account for most of the influence exerted by other members of the group on learning in young kea (Diamond and Bond 1999).

In Stöwe and Kotrschal's (2007) study of ravens the presence of a conspecific delayed explorative birds' approach to novel objects but facilitated the approach of aversive ravens to novel objects when they were in the company of siblings. The approach behaviour of the individual determined whether social context facilitated or delayed exploratory behaviour (Stöwe and Kotrschal 2007). The sibling relationships of the kea in this study were unknown but may have been a factor in the responses of individuals as shown for ravens. Further study would be required to investigate the influence of sibling relationships on the behaviour of kea with different personality types. Social context has also been shown to affect the exploratory behaviour of great tits (van Oers *et al.* 2005). Aversive males were more responsive to the conspecific's activity than explorative males (van Oers *et al.* 2005). Explorative great tits, however, seemed to remain unaffected by the presence of a conspecific (van Oers *et al.* 2005). Explorative birds increased their visits to feeders indicated by a tutor bird but aversive birds did not (Marchetti and Drent 2000).

Blood Lead Concentrations

Blood lead levels differed significantly between the two sites but this is more likely due to a difference in the availability of lead between the two sites than a difference in kea behaviour. MANP, unlike AMCNP, has no permanent settlement - only scattered huts and outbuildings.

The negative relationship between blood lead concentration and body condition may be the result of the effect of lead on kea physiology. Anorexia (the lack or loss of appetite for food) is a symptom of lead toxicosis in birds (Platt 2006). Kea suffering from the deleterious effects of lead, although they may not be showing obvious clinical signs, could show an overall loss of condition detectable by muscle palpation. The relationship between blood lead level and condition were not significant and the statistical power was low (R^2 = 0.065, P = 0.064). This may be because condition scores used in this study are too coarse to detect differences in muscle condition resulting from the effects of subclinical lead toxicity or that such effects are not detectable by this method alone.

In the information theoretic models based on the behavioural data set, the combination of biological character and social context is the strongest predictor of behavioural diversity (Table 4). This difference in the predictive importance of combined biological character and social context between the behavioural data set and the lead data set is likely due to the absence of several key individuals from the lead data set. These kea were included in the behavioural data set but did not have blood samples taken for lead analysis so were not included in the lead data set (Table 3). These individuals participated in a number of trials where conspecifics were absent, so their exclusion from the lead data set likely reduced the effectiveness of the presence of conspecifics as a predictor in the information theoretic models.

Based on these results it is expected that kea exhibit the same behavioural response to lead objects as they do to novel objects, i.e., since a kea's behavioural diversity and blood lead levels are predicted in the same way, it appears that the same behaviour driving the behavioural diversity exhibited by a kea towards novel objects also drives its behaviour towards lead, as reflected by its blood lead levels.

With repeated exposure objects cease to become novel and animals become habituated. Since group compositions during the novel object experiments in this study were not

controlled, some kea participated in more than 1 trial involving the same novel object. The behavioural diversity of these kea changed significantly with repeated exposure to the same novel object (Figure 14), reaching its maximum at the third exposure and then decreasing. Johnston (1999) found that wild kea repeatedly presented with the same test object showed only minimal habituation. Ritzmeier (1995) found that captive kea continued to explore an object after repeated exposure, but that the duration of their exploration was reduced. Although the behavioural diversity of kea repeatedly exposed to the same novel object in this study decreased after the third exposure, this may not occur with lead objects. The characteristics of lead not shared with the novel objects in this study, such as malleability and taste, make lead more rewarding to kea and are likely to override effects of habituation.

A major contrast between the context of novel object trials in this study and a roof with lead fixtures is availability. Unlike the novel object trials, in which only 1 object was presented at a given time, a roof has many lead head nails spread over a large area so availability is not a limiting factor to kea's exploration. If an aversive kea is in the presence of other kea that are manipulating lead fixtures on a roof, such as multiple lead head nails or strips of flashing that span the roof's length, the aversive kea will have many opportunities for exploration of these objects available to it. It will not be excluded from making contact with these fixtures by other kea as it may be in the case of a novel object trial, where only 1 object is available to all kea present.

My study did not include kea in the nestling stage, but two nestlings were banded and fitted with transmitters as part of the University of Vienna Kea Research Project, and had blood samples taken. The nestlings had elevated blood lead levels (32.8 and 42.4 μg/dl) within the range of the other birds. One of these birds was found dead as a fledgling of approximately 4 months of age, evidently killed by a cat (B. Gartrell unpub. necropsy report). The other participated in several novel object trials as part of the present study. The elevated blood lead

concentrations of these birds in the nest indicate that kea in areas like AMCNP where their habitat overlaps with that of humans may be exposed to lead from a very early age. If they are fed lead-bearing material by their parents from sources such as human rubbish, lead exposure may begin at the nestling phase (McLelland *et al.* in press). One actively breeding adult male kea at AMCNP was observed in a previous season feeding at a rubbish source and then flying immediately to its nest. The presence of a material that appeared to be regurgitated white bread near the nest entrance may also support the theory that breeding adult males provide their mates and chicks with food directly sourced from rubbish areas (*pers. obs.*).

Another possible explanation is that the developing chick is exposed to lead within the egg (McLelland *et al.* in press; Burger and Gochfeld 1993). Blood lead concentrations of breeding females previously exposed to lead, for instance from chewing lead head nails or flashing as a young bird, may increase due to the release of lead from bone during egg formation (McLelland *et al.* in press). Once absorbed, lead is deposited in a range of tissues, primarily liver, kidney and bone (Pain *et al.* 2005). Lead in liver and kidney has a turnover rate of weeks to months, whereas in bone lead is retained for years, therefore reflecting both acute and lifetime chronic exposure from all sources (Pain *et al.* 2005). Lead in bone is physiologically incorporated over the lifetime of the bird (Pain *et al.* 2005). Wilson *et al.* (2007) found that blood lead concentrations of female Pacific common eiders (*Somateria mollisima* var. *nigrum*) increased significantly during incubation. This increase indicated a chronic low-level metabolic release of lead related to reproductive physiology, particularly the mobilisation of stored lead via metabolism of medullary bone (Franson *et al.* 2000; Wilson *et al.* 2007). Medullary bone, a non-structural type of woven bone normally found only in the long bones of female egg-laying birds, acts as a labile reservoir for the supply of eggshell calcium (Dacke *et al.* 1993). Accumulated lead, chemically similar to calcium, is also stored in the medullary

bone of ducks, and may be simultaneously mobilised with the calcium during eggshell formation (Finley and Dieter 1978; Franson *et al.* 2000; Wilson *et al.* 2007).

It is unlikely that breeding adult male kea, which are adept foragers (Diamond and Bond 1999), would ingest lead in the course of securing food. Adult males observed foraging in rubbish areas are highly selective, taking only edible items such as fat, protein, and carbohydrate (Diamond and Bond 1999; *pers. obs.*). Judging from their foraging aptitude it seems improbable that they would ingest inorganic objects except by accident. Lead toxicosis is a cause of death in adult male kea (Jarrett 1997; McLelland *et al.* in press). Although adults do spend time on the roofs of buildings they do not appear interested in chewing the fixtures as fledglings and juveniles are (*pers. obs.*). Accidental ingestion of lead in the form of shot or bullet fragments from animal carcasses is, however, a risk. A juvenile male kea was found dead at St Arnaud in October 2000 and necropsy revealed a partially digested lead shot pellet in his stomach, and lead levels confirming lead toxicosis (R. Norman unpub. necropsy report). Both lead shot pellets and bullet fragments have been shown to expose several avian species to lead due to ingestion from hunter-killed animal carcasses (Fisher *et al.* 2006). Chamois and tahr are shot as part of pest control efforts and recreationally, and hares, rabbits, cats, and possums are shot as pests at AMCNP (*pers. obs.*) and kea are known to feed on carcasses (Diamond and Bond 1999; Temple 1996; *pers. obs.*) which presents the risk of lead ingestion from animals that have been shot. Rubbish sources are likely to be more reliable in areas of human habitation than carrion however, and adult males feeding at rubbish areas at AMCNP have been observed visiting these sources on a daily basis (*pers. obs.*). Therefore if adult males rely more heavily on rubbish sources than carrion for food, this reduces the likelihood that males ingest lead and pass it on to their mates and offspring. Further research is required to discover the true source of lead, as it is currently unclear whether the elevated blood lead

levels detected in the two nestlings resulted from ingestion or equilibration of lead from the egg in soft tissues, blood, and bone compartments (B. Gartrell *pers. comm.*).

Concentrations of > 20 µg/dl lead in whole blood are indicative of lead intoxication in psittacines, and concentrations of > 40 to 60 µg/dl are diagnostic of lead toxicosis (Platt 2006). Some birds, however, have exhibited clinical signs and responded to therapy with blood lead levels as low as 10 µg/dl, and others have shown no clinical signs with much greater levels (Dumonceaux and Harrison 1994). None of the kea tested exhibited overt clinical signs of lead toxicosis at the time of sampling. One juvenile male (blood lead concentration 24.7 µg/dl) was observed exhibiting ataxia with a wide-based stance the day after sampling (McLelland *et al.* in press) but was not observed by the author. The bird was not recaptured or observed again on that trip or in subsequent seasons. Although the absence of obvious clinical signs in the kea tested in this study may suggest a tolerance to high blood lead concentrations, this does not mitigate the sub-clinical effects of low-level lead exposure (McLelland *et al.* in press). Even low levels of lead (< 10 µg/dl) have been shown to cause damage to the central nervous system in chickens (Lurie *et al.* 2006). In humans it is suggested that blood lead levels > 2.0 µg/dl should be regarded as elevated due to the effects of even very low lead levels on biological processes, mainly the nervous system (Gilbert and Weiss 2006). Burger and Gochfeld (e.g., 2005) have carried out in-depth studies on the effects of lead exposure on herring gulls (*Larus argentatus*) in the wild and the laboratory. They found that experimental dosage with low levels of lead affected locomotion, food begging, learning, thermoregulation, and individual recognition in the lab and in the wild (Burger and Gochfeld 2005). Differences between control and lead-affected chicks were pronounced for more complicated tasks, such as learning the location of hidden food, finding and staying in the shade, and recognising caretakers or siblings (Burger and Gochfeld 2005). They observed that lead-exposed chicks had lower survival in comparison to control chicks in the wild due to abnormal behaviour

(Burger and Gochfeld 1994), and they concluded that that lead profoundly affects neurobehavioural development, and that environmentally relevant lead levels can significantly affect survival (Burger and Gochfeld 2005). Gorissen *et al.* (2005) found that exposure to heavy metals, including lead, diminished the singing behaviour of wild great tits, which may affect breeding behaviour and be a useful indicator of environmental stress at the population level.

The Implications of Exploration-Avoidance

Unfortunately, explorativity may have a heavy cost where kea and human habitats overlap. If explorative kea are the first to investigate sources of novelty they may be subject to an increased risk of injury or death. If they facilitate exploration in aversive kea this increases the risk to those kea as well. Explorative kea that investigate dangerous items such as possum traps, large water containers, toxins such as lead or 1080 pellets are less likely to survive than aversive kea, potentially resulting in a population skew towards aversive kea. This may be detrimental to the species if explorative individuals also initiate exploitation of beneficial resources such as natural food particularly during resource poor seasons or years. If exploration-avoidance is linked to innovation this may come at a cost to the species. Innovative-explorative kea that learn to exploit new resources such as sheep risk being shot, and those learning to open rubbish bins may risk illness or death from exposure to toxins or pathogens, choking hazards, or entrapment. Explorative kea may also be innovative. An adult male that learned to open rubbish bins at AMCNP also participated in novel object experiments (this study), and was scored as an explorative bird (in the middle of the explorative end of the scale, mean latency score 1.9). Another adult male that attempted to open rubbish bins at AMCNP (G. Gajdon *pers. comm.*) also investigated and was killed in a Timm's trap (a kill trap for possums). Timm's traps are made with bright yellow plastic

casings, a highly attractive colour to kea (Johnston 1999). A kea would have to be highly explorative to enter the trap and trigger it.

Previous studies of kea ecology, behavioural ecology, and cognition have been carried out in areas where kea are known to be at risk from lead exposure. Jackson's studies of kea ecology and Diamond and Bond's behavioural studies at Arthur's Pass, and ongoing studies by Gajdon *et al.* of kea cognition at AMCNP and Fox Glacier have been conducted in areas where kea have elevated lead levels (Jarrett 1997; McLelland *et al.* in press; McInnes *et al.* in prep; this study), or in the cases of Arthur's Pass and AMCNP, died of lead poisoning (Jarrett 1997; McLelland *et al.* in press). Lead has been shown to affect development, behaviour, and cognitive ability in other species including birds (e.g., Kertész *et al.* 2006; Burger and Gochfeld 2005). It is likely that kea suffer the same ill-effects from lead exposure as other species and, although kea that have been exposed to lead may not show clinical signs, their behaviour and cognitive ability may be affected. The study of kea in areas with anthropogenic lead sources may not reflect the normal range of kea behaviours and capabilities. If lead differentially affects personality types, for example by putting explorative birds at greater risk due to higher lead levels, the ratios of personality types may be skewed in populations living in or near areas of human habitation. Studies of kea behaviour in more remote areas with lower risk of lead exposure may provide a useful comparison for existing ones.

Lead is a known cause of death in kea (Jarrett 1997, McLelland *et al.* in press) and as such affects kea survival. As lead is still ubiquitous in areas where kea and human habitats overlap it poses an ongoing hazard to kea throughout their distribution. Kea live in a highly seasonal and periodically severe environment, the dangers of which are compounded by various anthropogenic hazards including lead exposure. Kea are a long-lived and slow-reproducing species at a high risk of decline from even a small reduction in its survival rate - an imposed reduction in numbers could result in non-recovery (Spurr 1979).

In the absence of humans the kea's behavioural makeup has proven to be of great advantage, ensuring its survival in a severe and changing environment. Neophilia, behavioural flexibility, persistent exploration, and innovation have even enabled it to survive the invasion of New Zealand by humans and an entourage of alien species. With the incessant spread of threats however – possums have only recently invaded parts of Fiordland, and stoats have been found in higher numbers in alpine areas than in adjacent beech forest (Smith *et al.* 2007) – even the kea's adaptability may not be sufficient to ensure persistence. In the presence of humans, kea's tendencies can also prove to be a disadvantage. At some point, the costs of the risks kea take begin to outweigh the benefits.

Acknowledgements

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