The Effect of Light on the Behaviour of Captive Brown Kiwi *Apteryx mantelli;* Implications for Captive Management

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Abstract

The impact of light intensity and spectrum on the behaviour of captive brown kiwi *Apteryx mantelli* was examined through behavioural observation. This topic was chosen as most animals have a significant response to light and there are currently no guidelines for the light regimes of nocturnal houses or brooder rooms that house brown kiwi. In the first experiment the amount of time that a kiwi spent in enclosure areas illuminated by four different colours was observed. The behaviour of the kiwi was not affected by colour but significantly more time was spent in enclosure areas that were darker and close to the edge of the enclosure. A second experiment investigated the amount of time that eight captive display kiwi spent in areas of their enclosure based on illumination intensity; again more time was spent in darker and peripheral areas as well as in areas of moderate to high structural coverage though these factors were interacting and did not singularly explain where time was spent in the enclosure. Finally the effect of early brooder light exposure on the later outdoor emergence times of nine neonatal brown kiwi was observed. Chicks that were housed for their first month of life in brooders diurnally lit by 150-200 lux emerged sooner after sunset once they were later housed in outdoor pens; this is compared with chicks housed in brooders brighter than 300 lux. Overall, light intensity and structure appeared to be the most significant environmental factors though much individual variation was found. Based on my results nocturnal houses that are no brighter than five lux and have at least 50% structurally covered and peripheral areas are most likely to be preferred by kiwi. Brooder boxes may need to be dimmed if a long-term behavioural effect is occurring from current brooder light regimes. These results support the widely held belief that kiwi do not rely on vision for information about their surroundings but may have good perception of light intensity as a result of having high rod photoreceptor density. It is more likely that kiwi rely on highly developed tactile and olfactory senses than vision. Results may be applicable to nocturnal mammals that also show high predator avoidance behaviour and/or do not rely on vision, such as some primates and rodents.

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Table of contents

List of figures and tables

Chapter 1

Chapter 2

Chapter 3

Chapter 1: Introduction and review of current literature

1.1: Introduction

The topic of this thesis is whether exposure to light affects the behaviour of brown kiwi *Apteryx mantelli*. Brown kiwi are a flightless, nocturnal bird endemic to New Zealand that belong to the ratite order Struthioniformes. They share ancestry with the emu *Dromaius novaehollandiae*, ostrich *Struthio camelus*, tinamous family Tinamidae, and cassowary genus *Casuarius*, and the extinct moa genus *Dinornis*, and elephant bird *Dromornis stirtoni* (Cooper et al, 1992). The family Apterygidae is thought to be 40-80 million years old and consists of five species of kiwi (Baker et al, 1995). Brown kiwi are found in a range of habitat types including forests, farmland and shrubland throughout the North Island of New Zealand as seen in Figure 1.1 (Robertson et al, 2011).

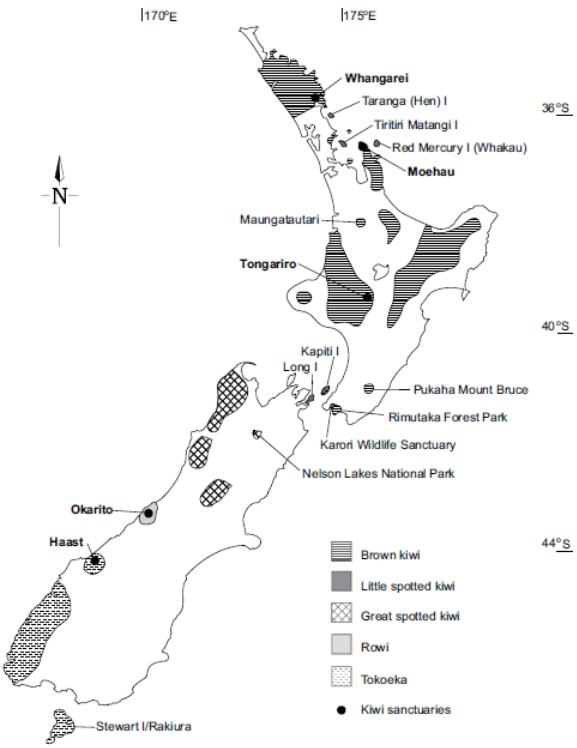


***Figure 1.1**: Distribution of Apteryx in New Zealand including sanctuaries (Robertson et al, 2011)*

Kiwi are unique having some characteristics more commonly associated with mammals, including “nocturnal habits, use of burrows, hairlike features, facial bristles, two functional ovaries, well-developed sense of smell, lower body temperature, near absence of wings, and consequent low dispersal power” (Baker et al, 1995). Kiwi exhibit reverse sexual dimorphism as female kiwi are larger than males and have a proportionally larger bill; they lay eggs that are four times larger than expected based on their body weight (Prinzinger and Dietz, 2002).

Brown kiwi are endangered due to their rapid rate of decline, largely as a result of predation. In 2008, the total population of brown kiwi was estimated at 25000 and their rate of decline is estimated to be 7.3% per year (Robertson et al, 2011). Mammalian predation is a serious threat to kiwi populations, and populations that were once abundant have been drastically reduced through predation from stoats, ferrets, rats, possums, dogs and cats (Robertson et al, 2011). Extensive predator control is an essential conservation tool for kiwi, along with placing kiwi in predator-free areas such as offshore islands and by rearing kiwi as part of the Operation Nest Egg program. Operation Nest Egg (ONE) involves collecting kiwi eggs from the wild and hatching them in incubators, then rearing the young and releasing them into the wild sometime between adolescence and maturity depending on the environment they are released into. This program has had great success, increasing the population of critically endangered Okarito rowi kiwi by 25% over the first six years of its implementation and allowing for a 12.5% annual increase in brown kiwi populations (Colbourne et al, 2005; Robertson et al, 2011). The main reason behind this success is that the ONE kiwi eggs have a high success rate of hatching in incubators, and neonatals are either raised in captivity until they are large enough to defend themselves or released at an early age to predator-free areas.

Captive management is a key issue for kiwi conservation because many kiwi are kept in captivity as part of the ONE program, in off-display breeding pairs and on display for advocacy purposes (Barlow, 2011). Brown kiwi are the most numerous species held in captivity with there being 95 captive brown kiwi both on and off-display in 2011 (Barlow, 2011). Captive kiwi are managed essentially as their own population, with the genetics, population size, husbandry techniques and founding population of captive kiwi being closely managed (Barlow, 2011). The long-term goal is to create a “self-sustaining, demographically stable” captive population that is genetically healthy (Barlow, 2011). At the moment there are few specific guidelines for the light regimes of kiwi nocturnal houses, though all facilities housing kiwi must comply with the DOC Conservancy Permitting Process (Fraser and Johnson, 2011). There are also no regulations for the light regimes that ONE kiwi are exposed to during their time in brooder rooms. The

captive management plan may therefore benefit from research into the impact of different environmental variables on the behaviour of display kiwi and juvenile kiwi involved in Operation Nest Egg.

Kiwi behaviour has not been the subject of extensive research, and neither has the relationship that kiwi have with light or nocturnal house lighting in general; however light has extensive control over the endocrine system and overall functioning of most avian species (MacDougall-Shackleton et al, 2009). Little research appears to have been done on the general effect of light on the behaviour of nocturnal birds, and the research that has been done suggests that animals have highly variable reactions to light intensity, duration and wavelength (Trent et al, 1977; Nash, 2006). These reactions appear to be the result of adaptive life characteristics such as foraging method, habitat and time of day that they are active (Roennberg and Foster, 1997). In this review I will discuss the sensory abilities of kiwi, patterns of kiwi behaviour, the relationship between light and behaviour in birds, and the relationship between light and behaviour in nocturnal animals specifically. This overview will assist the formation of my research questions, hypotheses and methodologies.

1.2: The sensory abilities of brown kiwi

Animals must have a balance between the sensitivity and resolution of their vision, and eyes that "maximise information gain at low light levels need to be large" (Martin et al, 2007). As a nocturnal, flightless bird with less weight constraints than birds that fly, it would be expected that kiwi have large eyes to compensate for their dark environment. This indeed appears to be the case with most bird species, however kiwi are the exception to this rule as they have proportionally small eyes compared with other nocturnal birds (Martin et al, 2007). Kiwi seem to be excellent at perceiving light intensity though; their relative aperture or light-gathering ability has a value of 0.95 that is similar to other nocturnal birds, meaning that they see images at a maximum brightness that is equal to other nocturnal birds and is brighter than diurnal birds (Martin et al, 2007). Kiwi have a monocular field of vision as well as a narrow binocular field of vision totalling 125°, that they cannot see beyond (Martin et al, 2007; Cunningham, 2007). This means that they can see ahead but cannot see the ground or their bill tip, and have a much more limited field of vision than most birds, particularly other nocturnal birds (Cunningham, 2007; Martin et al, 2007). Figure 1.2 illustrates this.

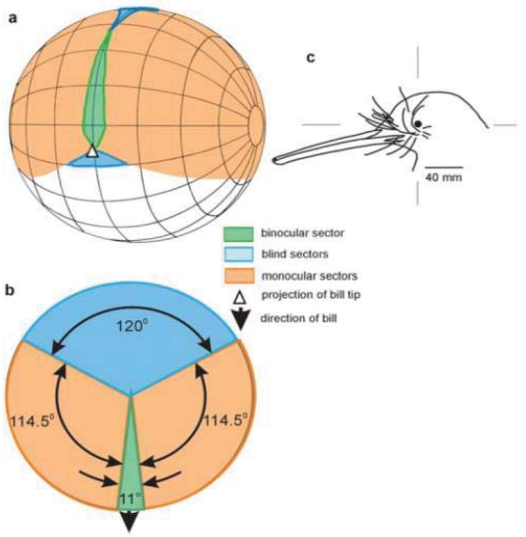


***Figure 1.2**: The field of vision of kiwi (Martin et al, 2007).*

The overall shape of kiwi eyes is round as opposed to the tubular shape of some nocturnal birds such as owls (Martin et al, 2007). This overall shape is more like the eyes of their ratite relatives, though the retinal structure of kiwi is more similar to owls than ratites (Bowmaker and Martin, 1978; Hall and Ross, 2007; Corfield, 2009). Because of the rounded shape of their eyes kiwi have a small corneal diameter in relation to axial length (Howland et al, 1992; Hall and Ross, 2007). This relationship can be seen in Figure 1.3.

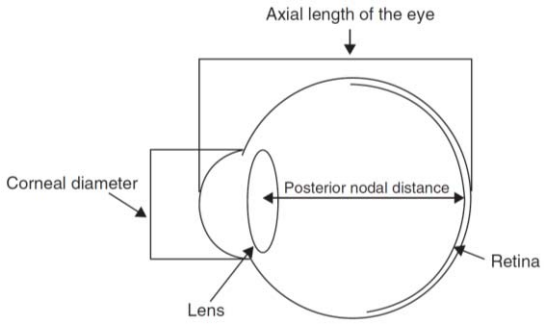


***Figure 1.3**: A schematic structure of a vertebrate eye (Hall and Ross, 2007).*

A smaller cornea and longer axial length indicates an adaptation towards visual acuity and is commonly found in diurnal birds (Hall and Ross, 2007). In comparison, animals with nocturnal vision typically have longer cornea in relation to axial length and are more adapted to visual sensitivity (Hall and Ross, 2007). Based on this kiwi seem to have developed some visual acuity, however their limited proportion of cone photoreceptors probably overshadows this as discussed below.

Kiwi appear to have undergone “adaptive regressive evolution” to suit their nocturnal, flightless lifestyle as they are highly diverged from their ratite relatives (Hall and Ross, 2007; Martin et al, 2007). As indicated by their eye size and structure, they seem to not rely on vision and probably have limited visual acuity but good perception of light intensity (Cunningham, 2007). Though in other cases of regressive evolution animals have completely lost their visual abilities, kiwi may still have limited vision because some ability to view their surroundings may be beneficial while they are foraging (Martin et al, 2007). As kiwi are flightless they lack weight constraints to limit the size of their eyes, making it more surprising that they should have eyes that are comparatively much smaller than other nocturnal birds (Martin et al, 2007). However, it is likely that a lot of metabolic energy would be required to maintain eyes that are powerful enough to operate effectively in the dark surroundings of their natural habitat compared with other senses that require less energy to provide sufficient information (Martin et al, 2007). Kiwi have evolved complex tactile and olfactory senses that they rely upon (Cunningham, 2007); this is more similar to nocturnal mammals such as primates and rodents than to nocturnal birds (Martin et al, 2007). Therefore these animals appear to have separately adapted their senses to suit the dim environment of the forest floor where reliance on vision may be less useful (Martin et al, 2007).

The photoreceptors that brown kiwi possess are an indicator of how well kiwi can perceive light intensity and wavelength. Photoreceptors are cells that receive visual information about light intensity or wavelength; a large proportion of cone cells indicates good range of colour perception while a large proportion of rod cells suggests excellent photon sensitivity (Bowmaker and Martin, 1978). Accordingly, nocturnal animals normally have more rod cells that perceive light at low levels and have poor colour vision, while diurnal animals have more cone cells and better colour vision but poor vision at low light levels (Bowmaker and Martin, 1978). Brown kiwi have a thick layer of tightly packed rod cells and have few cone cells suggesting that they are better at detecting light intensity than colour (Martin et al, 2007). Tightly packed rod cells increase the probability that a photon of light will be captured by these cells, again suggesting that kiwi have very good light intensity perception (Martin et al, 2004). However, as high visual discrimination is associated with cone cells, kiwi appear to lack the ability to see objects in fine detail (Bowmaker and Martin, 1978).

The perception of wavelength and intensity are linked as animals have a range of wavelengths that they are able to see best, and those wavelengths that are poorly perceived must be more brightly illuminated in order to see them (Bowmaker and Martin, 1978). Brown kiwi have a

large number of rod cells that are poor perceivers of the red wavelength (Martin et al, 2007); tawny owls *Strix aluco* have similar types and structure of rod and cone cells, thus kiwi may have similar wavelength perception to the tawny owl (Bowmaker and Martin, 1978). This owl has the highest sensitivity around the green spectral wavelength range, moderate sensitivity of blue and yellow wavelengths and poor sensitivity of the red spectrum (Bowmaker and Martin, 1978). Kiwi may accordingly have the best perception of green, moderate perception of blue and yellow and poor perception of red light. The fact that kiwi have mostly rod cells is likely to be the basis of the widely-held belief that kiwi cannot perceive red lighting. As a result, several facilities around New Zealand use red lighting in kiwi nocturnal houses and red flashlights for outdoor kiwi-spotting (Representatives from ten New Zealand wildlife institutes, personal communications, June 2009).

Being nocturnal, kiwi have had to adapt their senses to an environment of low light and they are thought to rely quite heavily on olfaction (Castro et al, 2010). This assumption is partly based on the fact that kiwi forage by probing their bill into the ground and have nares at the tip of their bill, and partly because they have a highly developed olfactory chamber and olfactory bulb in their brain (Cunningham, 2007). Research data indicates that chemicals may be used by kiwi to mark territories, which would be logical as they are highly territorial (Castro et al, 2010). This suggests that olfaction may be an important sense for them. Research has not demonstrated convincingly that olfaction is the most important sense that kiwi use to find prey though (Cunningham, 2007). Auditory cues seem to make little difference to their foraging habits, but they may be important to the overall behaviour of kiwi (Cunningham, 2009). This is suggested by their loud calls, their large ear openings and the immediate lifting of their heads in response to the approach of people (Cunningham, 2009). Recent research has found that kiwi have “specialised vibration and pressure-sensitive mechanoreceptors” referred to as Herbst corpuscles in their bill tips, and location of prey may be possible by using this vibrotactile sense (Cunningham, 2007). These corpuscles are contained within pits resembling a honeycomb in structure and they relay tactile information to their highly developed “telencephalic sensory end-station” (Cunningham, 2007). This tactile sense may work in conjunction with or be dominant over olfaction. The sensory pits are also present in the order Scolopacidae, indicating that convergent evolution has occurred (Cunningham, 2007). It is logical that kiwi have developed this vibrotactile sense, as they are found in many diverse habitats with a range of climates so being able to perceive a number of sensory cues would be beneficial (Cunningham, 2007). This supports the theory that kiwi may not have the need for highly developed vision if a mechanoreceptor is their predominant sense.

1.3: Patterns of kiwi behaviour

Kiwi have an unusual reproductive cycle as they breed during winter and have an extended laying season from approximately mid-winter until mid-spring, with the males incubating the eggs. They have pairs that range from being monogamous to having cooperative breeding with other kiwi. Pairs hold territories anywhere between 3-14 hectares in size depending on population density (Taborsky and Taborsky, 1995). Kiwi are aggressive and are highly defensive of these territories (Cunningham, 2011). They have a diverse range of habitats, being found in open farmland, pine forest, tussock grassland and dense native forest (Colbourne and Kleinpaste, 1983; Potter, 1989; Taborsky and Taborsky, 1995). Much of their behaviour appears to be innate with kiwi chicks raised in captivity having no apparent behavioural differences to kiwi chicks raised in the wild; subadult ONE kiwi also have the same probability of survival to first reproduction as wild juvenile kiwi that have survived infancy (Colbourne et al, 2005). Kiwi chicks move several kilometres from their burrow at 4-6 months of age before they disperse from their home nest when they are over nine months old; they may then travel more than 25 kilometres (McLennan, 1997; Colbourne et al, 2005).

Kiwi are distinct in that they sleep in burrows and are predominantly nocturnal, though some kiwi populations are known to emerge during the day. In some cases this is thought to be the result of food shortage caused by drought, and in other cases such as with the Stewart Island Tokoeka they may have evolved in the absence of predators. During an average night of activity, kiwi can emerge any time between 26 minutes and 5.5 hours after sunset (McLennan, 1988). Kiwi observed in their natural habitat were found to forage for a median of 74.3% of the time after emergence, spend 11.3% of the time walking, investigating obstacles or showing escape behaviour, display vigilant behaviour for 4.3% of the time, and exhibit comfort behaviour for 0.2% of the time (Cunningham, 2011). Comfort behaviour refers to preening, scratching or shaking of body or defecation. Time was spent foraging much more than any other behaviour suggesting this is a large priority for kiwi (Cunningham, 2011). Probing appears to be the predominant way that kiwi gain information from their environment and is the main method that they use for foraging. During summer and winter they spend the most time in leaf litter and roots, but in winter also spend much time beneath supplejack *Rhipogonum scandens* (a coniferous vine that grows very thickly) (Cunningham, 2011). Adult kiwi mostly travel between 0 – 150m per hour but can travel up to 433m in an hour (Keye et al, 2011). Taborsky and Taborsky (1995) suggest that where kiwi choose to spend their time is largely the result of “availability of food and shelter sites”, indicated by their wide range of

habitats. Male and female kiwi pairs mostly do not forage together but spend approximately 20% of their time together per night (Sales, 2005). Male and female kiwi have loud and frequent calls with which to communicate their location to each other.

1.4: The relationship between light and behaviour in birds

Understanding the relationship between kiwi and light requires a general understanding of avian relationships with light. Light has a far-reaching impact on the behaviour and physiology of most animals. It controls many circadian and circannual activities including food storage, activity levels, song initiation and breeding timing (MacDougall-Shackleton et al, 2009). Most animals have a reaction to light intensity, duration and/or spectrum that is either behavioural or physiological. The relationship that animals have with light is closely linked with life cycle stages and adaptation to the environment; animals can use light to cue behaviours appropriate to their daily and seasonal cycle (MacDougall-Shackleton et al, 2009). It is highly useful for animals to use changes in light conditions to anticipate and "exploit" seasonal and environmental changes, thus increasing the probability of survival and reproductive success (Roennberg and Foster, 1997).

Circannual rhythms have a significant impact on the physiology and behaviour of most species and are closely linked with the life cycles of animals. Circannual rhythms are "self-sustained endogenous rhythms with a period length of about one year that affect the morphology, physiology and behaviour of an organism" (Wikelski et al, 2008). They regulate essential processes such as "reproduction, moult, hibernation, migration, body weight and fat deposition/stores" by synchronising with environmental features such as photoperiod, lunar cycle and weather conditions (Wikelski et al, 2008). Synchronisation allows those processes to occur at the optimum time of year (MacDougall-Shackleton et al, 2009). Environmental conditions can be highly unpredictable and can vary significantly between habitats that are close in proximity. Some species therefore rely more on environmental factors to determine their circannual rhythm than others, suggesting some flexibility in circannual timing; this flexibility may depend on how well environmental factors are predictors of the season in their habitat (Wikelski et al, 2008).

Circadian rhythms are daily patterns of activity that are maintained by an endocrine feedback cycle and are therefore mostly endogenous (Wikelski et al, 2008). This is illustrated by the fact that a 24 hour circadian rhythm can be maintained to within a 20-28 hour degree of accuracy

in the absence of environmental cues for many animals; after a long period of time the “days” of cue-deprived animals typically become longer or shorter (Sothern et al, 2009). Circadian rhythms are closely linked with photoperiod though, as information about light conditions is used to alter physiology and behaviour. For most animals circadian rhythms are controlled by the suprachiasmatic nucleus in the hypothalamus (Chalet, 2007). Nocturnal and diurnal animals are active at opposite times of the day but experience some daily cycles at the same time, such as having peak melatonin levels and the highest sensitivity to light at night (Chalet, 2007). These factors are said to be activity-independent as they are not affected by activity levels of animals, however high levels of melatonin are thought to reduce the activity of diurnal animals (Chalet, 2007). Other circadian cycles occur at opposite times in nocturnal and diurnal animals and are thus dependant on activity levels, such as low levels of serotonin and low body temperatures associated with rest (Chalet, 2007).

Most birds and mammals are photoperiodic so their life cycle is closely linked with melatonin secretion (Takayoshi et al, 2005). Photoperiodic information is processed through a large and complex set of neurological pathways that together enable appropriate responses from animals (Takayoshi et al, 2005). Melatonin is an essential component of the photoperiod cycle, and there is much reason to believe that melatonin helps to regulate several seasonal processes, including gonadotropin secretion and gonadal activity (Takayoshi et al, 2005; Chalet, 2007). Photoperiod is involved in many of the endocrine pathways of animals, for example it is thought to affect the negative feedback pathway involved in reproductive hormone release (Wang et al, 2002). Birds experience photosensitivity or an increased release of gonadotropin-releasing hormone in response to increasing day length during spring; they also experience photorefractoriness or a lack of response to the stimulatory effect of long days when days reach their longest (MacDougall-Shackleton et al, 2009). While the total duration of light exposure is important to animal functioning, it is generally agreed that “timing of light exposure, rather than the total amount of light, is critical to the organism’s perception of day length” (Wang et al, 2002). It is not known how important photoperiod is to the functioning of kiwi, and knowledge of this would indicate how close in general their relationship is with light.

In addition to light duration, light intensity also has a significant impact on the functioning of animals, and is linked with the activation of neurological pathways and behavioural responses in birds. As previously discussed, photon reception occurs through rod photoreceptors, and there seems to be a correlation between quantity of rods and ability to perceive light (Bowmaker and Martin, 1978). Light intensity can have a range of effects on the behaviour of

animals depending on their ecology. For example, sunlight is understood to initiate song in many species of birds and artificial light has been shown to have the same effect, i.e. brighter nocturnal light as a result of light pollution can cause early onset of bird singing, an effect demonstrated by American robins *Turdus migratorius* (Miller, 2006). In a captive setting, inappropriate light intensity can cause stress for animals. Social communication in hens is affected by light intensity with unfamiliar hens of unequal rank having a shorter feeding duration in low lighting and facing each other less during the inspection period; this perhaps is avoidance behaviour as a defence mechanism (Kristensen et al, 2009). Hens exposed to darker lighting also exhibit more signs of stress. The opposite may be the case for the nocturnal kiwi, as bright illumination may cause stress, impacting natural behaviour. Research is therefore necessary to determine how different species respond to environment light levels, as reactions can vary greatly.

1.5: Circadian rhythm and behavioural patterns of nocturnal animals

When examining the relationship between kiwi and light the first obvious issue is that kiwi are nocturnal and must therefore be compared with other nocturnal birds and mammals. It appears difficult to isolate light as the cause of activity patterns though and research suggests differences among nocturnal animals in their responses to light intensity, duration and wavelength (Trent et al, 1977; Petren and Case, 1996; Bulyuk et al, 2009). Illumination intensity can affect the amount of time that nocturnal animals are active for, as well as specific behavioural patterns (Trent et al, 1977; Nash et al, 2006; Bulyuk et al, 2009). Little is known about light perception of nocturnal animals, however the majority of them have a large number of rod photoreceptors that are effective at detecting low light levels, suggesting that they are sensitive to changes in light levels (Bowmaker and Martin, 1978). Little is also known about the endocrine response of nocturnal animals to light; several hormones appear to be responsible for inducing activity in both nocturnal and diurnal animals including neuropeptide Y and serotonin (Chalet, 2007). Nocturnal and diurnal animals also have in common the secretion of melatonin during darkness by the pineal gland (Chalet, 2007).

Nocturnal animals for which vision is a dominant sense such as some primates and owls, presumably benefit from nights that are more brightly illuminated in order to navigate and see predators or prey (Nash, 2006). The spectral tarsier *Tarsius spectrum* increases foraging time, travelling and calling in response to increased moonlight, optimising time in relation to

improved visibility (Nash, 2006). Significantly more reed warblers (*Acrocephalus arundinaceus)* embark on nocturnal premigratory flights when at least half of the moon face is showing; flights such as these may allow the fledglings to become familiar with their breeding environment and to choose the best location, and therefore reed warblers may prefer to fly on nights when there is higher visibility (Bulyuk et al, 2009). Various species in the genus *Caprimulgus* synchronise nesting cycles with lunar cycles so the "first two weeks of the nesting period coincides with the period with the most moonlight" (Brigham and Barclay, 1992). Higher activity in the common poorwill *Phalaenoptus nuttallii* is positively associated with moon height, however nesting cycle was not synchronised with the lunar cycle (Brigham and Barclay, 1992). It appears that the higher activity of the poorwill in response to brighter nocturnal light is to improve hunting success (Brigham and Barclay, 1992). These animals all have highly developed nocturnal vision that they are able to use to their benefit, being less vulnerable to predation.

Increased predation risk is thought to reduce activity in many animals during brighter moonlight. The nocturnal rodents Darwin's leaf-eared mouse *Phyllotis darwini* and Merriam's kangaroo rats *Dipodomys merriami* both feed from distances further away from their burrows during nights of darker illumination (Vasquez, 1994; Daly et al, 1992). At brighter moonlight intensities they have heightened evasive reactions, decreased food consumption, increased use of structurally covered areas and are more central-place foragers (Vasquez, 1994; Daly et al, 1992). This pattern is found in most desert rats also (Nash, 2006). Gerbils *Gerbillus allenby* have decreased activity time and more use of covered areas in response to brighter nocturnal lighting, and are more highly predated on during this time; neotropical fruit bats *Artibeus jamaicensis* also show decreased foraging time in these conditions (Nash, 2006). These animals are highly vulnerable to predators, have limited visual abilities or in some cases live in environments that have little structural coverage offering protection. It seems that the circadian rhythm and behavioural response of nocturnal animals to light is variable and dependant on several factors including their reproductive cycle, how dependant on eyesight they are, their necessity to forage, the amount of structural coverage offered by their environment, and how heavily they are predated on.

1.6: Research on captive nocturnal animals in relation to light

Environmental features in an enclosure can be hugely important to an animal's behaviour and careful research is necessary so these features mimic that of an animal's natural habitat. Factors such as light regimes, enclosure size and number of visitors may all negatively impact on the behaviour of captive animals, and there are several illustrations of this that have been found in research. Indian blackbuck *Antelope cervicapra* appeared to have significantly heighted stress during days of high visitor density (weekend days when visitor numbers averaged 3382 per day) (Ragagopal et al, 2011). Additionally, Cheetahs *Acinonyx jupatus* were more likely to be observed pacing in smaller enclosures (Quirke et al, 2012). Captive nocturnal animals that are heavily predated on in the wild may be expected to show lower levels of activity when their enclosures are more brightly illuminated as a natural evasive response. The question of whether this relationship exists with the slow loris *Nycticebus coucang* was investigated by Trent et al (1977), who studied loris activity in a captive environment to determine the effect of light intensity on activity levels. Results suggested that low light intensities were associated with higher activity levels. Trent et al (1977) proposed that a "threshold phenomenon" occurred, i.e. lights brighter than a particular level may have been associated with low activity levels. This was suggested by the observation that there was no change in moderate activity at moderate illumination levels, and is consistent with the crepuscular/nocturnal niche. Higher activity levels may be indicative that the lorises were more comfortable with their surroundings, though high activity levels can also be associated with stress.

In some instances there may be several aspects of lighting regimes that explain unusual behavioural patterns in captive animals. This was found with the nocturnal primate potto *Perodicticus potto* whose activity levels were observed and ranked; results suggested that the activity of pottos was affected significantly by humidity and lighting alterations (Frederick and Fernandes, 1994). These changes involved night lights being swapped from two blue fluorescent to four white incandescent lights and adding a 75% light filtration, while changing the day lights from four fluorescent and three incandescent white lights to six fluorescent white lights. After this change there was a significant increase in nocturnal activity. It appears that they reacted to alterations of both their day and night lighting with increased activity. Light levels were very dim as a result of these light alterations, so results suggest that pottos may be quite sensitive to light and only become active when it is fully dark; this is consistent with observations from their natural habitat. It is also possible that they reacted the most

strongly to the most noticeable change in their lighting setup of the several that were trialled. These captive pottos may not have previously been active to their full capabilities due to their light regime, highlighting the benefits of investigating captive housing setups.

Some nocturnal animals use brighter lighting to their advantage in both natural and captive environments. One example of this is the geckos *Lepidodactylus lugubris* and *Hemidactylus frenatus* that develop better body condition and have greater reproductive success when housed in enclosures with artificial lights, and when they spend more time in areas close to enclosure lighting (Petren and Case, 1996). This is because these species are insectivorous and insects commonly aggregate around light sources. In artificial enclosures, as in their natural habitat, both species spend most of their time close to lights while attempting to remain hidden as much as possible and exhibiting "sit and wait" behaviour (Petren and Case, 1996). This example illustrates how several factors can contribute to the behaviour of nocturnal animals in relation to light; these geckos have adapted to spending much time in brightly lit areas with high insect abundance while risking being seen by predators. This response to light is to be expected from an insectivorous animal that is able to move quickly, can hide from predators easily and can forage on flying insects.

The overall message from research involving enclosure lighting seems to be the importance of researching light regimes and the significant impact that light regimes can have on captive animals. Inappropriate light regimes can impact the health, activity levels and reproductive success of animals. Again the research examples have illustrated that responses to light vary greatly depending on their ecology, and that several factors in combination may explain their behavioural responses to light. In all research examples discussed the captive nocturnal animals had a significant response to light regimes, though their responses varied as a result of several contributing factors. While captive nocturnal geckos aggregate around brightly lit areas, I would not expect this response from kiwi that forage solely on ground-dwelling insects. Instead kiwi are more likely to behave like captive loris and pottos who become more active with reduced light intensity; kiwi are slower moving and more conspicuous than smaller animals such as geckos so probably exhibit increased amounts or different types of predator avoidance behaviour.

1.7: Research aims

I have evaluated examples of literature that relate to my investigation of the relationship between brown kiwi and light. The common theme among all papers seems to be that light has variable impacts on animals due to different environmental adaptations and circannual cycles; overall, animals have a complex relationship with light. Studies on the relationship between nocturnal animals and light appear to be limited. Several studies that I reviewed investigating nocturnal activity and light intensity had results suggesting animals were more active under brighter illumination at night (Brigham and Barclay, 1992; Petren and Case, 1996; Bulyuk et al, 2009) while others found higher activity levels associated with darker illumination (Trent et al, 1977; Frederick and Fernandes, 1994; Vasquez, 1994). This may be explained by the subject animals weighing the risk of predation with the efficiency enabled by brighter light, though other species differences may account for these behavioural differences.

There seem to be gaps in the knowledge of the lighting requirements of captive animals, particularly the lights used in nocturnal houses. There are also large gaps in the knowledge of kiwi behaviour and physiology, for example how they respond to light intensity, duration and spectrum. The eyesight of kiwi has not been fully researched, though it appears that they have a good ability to detect illumination levels (Martin et al, 2007). There are numerous brown kiwi in captivity, either in breeding pairs, on display in nocturnal enclosures or as part of the Operation Nest Egg juvenile rearing program. Their light regimes have the potential to negatively impact their behaviour and/or physiology, as bright nocturnal light levels may cause stress and/or restrict the activity levels and habitat use of nocturnal animals. They may also supress melatonin levels, potentially disrupting circadian and circannual cycles (Daly et al, 1992; Vasquez, 1994; Ashley et al, 2012). If any such behavioural or physiological effect is lasting, this may have conservation implications for the juvenile or adult kiwi that are exposed to captive light regimes and are later released into the wild as it may affect their interactions with the environment and other animals. Nocturnal house light regimes may also have conservation implications for captive breeding pairs that are exposed to artificial light regimes if they negatively impact the reproductive capability of these breeding pairs or have long term effects on any offspring.

There are currently only limited guidelines for the lighting regimes of kiwi, as the guidelines state that “Nocturnal houses should be bright enough… for visitors to see the kiwi clearly while still being dark enough to encourage the birds to forage in the enclosure”, and should attempt

to mimic seasonal photoperiodic cycles (Fraser and Johnson, 2011). Therefore a study investigating the impact of lighting on the behaviour of captive kiwi would be a valuable beginning to what is a highly complex topic. I aimed to research the effect of light exposure on the behaviour of captive brown kiwi. My first experiment looked at whether captive kiwi have a preference for different colours of illumination, my second experiment investigated where they choose to spend time based on enclosure illumination levels, and my final experiment looked at how indoor brooder light intensity affects the subsequent outdoor emergence times of juvenile kiwi.

Chapter 2: Proportion of time spent in nocturnal house areas based on illumination wavelength

2.1: Introduction

Very little is known about the impact of light intensity, wavelength or duration on the behaviour of kiwi. Illumination colour can have a significant effect on the behaviour of animals though its effect is highly varied, in part because the visual perception of animals is different between species. Animals can be monochromatic (having no colour ranging), dichromatic, trichromatic or tetramatic (being able to see four colour groups) (Bennett and Thery, 2007). Many Avian species in particular are tetrachromatic so can see colours in the ultraviolet wavelength, probably used for foraging, orientation and signalling (Bennett and Cuthill, 1994). These differences in visual perception are the result of the photoreceptor cells (i.e. “rods” and “cones”) in their retina; rod cells are specialised at perceiving light intensity at low levels and are thus effective for nocturnal vision, and cone cells allow for acuity and colour vision in brighter illumination (Bowmaker and Martin, 1978). Even closely related species can have differences in their photoreceptor cells, for example humans and rhesus monkeys have small but significant differences in the colour spectrum absorbed by their rod cells (Bowmaker and Dartnall, 1980).

The photoreceptor cells of animals are linked with their life history, and often “correlations between the relative abundance of the different cone types and the visual ecology of different species of bird have been observed” in relation to colour vision (Hart, 2001; Ham et al, 2006). As a result of adaptation, birds have demonstrated different reactions to colour; for example broiler chickens are more active in low-frequency fluorescent lighting than high-frequency and are more active in areas illuminated by red lighting than blue (Sherlock et al, 2010). Additionally Kear (1964) demonstrated with a range of Anatidae that juveniles have a very significant preference for pecking at green out of a range of colour spots, thought to be a behavioural response to naturally feeding on grass, plant and pond vegetation. The visual ecology of kiwi (and subsequent reaction to illumination colour) will be closely linked with their nocturnal habits.

Like most nocturnal avian species, kiwi have a high proportion of rod cells to optimise vision in low light where strong colour vision is not necessary (Corfield, 2009). It is a widely-held assumption that kiwi are unable to see the red wavelength spectrum, the basis of this being that their numerous rod cells are poor absorbers of colours with high wavelengths (Bowmaker and Martin, 1978). As a result, numerous wildlife facilities use red lighting in their nocturnal houses or use red flashlights for observing kiwi outdoors. However, this relationship seems to have never been confirmed, and it is possible that, if the red lighting is bright, they are able to perceive it. This is because rod cells perceive both light intensity and wavelength, meaning that wavelengths that are perceived weakly may be compensated for by being brighter (Bowmaker and Martin, 1978). For example, the rod cells of tawny owls have the highest absorption of pigment oil at 503nm meaning that they are able to best perceive light in the green spectrum (490-560nm), have moderate perception of blue (450-490nm) and yellow (560-590nm) wavelengths and are least able to see light in the red spectrum (635-700nm) (Bowmaker and Martin, 1978). Red light must therefore be brighter for tawny owls to perceive it at the same brightness as green light (Bowmaker and Martin, 1978).

No light-related research has been previously completed on kiwi though illumination colour has the potential to have a significant impact on their behaviour. Additionally, few guidelines exist for kiwi nocturnal house light regimes (Fraser and Johnson, 2011); research results may contribute towards the further development of the captive management plan for kiwi. In light of these factors I wish to investigate whether kiwi spend significantly different amounts of time in areas illuminated by different colours. As they are likely to have varying perceptual abilities of colour, and as illumination colour can have a significant effect on animal behaviour, I hypothesise that time spent in areas of varying illumination colour will be significantly different. The colour perception of kiwi is likely to be similar to that of the tawny owl as they have similar photoreceptors (Bowmaker and Martin, 1978; Martin et al, 2007); I therefore predict that the kiwi will spend the most time in areas illuminated by red, a moderate amount of time in blue and yellow, and the least amount of time in green at equal illumination intensities.

2.2: Methods

This experiment was conducted with an approximately 33 year old female kiwi that has been at the kiwi conservation facility Kiwi Encounter in Rotorua, New Zealand for 29 years. This kiwi is housed in an indoor nocturnal house enclosure where a reversed light cycle is used; during her "night" the enclosure was usually illuminated by six 30 watt Phillips PAR38 bulbs coloured blue, yellow, red or green. For this experiment four of these bulbs (one of each colour) were used, as the kiwi was familiar with this light setup. These bulbs were positioned to have one colour illuminating a different section of the enclosure. The bulbs were rotated through the four positions for three repetitions, lasting 12 days (see Appendix A). The first sequence from left to right was green, red, blue and yellow, the second was red, blue, yellow and green, the third was blue, yellow, green and red, and the fourth was yellow, green, red and blue. Appendix A illustrates this setup and the following photo illustrates the light positioning.

Figure 2.1*: Lighting setup of the experiment subject kiwi with the four lighting colours shown.*

This experimental design was used as I wished to have a design where the kiwi was given the option of being in nocturnal house areas illuminated by either one of four colours. Colours were rotated daily as I wished to prevent bias resulting from extraneous environmental

variables influencing where the kiwi spent her time; additionally the area size that each light illuminated varied due to the positions of light fittings so I wished to prevent bias as a result of this factor. A grid of the nocturnal house was created by measuring the length and width of the nocturnal house and marking every 1m interval along the back wall. From these intervals string was laid 10cm above the ground from the back wall to the front with a marker at every metre lengthways along the string. A level was used to ensure that the string was laid evenly. This resulted in a 4X8m grid of $1m^2$ squares, with some squares around the front and side walls having an area less than $1m^2$ due to the shape of the nocturnal house (Appendix A). I also divided the nocturnal house into four quarters by the colour that it was illuminated by each day and classified each $1m^2$ grid square into a quarter accordingly; for example grid square A1 was in quarter one and on the first day was illuminated by yellow, on the second day by green, and so on.

Drawings were made detailing landmarks in each of the grid squares in order to quickly identify the whereabouts of the kiwi. She was released into her enclosure from her nest box at approximately 8.30am every day when the “night” lights were turned on, at which stage she was shut out from her box. Access was allowed again at 5pm when the “day” lights were switched on. The positioning of her food tubes was also noted, and every day live insects were introduced into the enclosure with their release positions also noted. The position of the water bowl remained the same. The number of food tubes varied between 3-4, adjusted for daily consumption. The release position and number of food tubes varied daily and was evenly distributed; 22 of the 29 grid squares contained food at some stage on at least one of the 12 days of observation.

Throughout the kiwi’s “night” from outside the enclosure I noted the kiwi’s position by grid square at one minute intervals. Light intensity was measured in each grid square for all light sequences using an Extech HD450 data logging light meter, taking the measurement from several different positions in every grid square. Mean intensity for each grid square was calculated from this. The colour illuminating each grid square was also recorded daily. Light bulbs were changed every morning before the nocturnal lights were switched on and were kept in the same position. A total of five hours of observation each day for 12 days was completed with observations evenly distributed between 8.30am and 5pm to prevent bias; her circadian rhythm means that she is often the most active at 8.30am and sleeps from midday.

I wished to determine the proportion of time that was spent in each grid square of the enclosure. To do so I entered each minute of observation into a spreadsheet as shown in

Appendix B with grid squares given a number in reference to proportion of time. For example if during one minute the whole time was spent in square A1 by the kiwi then the A1 column received a 1 for that minute. If, however, time was spent in A1, A2 and A3 in that minute then A1, A2 and A3 each received 0.33 for that minute's observation. These proportions of time for each grid square for the entire day of observations were then added and this sum for each grid square was divided by the total sum of proportions. This calculated what proportion of each day of observations was spent in each grid square, and it was these data that I used to complete the statistical tests for the individual variables. In addition to inputting the mean light intensity, edge and structure category of each square, I also classified each grid square as being in light category one or two; light category one squares are darker than the overall mean light intensity of the nocturnal house and category two squares are lighter than the mean intensity. I additionally noted the position and duration of foraging behaviour to later test any potential bias caused by the presence of food.

Statistical tests completed were non-parametric as the initial Anderson-Darling test for normality resulted in a p-value of <0.005, suggesting the results were not normally distributed. A Kruskal-Wallis non-parametric test was therefore completed on all variables. The amount of time that the kiwi spent foraging in each grid square was not significantly different, suggesting that the presence of food did not significantly impact the amount of time spent in them (Kruskal-Wallis; $H(28)=28.0$, $p=0.46$). Tukey's post-hoc tests were also completed to provide a more detailed analysis of the mean results for each variable; however these results may not be as reliable as the non-parametric Kruskal-Wallis results. A multivariate General Linear Model was carried out to examine the combined effect of experiment day, illumination intensity, structure and edge category, and illumination colour on the proportion of time spent in grid squares.

2.3: Results

The main focus of this experiment was to determine whether kiwi have a preference for spending time in areas of a nocturnal house illuminated by four different colours. I also wished to determine whether more time was spent in any of the four quarters of the nocturnal house irrespective of their illumination colour; this highlighted whether there may have been a significant preference for a particular area of the nocturnal house, potentially confounding the results for proportion of time based on illumination colour. An initial Analysis of Variance (ANOVA) multivariate analysis found that edge category had a significant main effect on the proportion of time spent in individual grid squares (ANOVA; $F(1, 329)=5.70$, $SS(B)=0.051$, $p=0.018$). The edge category of an individual grid square accounted for 5.1% of the proportion of time spent there. Other variables did not have a significant effect; these variables included experiment day, illumination intensity, structure category and illumination colour, and results can be seen in Appendix C. There were no interaction effects between variables, I therefore proceeded to investigate variables separately.

The proportion of time that the kiwi spent in the four quarters of the nocturnal house was not significantly related to the colour of the light illuminating each quarter, seen in Figure 2.2 (Kruskal-Wallis; H(3)=2.20, *p*=0.53).

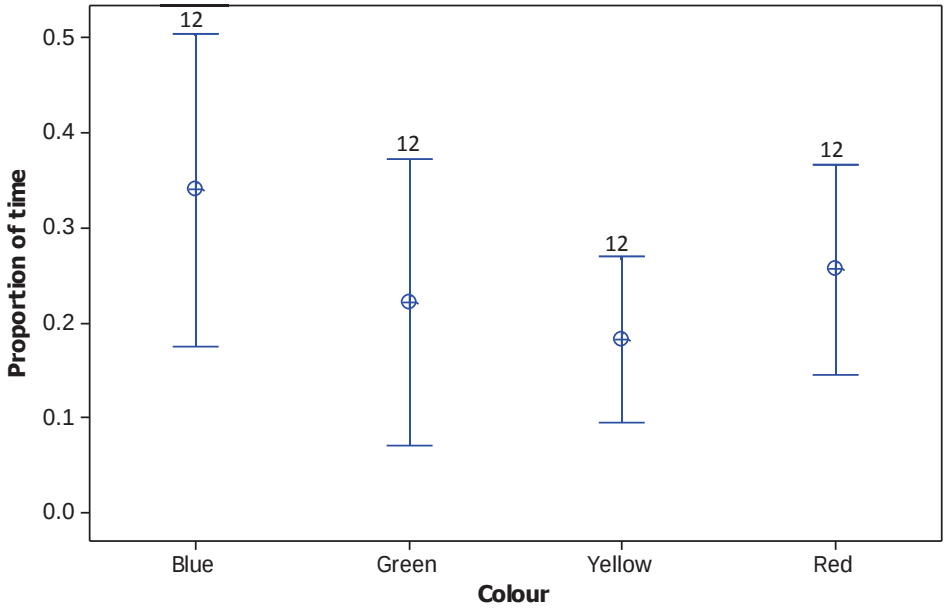


***Figure 2.2**: Mean proportion of time spent by a kiwi in each of four quarters of a nocturnal house in relation to illumination colour in increasing wavelength; this relationship was not significant, n for each group is shown above interval bars . 95% confidence interval, mean ± 2 standard errors.*

The kiwi spent a significantly different proportion of time in at least one of the four quarters of the nocturnal house (Kruskal-Wallis; H(3)=45.84, p<0.01). Significantly more time was spent in quarter one than four (Tukey post-hoc; F(3, 44)=6.29, p=0.01), however there was no significant difference in time spent in the other nocturnal house quarters as seen in Figure 2.3 (see Appendix D(a) for full results).

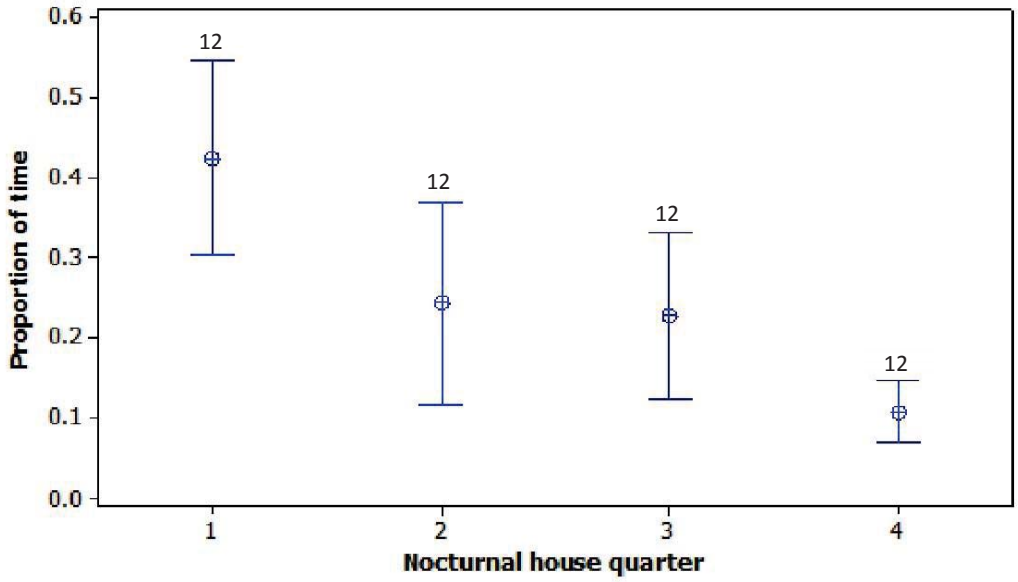


***Figure 2.3**: Mean proportion of time spent in each of four quarters of a nocturnal house by a kiwi with n for each group shown above interval bars; significantly more time was spent in quarter one (Kruskal-Wallis; H(3)=45.84, p<0.01). 95% confidence interval, mean ± 2 standard errors.*

These results suggest that while the colour of the nocturnal house lights may not have significantly impacted where the kiwi spent her time, there are other factors causing a preference for particular areas of the nocturnal house. These factors may include mean light intensity, amount of covering i.e. structural complexity, or what proportion of the quarter is on the periphery of the nocturnal house, which I will investigate next.

The kiwi spent significantly more time in darker grid squares with a median of 0.01 or 1% of time spent per day in grid squares that were illuminated by light dimmer than the median light intensity and 0.005 or 0.5% of time spent in lighter grid squares. There was a 95% probability of the difference between the medians being between 0.001 and 0.007 (Mann-Whitney; W(2)=33444.5, p<0.01). The mean light intensity of all four nocturnal house quarters did not vary significantly as shown in Figure 2.4 though they were close to being significantly different (Tukey post-hoc; F(3, 344)=2.39, p=0.068). However, the range of light intensities illuminating the four quarters was vastly different. Light intensity did not appear to explain proportion of time spent in nocturnal house quarters (figures 2.3 and 2.4). Differences in mean and median light intensity between nocturnal house groups can be accounted for by differences in grid square light intensities as all bulbs were 30 watts.

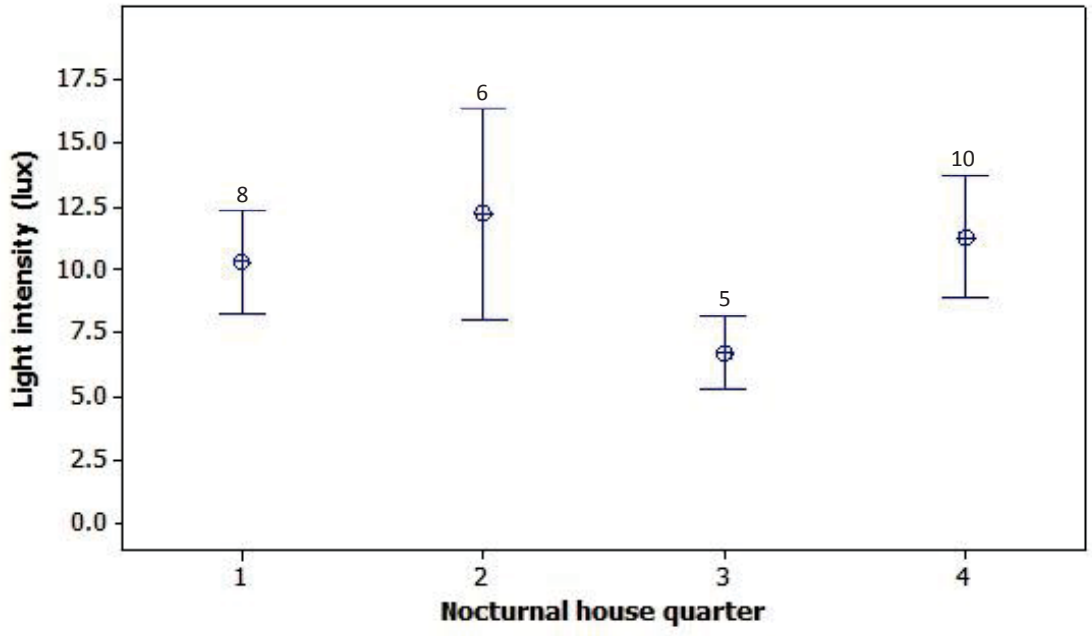


Figure 2.4*: Mean light intensity of all four quarters of a kiwi nocturnal house; there was little variation in mean intensity for each quarter but wide variation in the 95% confidence interval range. N is shown above each interval bar, mean ± 2 standard errors.*

Structure had no significant impact on where the kiwi spent her time (Kruskal-Wallis; H(2)=5.31, *p*=0.07). There may have been an interaction between structure and light, as Figure 2.5 indicates that a significant proportion of time was spent in darker areas that were structurally open. Please note that this data has not been corrected for proportion of availability of open, mixed and covered structure grid squares and that data is not independent.

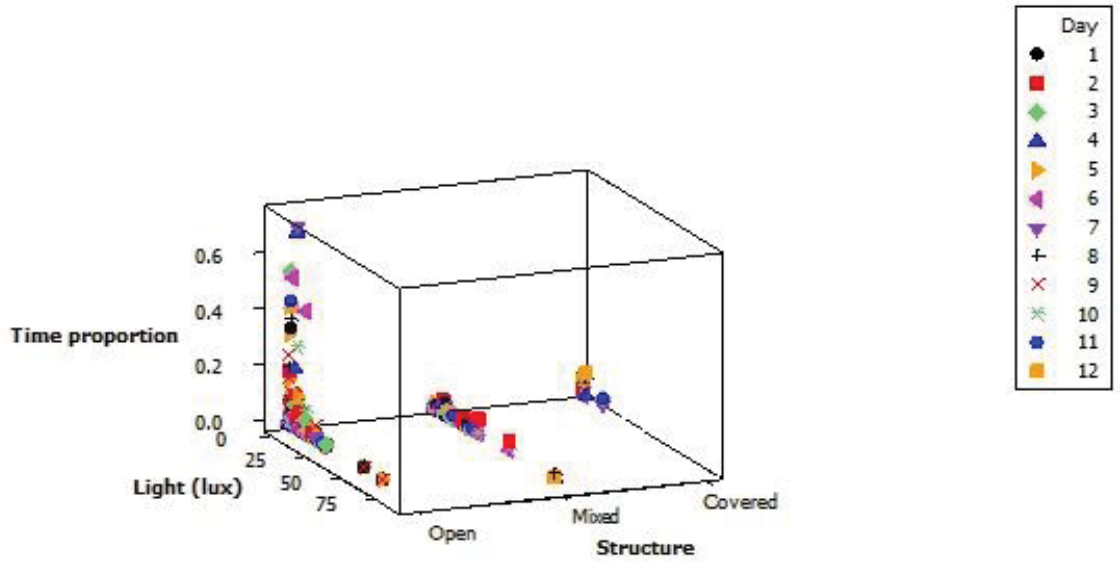


***Figure 2.5**: Time spent in individual grid squares of a nocturnal house by a kiwi based on structure; squares have varying light intensities and have an open (n=252), mixed (n=84) or covered (n=12) structure. Large proportions of time were spent in squares less than 25 lux with little or no covering.*

At least one of the nocturnal house quarters had a significantly different median structural complexity from at least one of the other nocturnal house quarters (Krusal-Wallis; H(3)=31.42, p<0.01). The only quarters that did not have significantly different structural complexity were quarters one and two (Tukey post-hoc test; F(3, 344)=14.1, p<0.01). These results can be seen in Appendix D(b) and in Figure 2.6. Structural complexity also did not appear to explain proportion of time spent in grid squares (figures 2.3 and 2.6).

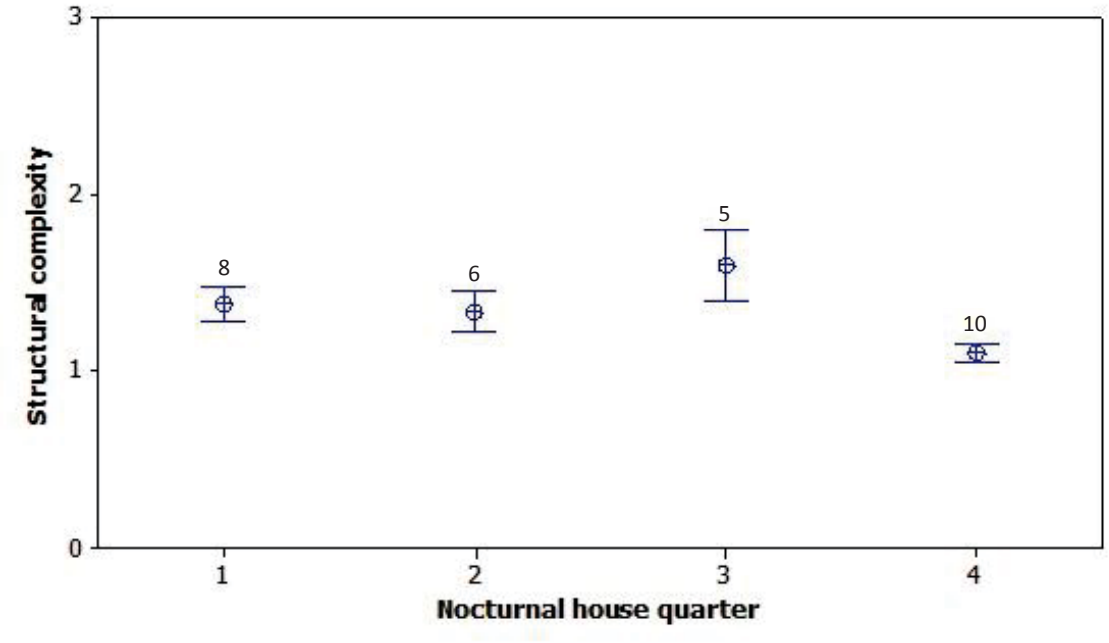


Figure 2.6*: Mean structural complexity of all four quarters of a kiwi nocturnal house ranging from 1 (fully open, no ferns or low bushes) to 3 (fully covered, kiwi obscured from view). For each quarter there was much variation in the mean and 95% confidence interval range. N is shown above each interval bar, mean ± 2 standard errors.*

The kiwi spent significantly more time in individual grid squares on the periphery of the enclosure (Kruskal-Wallis; H(1)=11.09, p<0.01). Figure 2.7 suggests that there is a relationship between the edge category and light intensity of grid squares; large proportions of time were spent in squares that were illuminated by less than 25 lux of light and were on the edge of the enclosure. There appeared to be a fairly even distribution of time spent in different areas of the enclosure during each day of the experiment, though on several days a lot of time was spent in a small number of areas. Please again note that results have not been corrected for proportion of availability of edge and centre grid squares and that data is not independent.

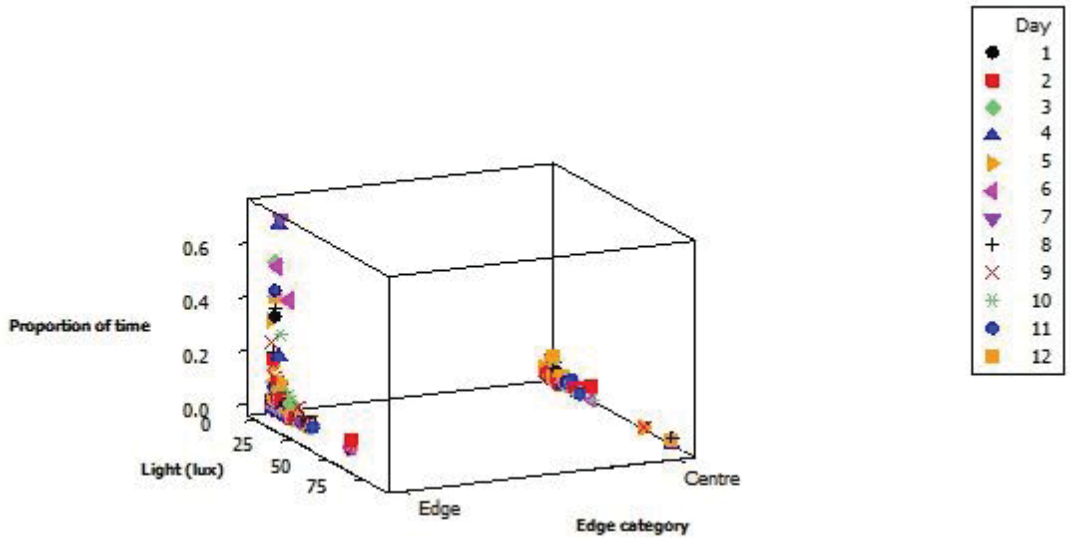


***Figure 2.7**: Time spent by a kiwi in grid squares on the edge (n=240) and in the centre (n=108) of a nocturnal house in relation to illumination intensity (lux) of the squares. Large proportions of time were spent in squares that were less than 25 lux and on the edge of the nocturnal house.*

There was a significant difference between the mean proportion of edge area of at least two of the four nocturnal house quarters (Kruskal-Wallis; H(3)=32.07, p<0.01); quarter three had significantly less area on the edge of the nocturnal house than the other quarters (Tukey post-hoc test; F(3, 344)=11.67, p<0.01). Figure 2.8 illustrates this relationship, see Appendix D(c) for full results.

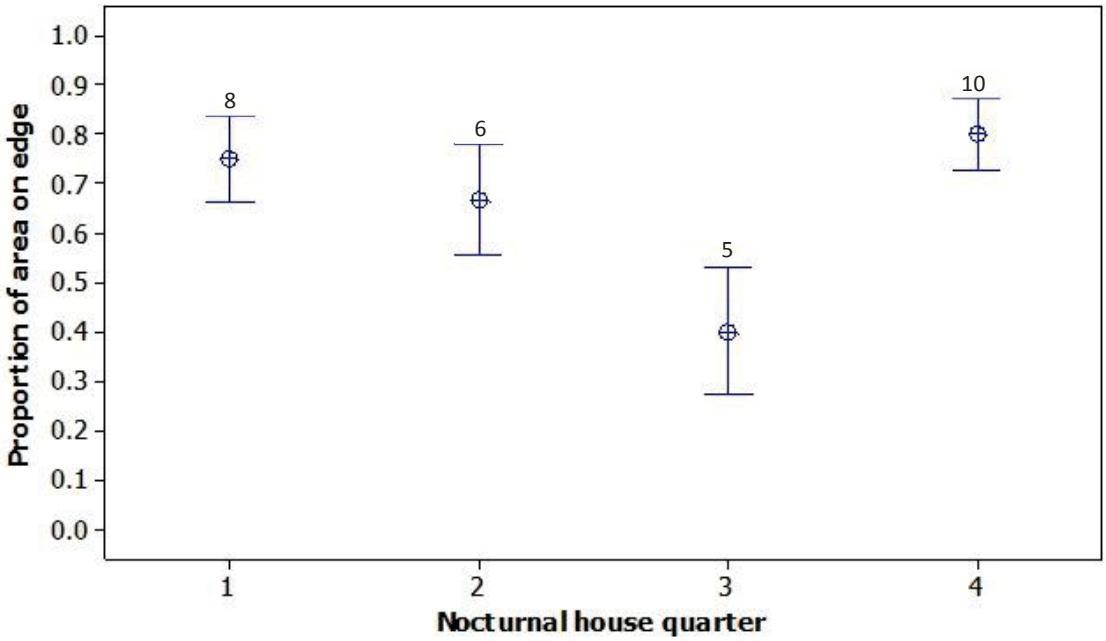


Figure 2.8*: Mean proportion of area on the periphery of the enclosure for all four quarters of a nocturnal house with n shown above each interval bar; proportion of area on the edge of the nocturnal house did not explain the proportion of time spent in each quarter as shown in Figure 2.4. 95% confidence interval, mean ± 2 standard errors.*

2.4: Discussion

It appears that no single factor explains the amount of time spent in each quarter of the nocturnal house. When data was compared between nocturnal house quarters, illumination colour did not significantly affect the amount of time spent in each quarter and the mean light intensity of each quarter was not significantly different. Significantly more time was spent in quarter one than quarter four; quarter one had significantly more structural coverage than quarter four, however it had significantly less coverage than quarter three suggesting that structure does not solely explain the large amount of time spent in quarter one. Quarter three had significantly less area on the edge of the nocturnal house which may have accounted for why more time was spent in quarter one despite there being less structural coverage in that quarter. Such an effect is unlikely to have occurred though, as the multivariate analysis results suggested that edge and structure did not have a significant interaction on the proportion of time spent in individual grid squares.

Illumination colour appeared to have no effect on the movement of the kiwi within her nocturnal house based on the non-significant relationship between illumination colour and time spent in an area. Additionally the mean time spent in areas illuminated by each of four colours was similar. This result may be explained either by the kiwi being able to see red lighting but having no strong preference or dislike for it, or by the kiwi not being able to see it but there being other factors that are more important. Light intensity and edge category appeared to significantly impact where the kiwi spent her time; significantly more time was spent in peripheral enclosure areas illuminated by lower light levels. Light intensity appeared to have a combined effect with both edge and structure category, as high proportions of time were spent in dark peripheral areas and dark open areas of the enclosure.

A possible explanation is that the eyesight of brown kiwi is not good enough to strongly perceive the colour of their surroundings. Corfield (2009) investigated the physiology of the brown kiwi's eye in comparison with that of a barn owl. His results suggest that kiwi have a large number of rod cells and very few cone cells, both being photoreceptor cells found within the retina. Cone cells aid in colour and daytime vision and rod cells are essential for nocturnal vision; this suggests that kiwi lack colour vision but compensate by having good perception of light levels**.** Corfield (2009) concluded that kiwi have illumination sensitivity that is "similar to that of other nocturnal birds and mammals and higher than that of diurnal birds". If kiwi have poor colour perception and good light intensity perception, the illumination colour of their surroundings may have less influence than brightness on where they spend their time. It is also

very possible that kiwi have poor eyesight in general. Howland et al (1992) point out the proportionally small eyes that kiwi have in relation to body size, particularly for a nocturnal animal. Howland et al (1992) investigated the visual accommodation abilities of kiwi, finding that kiwi are mildly far-sighted and have a poor close field of vision. They also found that the corneal radius of kiwi is similar to that of young chickens suggesting a lack of "corneal power" or ability to converge or diverge light. A lack of visual perception of surroundings would also explain why there was no significant effect of illumination colour.

There may be other environmental factors that have a more significant influence over where a kiwi chooses to spend its time. Both the edge category and illumination level of each enclosure grid square had a significant relationship with the amount of time spent in them; more time was spent in squares that were on the edge of the nocturnal house and were darkly illuminated. Structural complexity did not affect the amount of time that the kiwi spent in each grid square. There appeared to be an interaction between structure category and light intensity as well as between edge category and light intensity; much time was spent in parts of the nocturnal house that had little coverage and were dark, or were on the periphery and were dark. These results also suggest a stronger influence of illumination brightness on where kiwi choose to spend their time than colour of illumination, though as the results are based on data from one kiwi generalisations cannot be made. The increased time spent in peripheral areas by the kiwi may have been the combined result of several factors. For example, the nocturnal house used for this experiment had a periphery that was open in structure which may be easier for the kiwi to navigate. The kiwi also exhibited what was possibly minor pacing behaviour along the nocturnal house edges which may have affected results; a small amount of pacing is a common occurrence with captive wild animals (Mason et al, 2007).

Several factors may limit the validity of my experiment results. The sample size of one means that the results are not necessarily representative of the general population; additionally the kiwi is older, sometimes sleeps for several hours at a time and has been in captivity for many years. It is also possible that this particular kiwi is colourblind, or has become habituated to her enclosure to the extent that change of illumination colour needed to be for a long period to impact her behaviour. Each day of the experiment there were several grid squares out of the total of 29 that were illuminated by two colours due to unavoidable overlap of the bulb positions. This occasionally created difficulties when classifying these squares into one of the nocturnal house quarters as this process was based on illumination colour. I resolved this by classifying the two-coloured grid square into the smallest of the two possible quarters to standardise the size of the quarters and therefore the distribution of behavioural data.

Additionally the data was not independent as the location of the kiwi each minute affected the probability of where her location would be during the next minute. The positioning of food tubes varied between the days of the experiment but there may have been a bias towards spending time in the grid squares that contained food; as previously mentioned the amount of time spent foraging in each square was not significantly different suggesting that no such bias occurred. Noise from visitors may have also discouraged the kiwi from spending time in parts of the nocturnal house closest to the visitors. I was not aware of any such effect during the observation period however, and the glass used in the enclosures is relatively soundproof. The long periods of time spent by the kiwi sleeping in particular grid squares may have also created data outliers, potentially skewing results in favour of the characteristics of these few squares. This experiment has strong potential for repetition using a large sample of wild and captive kiwi that are a range of age and genders. Repetition using lights with known wavelengths would also be beneficial to understanding the relationship between wavelength and kiwi physiology and behaviour. A more specific focus on whether they can see or prefer red lighting may also be useful, for example by experimenting with a range of lights in the red spectrum.

2.5: Conclusions

It appears that illumination colour had little effect on the amount of time spent in different parts of an enclosure by this kiwi. While we should be cautious about extrapolating the results from a single animal to the general kiwi population, if they are applicable then these findings are of significance to the management of kiwi in wildlife facilities that operate their light regime on the premise that kiwi are not able to see red light. While this may be the case, kiwi may also not have strong enough visual abilities for light colour to significantly affect their behaviour. This study suggests there may be other environmental factors that are more of a determinant of where kiwi spend their time; the kiwi in my study spent significantly more time in areas that were darker or were on the edge of the nocturnal house. In the following chapter I will further investigate the effect of light intensity, edge and structure category on kiwi behaviour as results from this research suggested that there may be significant relationships between these variables.

Chapter 3: Proportion of time spent in nocturnal house areas based on illumination intensity

3.1: Introduction

Variation in light intensity has a significant effect on the behaviour and physiology of many animals. Most animals have significant biological and physiological relationships with light, commonly the result of life history adaptations. Nocturnal animals that are preyed upon will often have significantly altered behaviour under brighter moonlight; this may manifest as them being more evasive, being active closer to a burrow, reducing activity levels or spending more time in burrows (Trent et al, 1977; Daly et al, 1992; Vasquez, 1994). There are several examples where this has been found with nocturnal animals, for example with the kangaroo rat *Dipodomys merriami*, Darwin's leaf-eared mouse *Phyllotis darwini*, the loris *Nycticebus coucang* and the potto *Perodicticus potto* (Trent et al, 1977; Daly et al, 1992; Vasquez, 1994; Frederick and Fernandes, 1994). These behaviours are likely to allow for effective predator evasion. In the wild, kiwi are depredated by introduced mammals such as possums, stoats, rats, dogs and cats, causing their rapid population decline (Robertson et al, 2011). Kiwi are known to be "cryptic" and difficult to locate in the wild with highly cautious behaviour, seldom leaving their burrows until it is completely dark (McLennan, 1997). Much of brown kiwi predator avoidance behaviour appears to be innate; subadults that have been reared in captivity are as likely to survive until the age of first breeding as subadults raised in the wild that have survived infancy (Colbourne et al, 2005).

Kiwi have multiple senses that allow them to perceive the world. They have large quantities of rod photoreceptors that perceive light intensity and have few cone photoreceptors that perceive colours (Corfield, 2009). This suggests that kiwi are well able to pick up the illumination levels of their surroundings but are not able to easily distinguish colour. They have similar photoreceptors as the tawny owl so may have similar wavelength perception (Bowmaker and Martin, 1978; Corfield, 2009); kiwi may therefore be able to best perceive green wavelength and have limited ability to perceive the red wavelength as with the tawny owl. Kiwi are thought to be myopic and have proportionally small eyes compared with those of

other nocturnal birds (Martin et al, 2007). They have a vibrotactile sense that allows the perception of movement around them; kiwi also probably have a reasonably good sense of smell based on their large olfactory bulb (Cunningham, 2007). Being nocturnal it is unsurprising that they would develop senses that are more useful at low illumination levels. It therefore seems that while kiwi may have poor detection of colour, they may have good monochromatic vision at low light levels.

The lighting regimes of enclosures have the potential to impact the behaviour and physiology of captive animals. Light intensity affects the behaviour and physiology of a variety of captive animals including poultry, lorises and pottos (Trent et al, 1977; Frederick and Fernandes, 1994; Sherlock et al, 2010). Light that is too bright or dark in a nocturnal enclosure can affect activity levels and specific behaviours. Pottos *Perodicticus potto* become more active when their diurnal and nocturnal lights are dimmed, consistent with what is observed in the wild (Frederick and Fernandes, 1994). Slow lorises *Nycticebus coucang* become more active when their enclosure lights are dimmed and there seemed to be an illumination "threshold" level below which activity levels were much higher (Trent et al, 1977). Additionally, in my previous experiment a kiwi chose to spend more time in areas with darker illumination. It is likely, therefore, that light intensity affects the behaviour of kiwi in both natural and artificial environments.

It is possible that the light intensity of kiwi nocturnal houses significantly impacts their behaviour and physiology. Because kiwi predator aversion behaviour appears to be innate and because kiwi may have good perception of the light intensity of their surroundings, it may be beneficial to research the impact of nocturnal house illumination intensities on the behaviour of captive brown kiwi *Apteryx mantelli*. Kiwi are an iconic species in New Zealand and many are housed for advocacy and education purposes in captive nocturnal houses (Barlow, 2011). However, there are currently limited guidelines for the nocturnal house light regimes of kiwi (Fraser and Johnson, 2011). Much variability exists between nocturnal house light setups. Some enclosures have lights that vary in colour while others are uniform in colour; enclosures vary noticeably in their light intensities and in their duration of nocturnal lighting (Personal observations). To successfully breed and/or exhibit kiwi in captivity, the light regimes they are exposed to may be important, though the effect of light regimes on kiwi has not been previously investigated. I wish to compare the significance of light intensity with the significance of structural complexity and proximity to the enclosure edge when kiwi are choosing where to spend their time, and I predict that kiwi will spend significantly more time in darker enclosure areas. This research will provide baseline information on the importance of

illumination intensity to the behaviour of kiwi and indicate whether their display quality and captive well-being can be further enhanced; it may also assist the refinement of the captive management plan for kiwi.

3.2: Methods

Eight brown kiwi were observed at three captive institutes; three birds were on display indoors at Kiwi Encounter housed in individual enclosures, three were outdoor display birds in separate enclosures at Rainbow Springs and two were a male and female pair sharing an indoor enclosure at the National Aquarium of New Zealand. In total there were a young male and female, three middle-aged males, two middle-aged females and an older female kiwi. Figures 3.1 and 3.2 show examples of the indoor and outdoor enclosures that housed kiwi.

Figure 3.1*: The kiwi nocturnal house at the National Aquarium with examples of structural coverage and roost boxes seen.*

***Figure 3.2**: One of the outdoor kiwi display enclosures at Rainbow Springs.*

All indoor kiwi are kept under reverse light conditions with their lights being switched to darkness at 8.30am and switched back to bright lighting at 6pm. The kiwi at the National Aquarium were fed from food dishes at 10am and 3pm and did not have live insects released into their enclosure while I was there; the Kiwi Encounter/Rainbow Springs kiwi had food placed in their enclosure at the start of the day and had live insects released most days. For my observations, I recorded which grid squares the kiwi entered every minute in addition to recording where food was positioned in the enclosure and any extraneous environmental variables. From standing outside their pens during their night, a total of 1500 minutes of observation were completed for each of the five kiwi housed indoors. 600 minutes of these observations were within the first two hours of the indoor kiwi being active. This was done because I was limited to observing the three outdoor kiwi for their first two hours of activity. Hence, over five days I collected 600 minutes of behavioural data within the first two hours of activity for all kiwi. The 1500 minutes of observations of indoor kiwi were evenly distributed throughout the day to negate any bias towards natural daily activity patterns. Kiwi were equally detectable from all enclosure grid squares.

To record where kiwi spent their time in their enclosure during observations I created a grid of each nocturnal house. To do this, I divided enclosures into 1x1 metre grid squares by laying string that was marked at one metre intervals from the back to the front wall of the enclosure; string was laid every metre along the length of the enclosure until all areas of the enclosure were contained within a 1x1 metre square. Geographical objects within each of the grid

squares were drawn on a map of the enclosure to enable quick identification of each square. This was so the string could be removed while the kiwi were active. Light intensity measurements were made in several different positions within each square and a mean intensity was calculated. An Extech HD450 data logging light meter was used for this. Each grid square was classified as being either open in structure, having moderate coverage or being fully covered. The structure of enclosures largely consisted of ferns, tussock and flaxes. Grid squares were also classified as being on the periphery or in the centre of an enclosure and positioning of light bulbs was noted. Kiwi Encounter/Rainbow Spring enclosures were illuminated by between five and seven 30 watt Phillips PAR38 bulbs coloured blue, yellow, red or green. The National Aquarium enclosure was illuminated by six 30 watt Radium halogen lamp bulbs. A table listing the light intensity range, total number of edge and centre squares, total number of open, mixed and fully covered squares, and the total number of grid squares overall for each nocturnal house can be found in Appendix E.

I wished to calculate the proportion of time spent in each grid square of all enclosures by the eight kiwi. To do so I entered each minute of observation into a spreadsheet as shown in Appendix A. The proportion of time in each minute that was spent in a grid square was entered. For example, if in one minute the whole time was spent in square A1 by a kiwi, then the A1 column received a 1 for that minute. If, however, time was spent in A1, A2 and A3 in that minute then A1, A2 and A3 each received 0.33 for that minute's observation. These proportions of time for each grid square for the entire day of observations were then added and this sum for each grid square was divided by the total sum of proportions. This calculated what proportion of each day of observations was spent in each grid square, and it was these data that I used to complete the statistical tests for individual variables. I also classified each grid square as being in light category one or two; light category one squares were darker than the overall mean light intensity of the nocturnal house and category two squares were lighter.

Statistical tests completed were nonparametric as the results were not normally distributed (Anderson-Darling; $\bar{x}=0.020\pm0.093$, $p<0.01$). A univariate General Linear Model (GLM) was completed on the data of all kiwi combined; proportion of time spent in grid squares was compared with their light intensity, structure and edge category. As with Chapter 2, the GLMs are parametric so results from this test must be interpreted with caution. Non-parametric Mann-Whitney tests compared the proportion of time spent in grid squares in relation to light intensity, structure and edge category for individual kiwi as a more robust test of the abnormally distributed data. A multivariate GLM was carried out to examine the combined

effect of illumination intensity, structure and edge category on the proportion of time spent in enclosure grid squares; this was completed for individual kiwi.

The following figures illustrate the grid enclosure setup of the eight experiment kiwi with the positioning of kiwi in relation to each other and visitors shown.

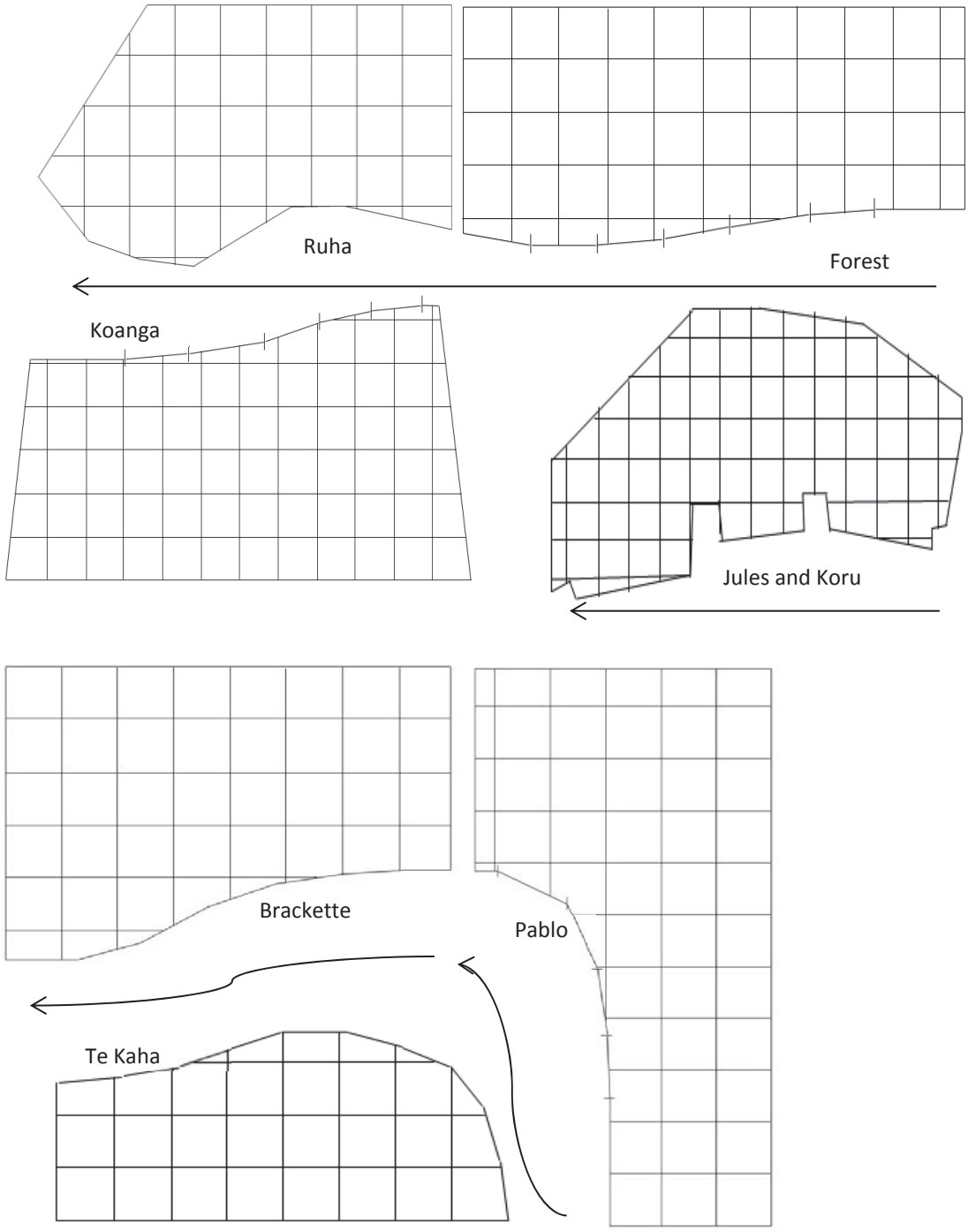


***Figure 3.3**: Enclosure grids of eight brown kiwi with positioning in relation to each other and visitors shown. Brackette, Pablo and Te Kaha were housed in the same room indoors at Kiwi Encounter but were physically separated; Brackette and Pablo's exhibits were separated by a fence and there were glass walls on either side of the pathway where visitors walk as shown with arrows. Jules and Koru were housed indoors together at the National Aquarium in an enclosure with a glass wall where visitors passed. Ruha, Forest and Koanga were housed outdoors at Rainbow Springs with a fence separating them from visitors. These three kiwi were physically separated though the enclosures of Ruha and Forest share a fence.*

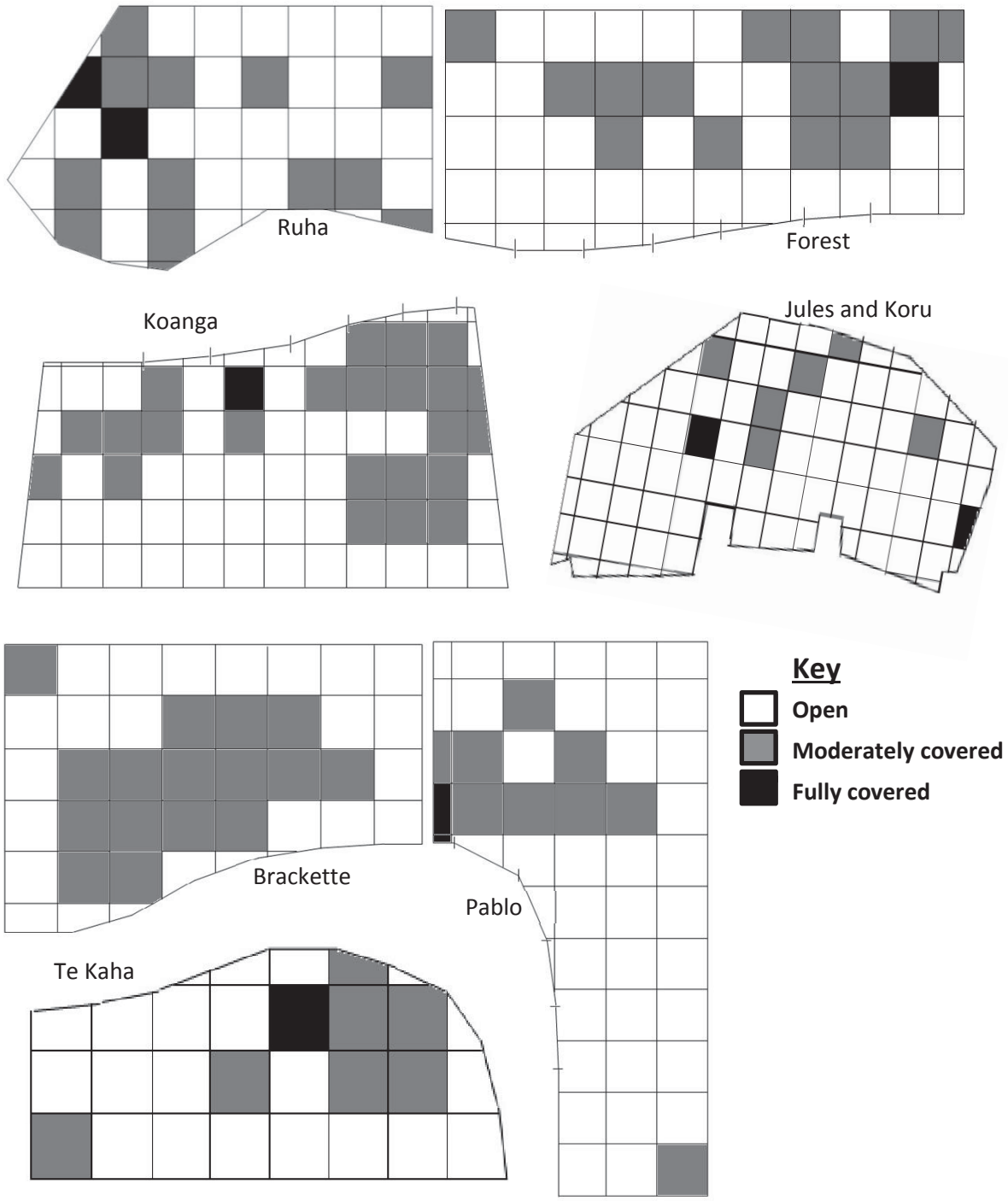
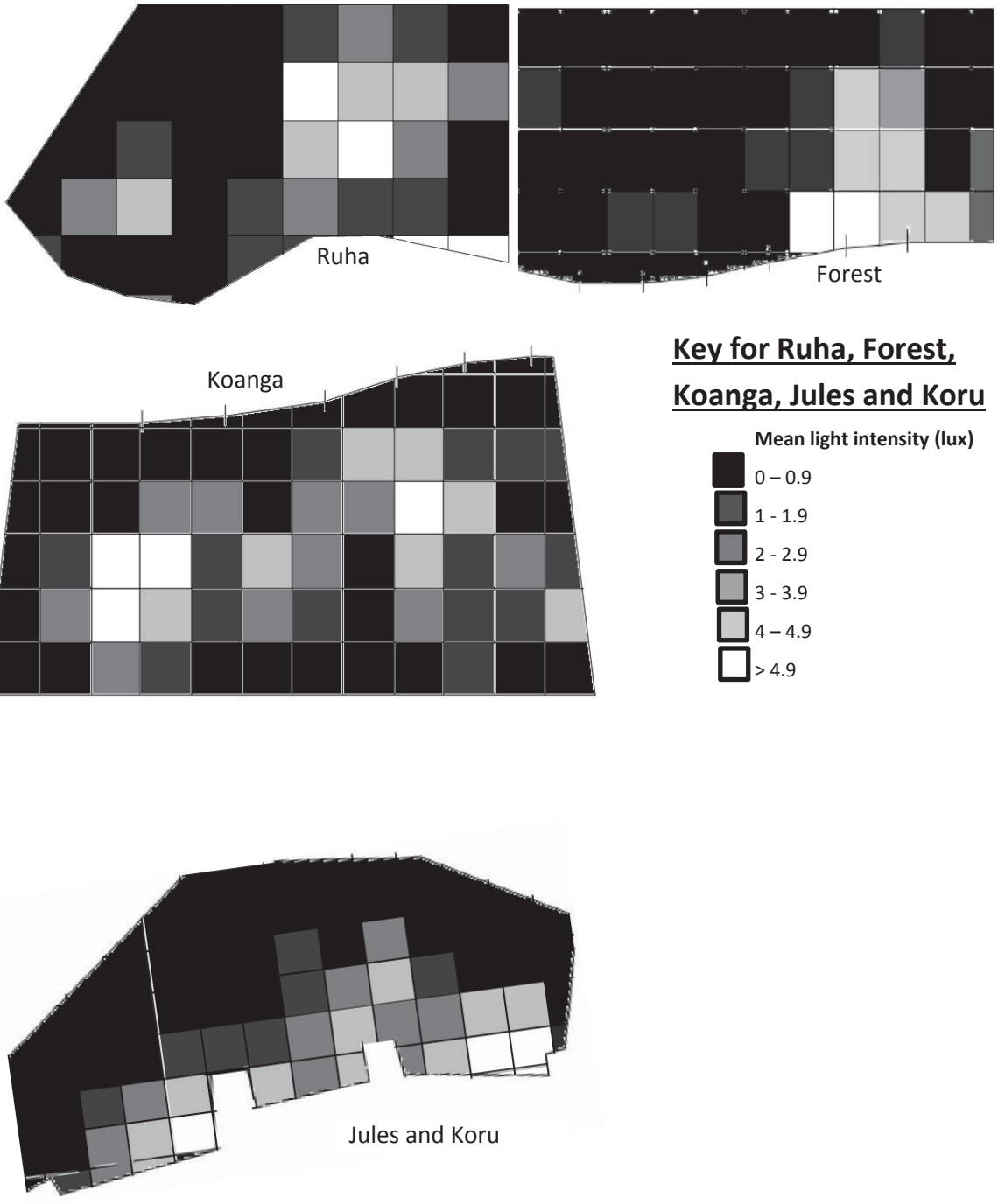


***Figure 3.4**: Structure coverage of the enclosures that eight brown kiwi are housed in with white indicating open grid squares (structure category one), grey indicating moderately covered squares (structure category two) and black indicating squares that are fully covered in structure (structure category three). It appears that some enclosures have proportionately more mixed and covered grid squares than others.*

Figure 3.5 shows the relative light intensities of the nocturnal houses with lighter squares having a lighter mean illumination. Please note that Jules and Koru, Ruha, Forest and Koanga have a different scale of shading to Te Kaha, Brackette and Pablo to represent the relative as opposed to absolute distribution of enclosure illumination.



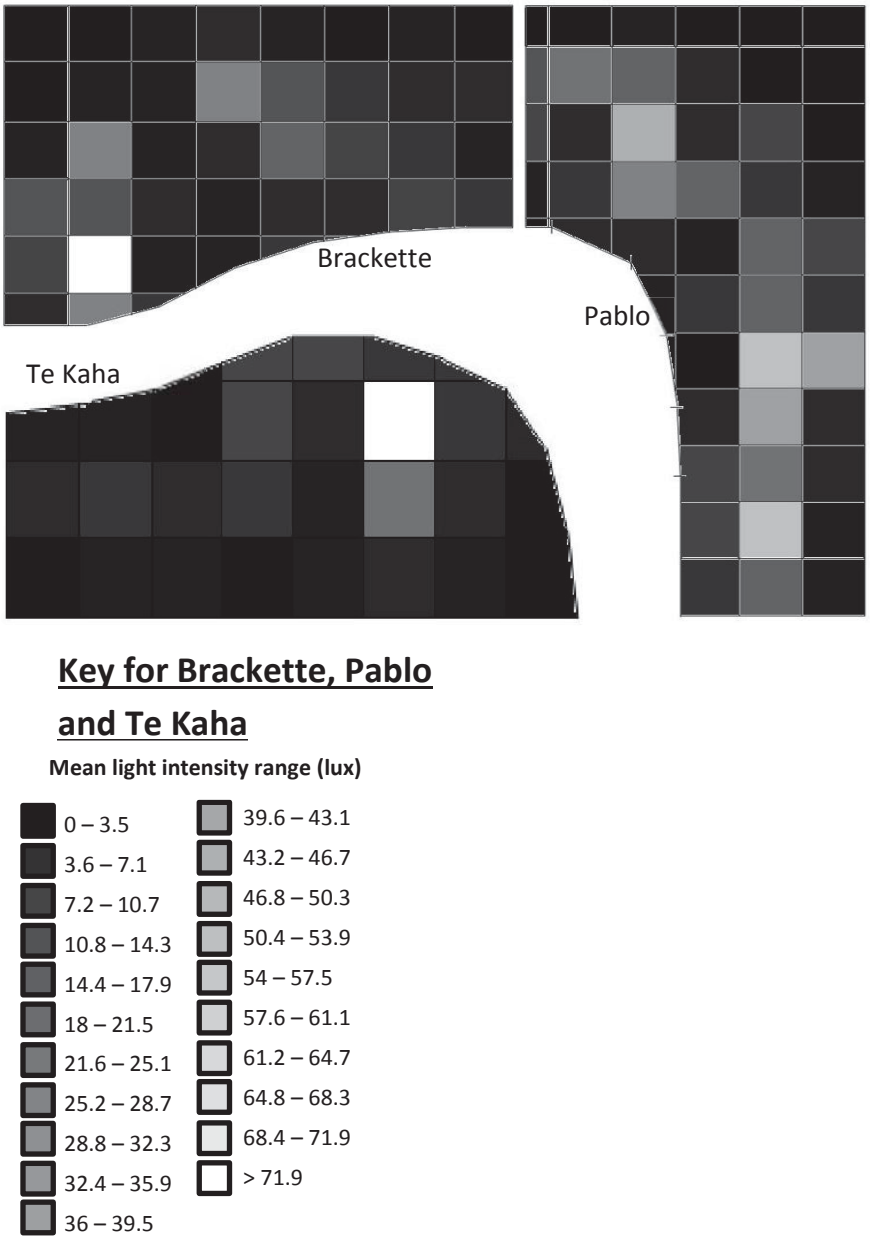


Figure 3.5*: Mean relative light intensities of the nocturnal houses of eight brown kiwi; please note that Jules and Koru, Ruha, Forest and Koanga had a different range of shading to Te Kaha, Brackette and Pablo due to having differing ranges of light intensities.*

3.3: Results

I investigated whether illumination intensity affected the amount of time that was spent in areas of an enclosure by eight brown kiwi, or whether amount of structural coverage and proximity to the enclosure edge were more important factors in determining time spent there. For the following statistical tests and graph representations, data used and displayed is the illumination level, structure or edge category, or amount of time spent in an individual grid square; therefore the term “nocturnal house area” is synonymous with individual grid squares and is used for simplicity.

It seems that different factors are together significantly impacting where kiwi are spending their time and that it is unlikely to be the result of a single factor. The univariate GLM multiple comparison analysis showed a significant three way interaction effect between the variables of individual kiwi, edge and structure ($F(2, 3159)=3.13$, $p=0.044$) on proportion of time spent in grid squares. There was also a significant two-way interaction effect of light intensity and edge ($F(9, 3159)=4.56$, $p<0.01$), and individual kiwi and edge ($F(4, 3159=6.031$, $p<0.01$), on proportion of time spent in grid squares. Further investigation in a post-hoc Bonferroni multiple comparison found that on average per minute observation, 1.7% less time was spent in open-structured grid squares than in squares with mixed coverage (0.017 ± 0.0019, $p<0.01$) and on average 6.9% less time was spent in mixed coverage squares than full coverage squares (0.069 ± 0.0050, $p<0.01$). It was also found that on average per minute observation, of the experiment kiwi, Te Kaha was more active than all kiwi aside from Brackette ($p<0.01$ for all), Brackette was more active than Jules ($p<0.01$) and Koru ($p=0.013$), and Ruha was more active than Jules ($p=0.048$). Finally, kiwi spent 1.1% longer on average per minute observation in grid squares in the centre of their enclosure compared with on the edge (0.011 ± 0.0031, $p<0.01$). These significantly interacting variables suggest that some validity is lost when examining variables separately for their impact on where kiwi spent their time; however as data was not normally distributed the GLM and Bonferroni results must also be viewed with some caution. I therefore went on to examine factors individually.

When data were combined kiwi spent significantly more time in darker illuminated grid squares (GLM; F(193, 3346)=8.70, p<0.01). Individually, Forest (W(1, 305)=26027.5, p=0.01) and Koanga (W(1, 489)=63610.0, p=0.02) spent significantly more time in areas darker than their median light intensity while Jules (W(1, 647)=97658, p<0.01) and Koru (W(486)=55394.5, p<0.01) spent significantly more time in lighter areas (Mann-Whitney non parametric test). The remaining kiwi showed no significant difference. Jules and Koru may have influenced the behaviour of each other as they were housed together and were laying and incubating an egg for several days of the observations. This may have also affected their results for the variables of light, structure and edge category, and for the amount of time that they were active. They were significantly less active on average than three of the six other kiwi, however I chose to include their data as their results were comparable with the other three kiwi and with each other.

Figure 3.6 shows that when more than 30% of time was spent in a grid square, that square was illuminated by 8 lux of light or less; grid squares illuminated by over 20 lux of light had no more than 10% of time spent in them. The data for proportion of time appear to match the pattern shown in Figure 3.13 with some kiwi spending large periods of time in a few areas and with other kiwi having a more even distribution.

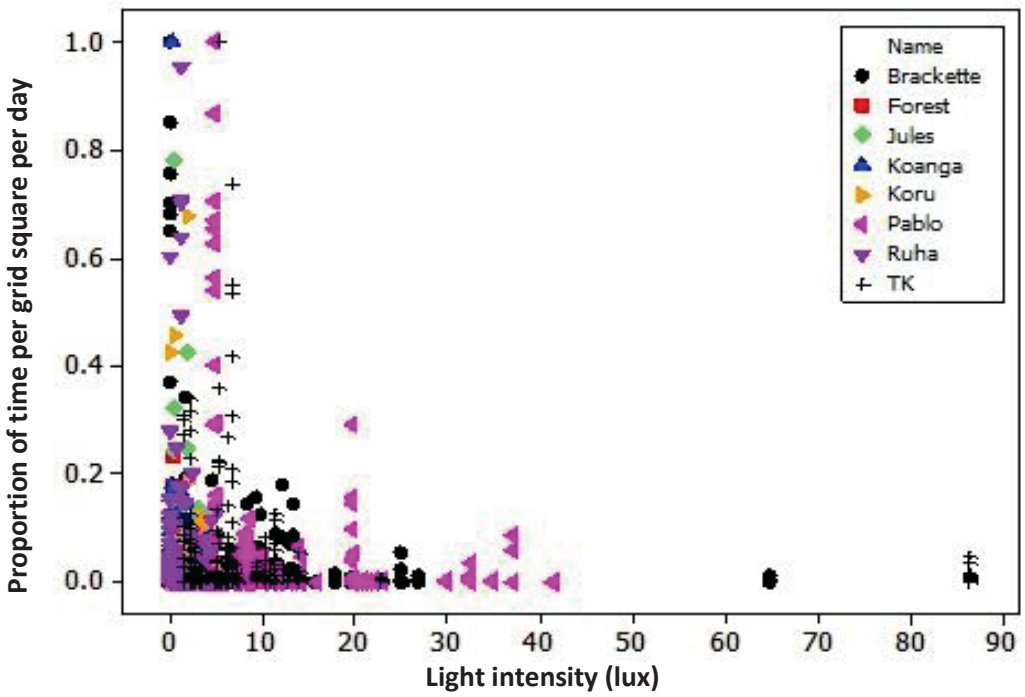


***Figure 3.6**: Proportion of time spent by eight brown kiwi in areas of a nocturnal house based on light intensity; areas illuminated by more than 20 lux had no more than 10% of time spent in them and areas where more than 30% of time was spent were no brighter than 8 lux.*

The mean light intensity data point for each grid square was divided by the mean light intensity for each kiwi's nocturnal house, to distribute the light intensity data more evenly and account for the fact that the range of light intensities varied for each kiwi. When light intensity data were adjusted for the mean there was a similar relationship with the larger proportions of time being spent in darker areas (Figure 3.7).

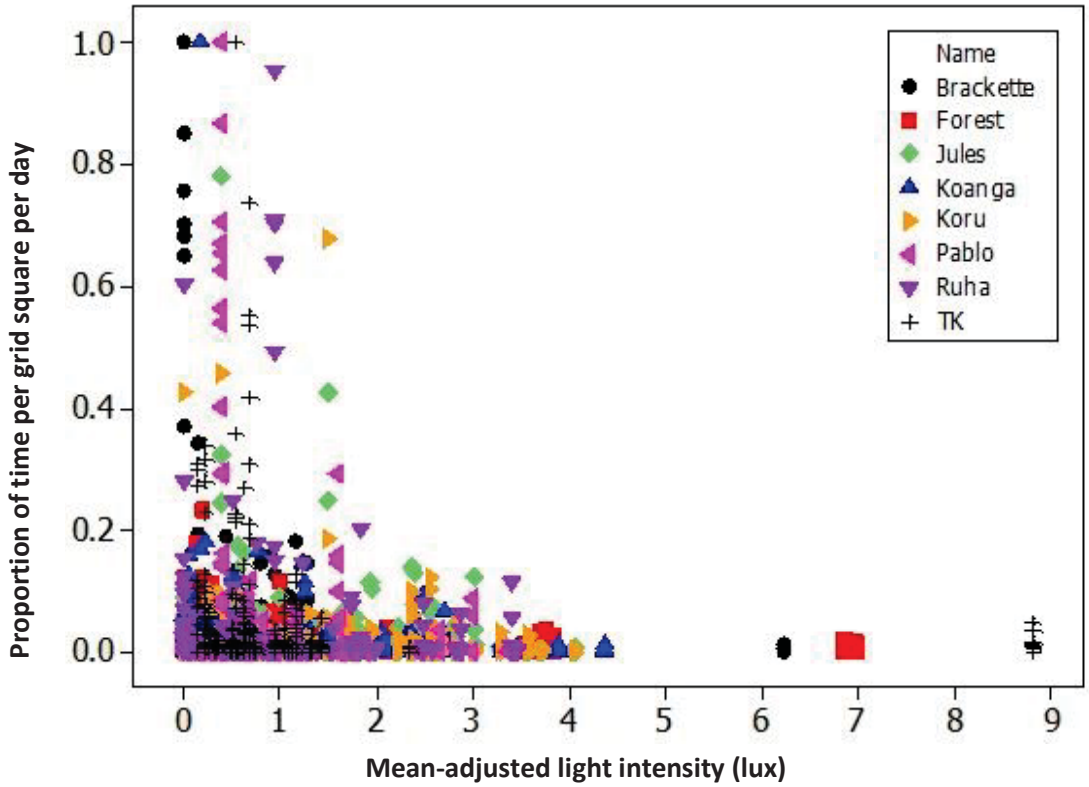


***Figure 3.7**: Proportion of time spent by eight brown kiwi in areas of a nocturnal house based on adjusted light intensity (lux); mean light intensity (lux) for each grid square was divided by mean light intensity (lux) for each nocturnal house. A more even distribution of time proportions at lower light intensities is demonstrated in this figure than in figure 3.6 but with a similar pattern of low time proportions at high light intensities.*

Kiwi appeared to spend variable amounts of time in areas brighter and darker than the mean light intensity (Figure 3.8); half of the kiwi spent more time on average in darker areas of their enclosure and half spent more time in lighter areas. There also seemed to be no apparent effect of whether kiwi were housed indoors or outdoors. The black lines represent the expected mean proportion of time spent in grid squares regardless of illumination. Please note that the expected mean amount of time varies between kiwi due to differing numbers of grid squares (ranging from 29 to 81, see Appendix C).

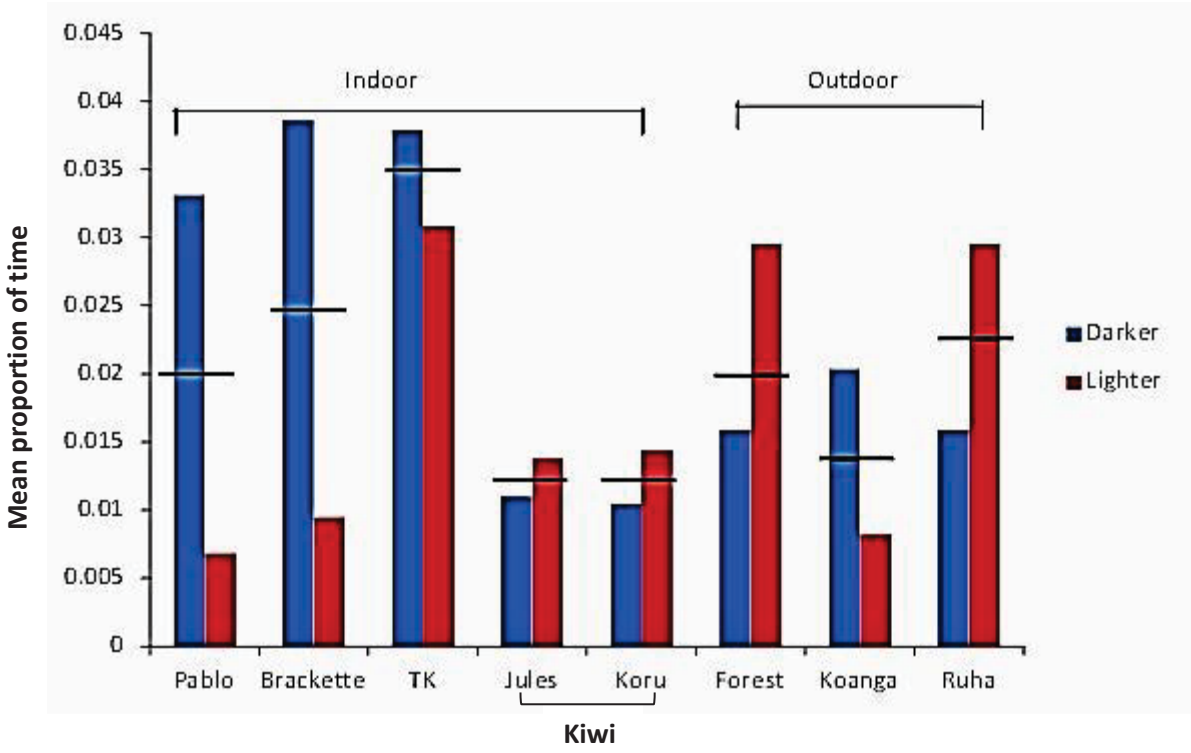


Figure 3.8*: Mean proportions of time spent by kiwi in areas darker and lighter than the mean enclosure light intensity with the location that kiwi were housed in shown; three of the five indoor kiwi spent more time on average in areas illuminated darker than the mean light intensity while two of the three outdoor kiwi spent on average more time in areas that were brighter. The black lines represent the expected mean amount of time spent in each grid square regardless of illumination, structure or edge category. Please note that Jules and Koru were housed together so may have affected the behaviour of each other.*

Significantly more time was spent by brown kiwi in areas that had mixed or fully covered structure when data were again combined (GLM; F(2, 3537)=46.58, p<0.01). As individuals, Jules (W(1, 647)=185944.5, p=0.01*).* Koanga (W(1, 489)=72608.5, p<0.01), Koru (W(1, 485)=104975.5) and Ruha (W(1, 351)=38900.5, p=0.01) spent significantly more time in areas with mixed and covered structure based on median proportion of time (Mann-Whitney non-parametric test).

An overall pattern for increasing mean time spent in mixed and covered areas can be seen in Figure 3.9. There was no apparent difference between indoor and outdoor kiwi for the mean proportions of time spent in open, mixed and covered areas.

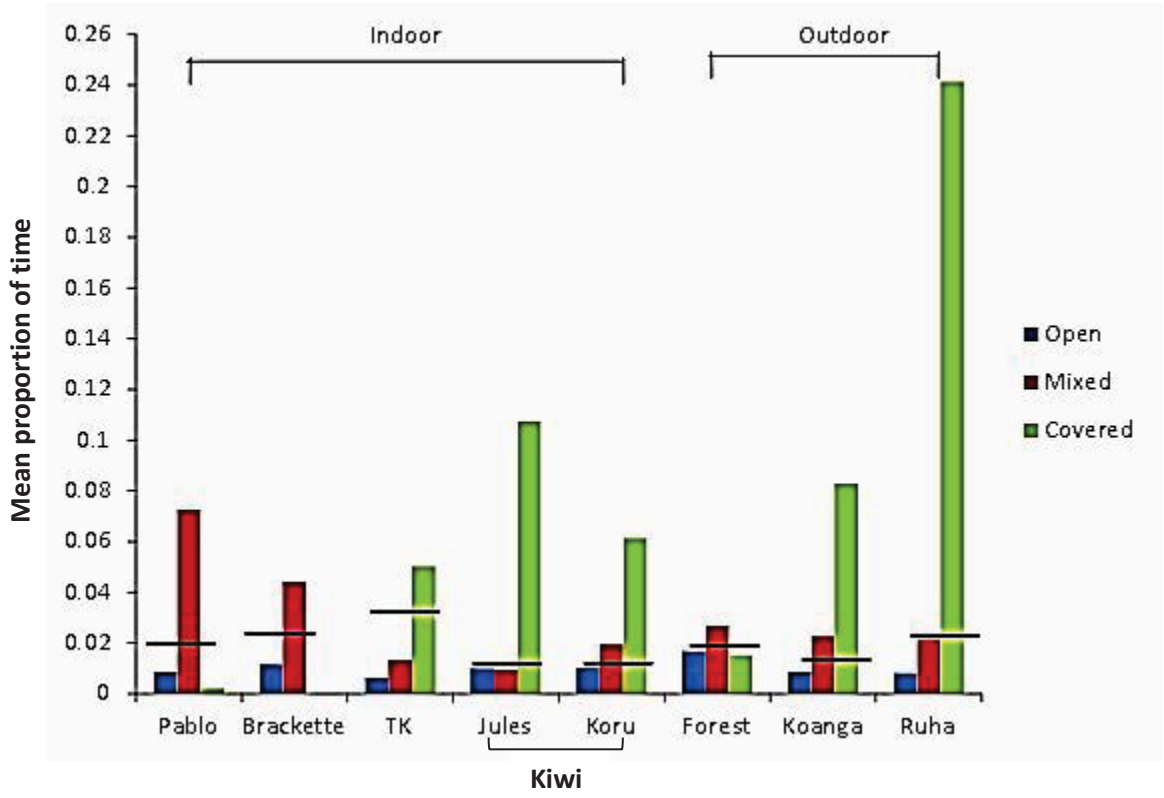


Figure 3.9*: Average proportions of time spent by eight brown kiwi in enclosure areas that were open, partly covered or covered; significantly more time on average was spent in covered areas with an evident pattern for increasing mean proportion of time with increasing coverage. The black lines refer to the expected mean proportion of time spent in each grid square. Please again note that Jules and Koru were housed together, and that Brackette had no completely covered areas in her nocturnal house.*

Unsurprisingly there were slightly more open-structured nocturnal house areas that had high light intensity illuminations (Figure 3.10); this was expected as less coverage should result in more light being able to illuminate an area at ground level. The high number of data points in each structure category should offset the potential for statistical bias caused by more time being spent in lighter or darker illuminated areas which may have affected the examination of structure as a single variable.

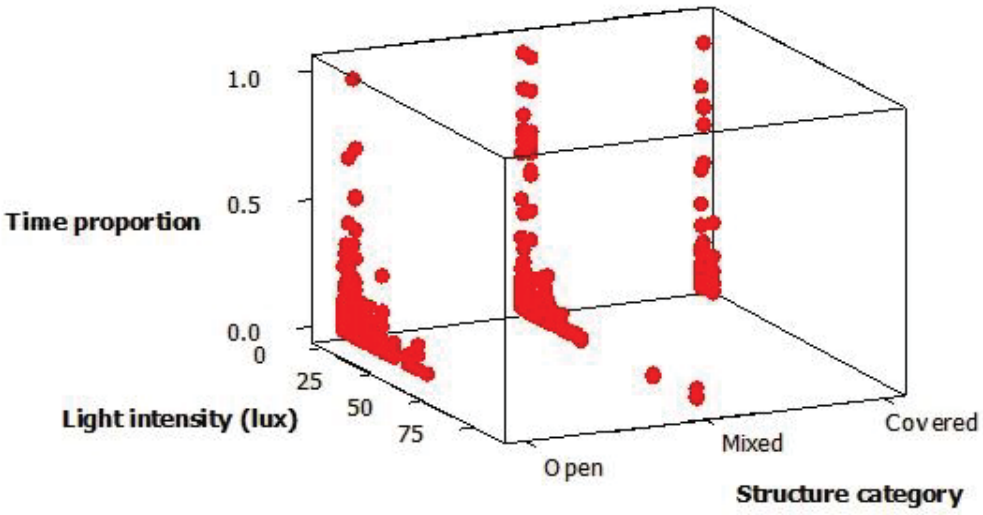


Figure 3.10*: Proportions of time in relation to light intensity (lux) spent by eight brown kiwi in areas of enclosure that were open, had mixed coverage or were fully covered. Significantly more mean time was spent in areas that were more covered in structure for the combined data. In this graph data points of high time proportions were much more commonly in the mixed or covered structure category.*

Significantly more time was spent in areas on the periphery of the enclosure for combined data (GLM; F(1, 3538)=13.05, p<0.01). Jules (W(1, 647)=102873.0, p<0.01), Koru (W(1, 485)=55964.5, p<0.01) and Ruha (W(1, 351)=35561.5, p<0.01) spent significantly more time in grid squares at the centre of their enclosure based on median time proportion and Pablo (W(1, 499)=78562.0, p,0.01), Brackette (W(1, 409)=46218.0, p<0.01), Te Kaha (W(1, 347)=45959.0, p<0.01), Koanga (W(1, 489)=60919.5, p=0.01) and Forest (W(1, 305)=27917.5, p<0.01) spent significantly more time at the edge (Mann-Whitney non-parametric test). This was in accordance with the mean proportions of time that they spent in these areas seen in Figure 3.11. Figure 3.11 illustrates that five of the eight kiwi spent a higher mean proportion of time in areas on the edge of the enclosure. There was no pattern for indoor or outdoor kiwi as groups spending more time in peripheral or central areas.

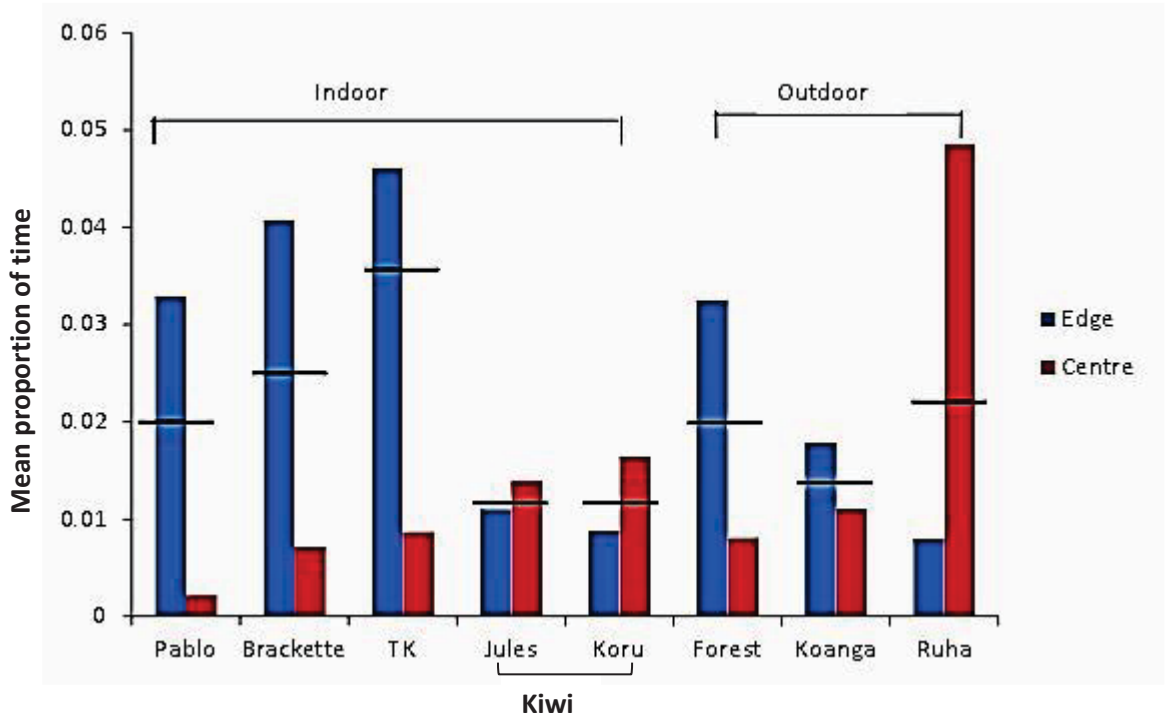


Figure 3.11*: Distribution of proportion of time spent by eight brown kiwi in areas on the edge and in the centre of enclosure; five of the kiwi spent a higher mean amount of time in areas on the edge of their nocturnal house than in the centre. Again note that Jules and Koru were housed together and incubating an egg for several days, and that the black lines represent expected mean proportion of time spent in each grid square.*

The distribution of light intensities was similar for areas on the edge of the nocturnal house as in the centre (Figure 3.12). There appeared to be more instances of high proportions of time spent in areas on the enclosure edge.

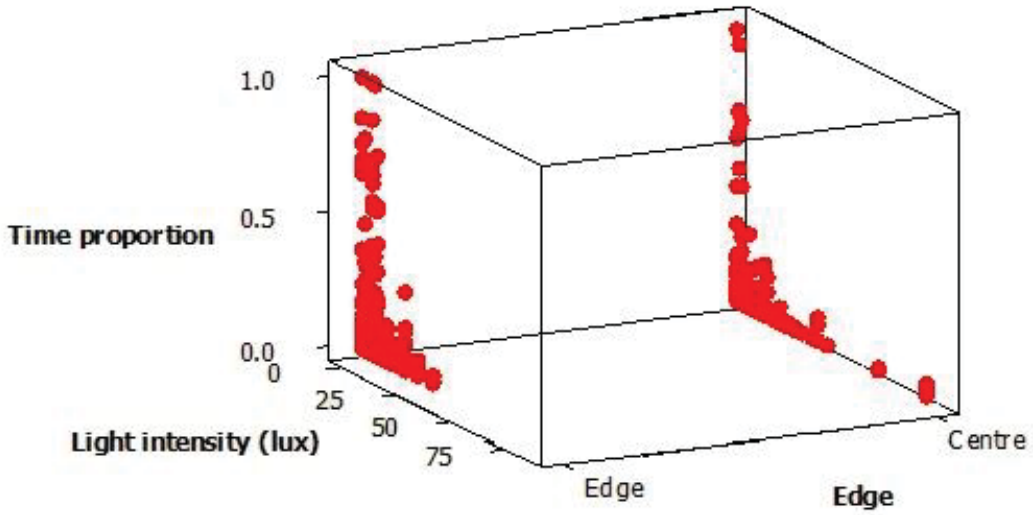


***Figure 3.12**: Proportions of time spent by eight brown kiwi in areas on the edge and in the centre of their enclosure; a larger number of areas on the enclosure edge appear to have had more than 25% of time spent in them*

The following graphs represent the mean proportions of time that were spent by the eight kiwi in different parts of their nocturnal house. Areas that are a darker shade had more time spent in them and arrows indicate the side that visitors view the kiwi from. Again Figure 3.13 illustrates that while some kiwi spent a small amount of time in a large number of areas, others spent a large amount of time in a few areas (also seen in figures 3.6 and 3.7). There appears to be no obvious pattern for any of the kiwi linking their proportions of time with the light intensities, structural coverage and proximity to the enclosure edge (also seen in figures 3.4 and 3.5). Additionally there appears to be no significant relationship between visitor proximity and proportion of time spent in a grid square. Proximity to each other may have had an effect on where they spent their time, particularly with Brackette and Pablo who appeared to spend a lot of time at opposite sides of their enclosure. Please note that the shading of the grid squares was non-linear.

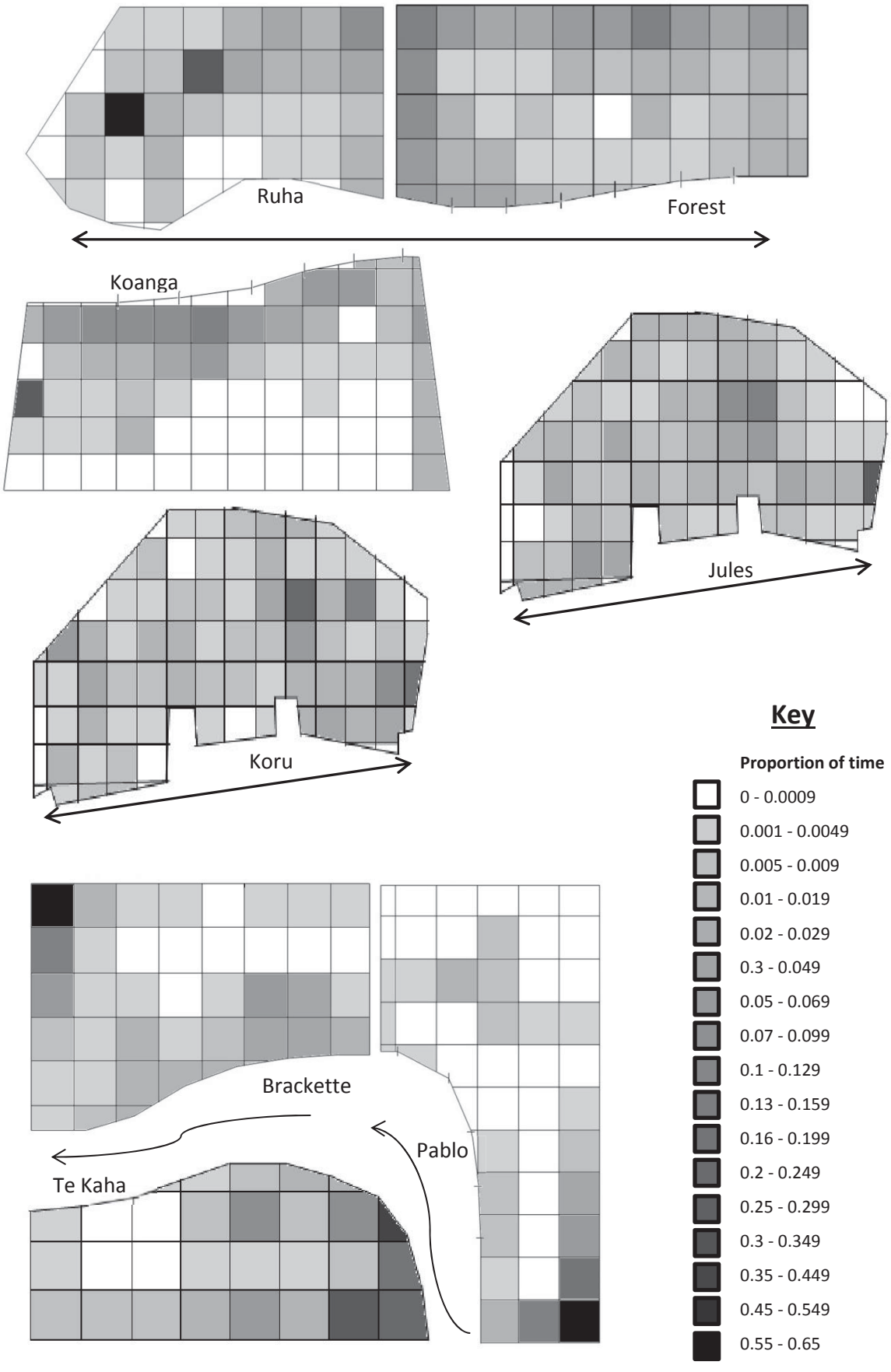

Ruha
Forest
Koanga
Jules
Koru
Key
Proportion of time
0 - 0.0009
0.001 - 0.0049
0.005 - 0.009
0.01 - 0.019
0.02 - 0.029
0.3 - 0.049
0.05 - 0.069
0.07 - 0.099
0.1 - 0.129
0.13 - 0.159
0.16 - 0.199
0.2 - 0.249
0.25 - 0.299
0.3 - 0.349
0.35 - 0.449
0.45 - 0.549
0.55 - 0.65
Brackette
Pablo
Te Kaha

***Figure 3.13**: Mean proportions of time that eight brown kiwi spent in each grid square of their nocturnal house with darker shading indicating more time spent in that area. Proximity of kiwi to each other is shown with the pathway of visitors illustrated with arrows; Brackette, Pablo and Te Kaha at Kiwi Encounter were housed indoors separately with Brackette and Pablo sharing a fence, there was also a glass wall along the pathway that visitors took separating them from the kiwi. Jules and Koru were housed together indoors at the National Aquarium with a glass wall separating them from visitors. Ruha, Forest and Koanga were housed outdoors at Rainbow Springs with fences separating them from visitors. The enclosures of Ruha and Forest also shared a fence.*

3.4: Discussion

Neither one of the three independent variables analysed (illumination intensity, structure and edge category) was the main determinant of the proportion of time spent in enclosure areas by kiwi. These variables had differing and interacting effects on where the kiwi spent their time and there appeared to be no single variable that was the main determinant of this, though kiwi appeared to prefer darker, more covered and peripheral areas overall. The individual preferences of the kiwi are one of several alternative factors that may have accounted for the individual variation seen. Kiwi spent different amounts of time in the edge and centre, in darker and lighter and in covered and open areas of their enclosure. They were also active for varying amounts of time and some spent a small amount of time in a large number of areas, again suggesting behavioural differences between individuals. It is possible that extraneous variables such as differing visual abilities and occasional ambient noise from particularly large groups of visitors may account for this.

Light intensity had a mixed relationship with the proportion of time that kiwi spent in enclosure areas. When data were combined kiwi spent significantly more time on average in areas illuminated by darker light intensity, though this was not the case for all individual kiwi. The three kiwi that were housed in enclosures that had some areas brighter than 10 lux generally spent less than 20% of time in them (Figure 3.6); at least 31% of these three enclosures were brighter than 10 lux so spending less than 20% of time in these areas is lower than expected. This may indicate that nocturnal houses should not use lights brighter than 10 lux. This is also supported by the fact that a full moon produces a maximum of two lux of light on a clear night (Vasquez, 1994); therefore wild kiwi are naturally only exposed to a maximum moonlight illumination of two lux. Captive nocturnal animals, including pottos and lorises, are known to avoid brighter areas of their enclosure (Trent et al, 1977; Frederick and Fernandes, 1994). This is probably a natural predator avoidance mechanism for them, as is the fact that the potto and loris are arboreal, having predominantly terrestrial predators (Trent et al, 1977; Frederick and Fernandes, 1994). Kiwi may have less of an instinct to avoid brighter areas than other nocturnal animals as their ancient predators were mostly avian, including the Haast eagle *Harpagornis moorei*, the Goshawk *Accipiter fasciatus* and the Whekau owl *Sceloglaux albifacies* (Holdaway, 1989). Avian predators are more likely to have powerful eyesight than terrestrial predators so can probably see terrain easily regardless of low light levels, particularly nocturnal avian predators with many light-sensitive rod cells (Ruggeri et al, 2010). This means that the use of structural coverage would have been a superior way for kiwi to

avoid avian predators than by solely avoiding darker areas. Kiwi may therefore have more of an instinct to avoid areas with little coverage.

Results suggested that kiwi may have a partiality for areas that are structurally complex. Though there were only nine nocturnal house grid squares in total that were completely covered in structure, significantly more time on average was spent in them by the kiwi than in other areas when data were combined; of the seven kiwi with fully covered squares in their enclosure a mean time of approximately 8.5% per day was spent in each of these squares, compared with an average of 1.5% that was spent in each of the squares that were fully open. Four of the kiwi spent significantly more time in covered areas, again suggesting individual variation for this variable. On moonlit nights nocturnal animals that are preyed upon will commonly spend less time out in the open and more time in areas that are darker or covered (Vasquez, 1994; Daly et al, 1992; Trent et al, 1977). Taborsky and Taborsky (1995) found that kiwi spend significantly more time in areas of marsh and seral or low-lying vegetation, mirroring the large proportion of time the kiwi spent beneath ferns, tussock and flaxes in my experiment. It is likely that low-lying vegetation provides more effective cover than just the shade offered by taller trees, perhaps providing better defence against past avian predators than darkness alone (Holdaway, 1989). Moderate structural coverage in nocturnal houses, particularly low-lying shrubbery, may be an appropriate compromise between allowing coverage for kiwi to seek refuge and enabling visitors to observe the kiwi. I would suggest that nocturnal house kiwi may benefit from having more partly or fully covered area than open area.

Captive kiwi may prefer to spend slightly more time around the edge of enclosures. Significantly more time on average was spent on the edge of the enclosures when data was combined; grid squares that had more than 50% of time spent in them were much more commonly on the periphery of an enclosure (Figure 3.12). Individually, five of the eight kiwi spent more time on the edge of their enclosure. Thigmotaxis, or a tendency to orientate towards touch stimuli, may explain the higher mean proportion of time spent on the edges of an enclosure overall (Simon et al, 1994). Animals that exhibit thigmotaxis, including many species of birds, rodents and fish, spend higher amounts of time close to touch stimuli as contact with outer walls enables the use of “tactile cues, in addition to olfactive and visual ones, to build up a spatial representation of the environment” (Simon et al, 1994). As kiwi vision is unlikely to be acute they perhaps benefit from using other senses to navigate in this way. The light perception ability of kiwi is likely to be very good due to a large number of rod cells allowing for photon reception; however their colour vision and image resolution is not

likely to be well developed (Howland et al, 1992). Kiwi have a well-developed sense of vibration that they use to sense their surroundings by “probing” the ground with their bill (Cunningham, 2007). Mechanoreceptors referred to as Herbst corpuscles contained within the bill tips of kiwi receive vibration and pressure information from the environment and relay this information to the brain (Cunningham, 2007). Kiwi also have at least a reasonably well developed sense of smell and are known to use scent to mark territories, acting as a warning to intruders (McLennan, 1988; Cunningham, 2009). These senses may be used particularly effectively around the enclosure edge to provide information of their surroundings. As with light and structure the results do not show a conclusive preference for edge or central enclosure areas, however kiwi may benefit from being housed in enclosures that have proportionally more periphery area than non-periphery area. They are also likely to be more visible to the public if they spend more time on the edge of the enclosure.

There were other environmental factors that may have affected the results that were achieved in this experiment. There may have been an effect of territoriality on the behaviour of kiwi housed next to each other with a fence separating them. The time proportion graphs suggested that Pablo and Brackette in particular spent more time on opposite sides of their enclosure (Figure 3.13). Kiwi who are separated by a fence are likely to be able to smell each other; as they are territorial by nature and can be aggressive it is possible that this would impact their behaviour (Cunningham, 2009). Further investigation would be necessary to confirm an effect. Whether kiwi were housed indoors or outdoors may have also been a significant factor for how much time they spent in areas of differing structure, light and edge category. However, kiwi housed indoors and outdoors showed no apparent difference between where they spent time based on the variables of light, structure and edge shown in figures 3.8, 3.9 and 3.11, and individual preference may have been a more important factor.

The experiment results suggest that the kiwi had distinct personalities that impacted what areas of the enclosure they spent their time in. The time that the kiwi as individuals spent in areas of differing structure, light and edge category varied significantly; this was also the case with their general area distribution as some kiwi spent a small amount of time in a large number of grid squares and vice versa. Individual personalities in animals can arise as a result of selection pressures that vary in response to environmental changes and selection for or against particular phenotypes (Dingemanse et al, 2004). In a captive environment this may mean that behaviours develop that would not necessarily be selected for in the wild, meaning that the results from the captive kiwi may not be an accurate reflection of how wild kiwi respond to light. It may also mean that kiwi enclosures need to be more specifically adjusted

to suit and/or enhance the behavioural patterns of display kiwi, for example by enticing kiwi to use a larger proportion of their enclosure if they normally spend time in a small area.

Several factors must be considered when taking into account the validity of these results. One of the major factors is that some of the squares making up the nocturnal house grids were less than 1x1 metre squared which may have reduced the chance that the kiwi would be observed in them. Additionally the independence of data is impacted by the experimental design as the presence of kiwi in a particular grid square affects the probability of their presence in the other grid squares of their nocturnal house. Also two of the kiwi were housed together so their behaviour may have affected each other; this is supported by their similar periods of time spent active and in similar areas, seen in figures 3.8, 3.9 and 3.11 as well as the proportions of time graphs in Figure 3.13. These two kiwi were incubating an egg for several days of the observation period which impacted their activity results as both kiwi had limited activity for this time. As these two kiwi were significantly less active than only three of the six other kiwi I chose to include their data. Additionally, the presence of food tubes may have affected the amount of time that was spent in some grid squares, as may have the position where live insects were released. However, the positions of food tubes were changed daily and there was no pattern in the behavioural data for kiwi spending more time in grid squares containing food. The presence of visitors passing their enclosures may have impacted their behaviour, though there was no obvious effect on where the kiwi spent their time based on Figure 3.13.

Ideally this experiment would have taken place in controlled conditions with a larger sample size, in enclosures of the same size with the same amounts of structural complexity and with identical proportions of the enclosure being on the edge. Kiwi would ideally all be housed indoors separately away from the public so there would be no effect of the weather and visitor interaction; as observations were made in early autumn and there was only one night of outdoor observations when it rained I did not perceive any bias for my experiment. The experiment of kiwi would ideally be all of the same age and gender and have been in captivity for the same length of time. In this experiment Pablo and Brackette may have still been acclimating to their new enclosure, though they had been housed in the enclosure for a month before my observations. More ideally still would be if the behaviour in relation to light could be closely observed of wild kiwi that were previously captive. This would provide an indication of whether the light regimes of nocturnal houses have conservation implications for kiwi if they are impacting potential reproductive success and survival. It must be noted that results from this experiment may not reflect the natural behaviour of brown kiwi or be applicable to other species of kiwi.

3.5: Conclusions

It appears that light intensity alone does not explain where kiwi choose to spend time, though kiwi spent more time in darker areas overall confirming my original hypothesis. Neither of the variables of light intensity, structural coverage and edge or centre location fully explained where the kiwi spent their time. However, they showed some preference for darker, more covered areas on the enclosure periphery. I would therefore recommend that kiwi nocturnal houses be illuminated by less than 10 lux of light, be long and narrow having at least 50% of area on the periphery of the enclosure (based on 1x1m grid squares), and have at least 50% coverage by low-lying foliage. Of the main variables that were examined, structure and edge appear to have the biggest impact on the behaviour of kiwi. It is possible that kiwi have a preference for spending more time in covered areas as a natural mechanism for avoiding ancient avian predators (Holdaway, 1989). Kiwi may benefit from spending more time on the edge of the enclosure as their sensing abilities may be heightened around the periphery (Simon et al, 1994). Individual preference seemed to also be an important determinant of where kiwi spend their time; this affected their relationship with the variables that I tested and whether they spent a larger amount of time in a smaller area or a smaller amount of time in a larger area. Further research would help to conclusively determine the significance of the variables examined, as the variables were interacting and there are several confounding factors that complicate the results.

Chapter 4: Effect of light intensity exposure on emergence times of juvenile brown kiwi

4.1: Introduction

Exposure of infant animals to unnatural light regimes has the potential to have lasting effects on their physiology and behaviour (Fosser et al, 2005; Ashby et al, 2009). This is unsurprising as light intensity, wavelength and duration have a close relationship with the physiology and behaviour of mammalian and avian species, and during juvenile development nervous systems are developing quickly and may be easily influenced by the environment (Boulos et al, 1996; Nayak et al, 2007). The effects of light regimes on young animals can be physiological or behavioural. For example, domestic chicks exposed to at least four hours of daylight illumination in a laboratory setting are significantly more likely to have normal ocular development and are less likely to have hyperopia and corneal flattening than those exposed to less than four hours of light; additionally it seems that there is a specific, early period of development before they have hatched when their circadian rhythm develops and can be manipulated during this time using light (Li et al, 2000; Hill et al, 2004). Domestic chicks housed in brooder boxes lit by one lux of light preen and rest more and forage less than those housed under brighter lighting, but have normal behavioural diurnal rhythms (Deep et al, 2012). It is therefore possible that the light regimes that brown kiwi chicks are exposed to when they are reared in brooder boxes may affect their behaviour and physiology temporarily or in the long term.

Many brown kiwi are involved in a captive rearing programme referred to as Operation Nest Egg (ONE) during which there is the potential for artificial light regime exposure to impact their behavioural development. Kiwi eggs are initially recovered from the wild and incubated until hatching; after three days juveniles are then moved to brooder boxes for one month. During this time they have access to an open area in addition to a covered, closed-off sleeping box. They are then transferred to an open pen with access to a sleeping box and vegetative cover where they stay until they reach one year of age, after which they are released into the wild (Colbourne et al, 2005). Alternatively they may be directly transferred to a predator-free sanctuary when they have reached one month of age. During their time in brooder boxes, kiwi are exposed to artificial light regimes that may affect their behaviour during the early stage of

development. It is possible that the illumination levels in the open area of the brooder boxes are significantly different and may be brighter than the illumination levels that kiwi chicks are exposed to naturally. It is also possible that the transitional changes in light levels throughout the day are significantly different between brooders. Such light regimes during the early stages of development of kiwi may have subtle impacts on their future behaviour when released back into the wild. For example, several species of nocturnal flying foxes (*Pteropus* spp.) and kangaroo rats (*Dipodomys* spp.) have been observed to emerge significantly later as a result of longer twilight periods (White and Geluso, 2007; Welbergen, 2008).

Despite the recognised effects of light on the development of diurnal species, little research has been completed on the long-term implications of the light regimes of juvenile nocturnal animals. Many kiwi are housed in captivity as part of Operation Nest Egg, however there are currently few guidelines as to the light intensity, duration or wavelength of the light that they are exposed to while in brooder boxes (Fraser and Johnson, 2011). I therefore aimed to examine how brooder box illumination intensity affects the emergence time of juvenile kiwi in outdoor pens. I predict that chicks housed in brighter brooder boxes for one month will emerge earlier than chicks housed in darker brooders. The rationale for this hypothesis is that in their brighter brooders kiwi may become more sensitised to being active at brighter light levels. Some nocturnal animals that live in burrows use light-sampling behaviour during dusk to determine their time of emergence (White and Gelusen, 2007); it is therefore possible that ONE kiwi regularly exposed to brighter illumination in their brooders may become more habituated to being active in brighter light as a result of light-sampling behaviour. These kiwi may become more willing to emerge before full darkness when released into their outdoor pens. This may have conservation implications if this behaviour is lasting, for example if they become more vulnerable to predation by being more visible when emerging before full darkness.

4.2: Methods

Nine juvenile brown kiwi that were part of the ONE kiwi recovery program at Kiwi Encounter in New Zealand were used for this experiment. At three days of age after hatching, the experiment kiwi was moved to a brooder box; the setup of these boxes is shown in Figure 4.1.

Figure 4.1: *Coverage of juvenile kiwi brooder boxes by 50% shade cloth. This shade cloth was used for three of the nine neonatal kiwi for a one month duration while they were in the boxes.*

During their time in the brooder room the brooder boxes housing three of the kiwi were covered with 50% shade cloth, i.e. cloth that reduces light intensity by 50%, while the brooders of the other six remained uncovered. Light intensity measurements were taken at three different positions within the brooders outside of the covered resting box using a light meter that measured accuracy to within 0.1 lux. The mean light intensity of each brooder was calculated from this. Illumination of the brooders during the day was provided by incandescent 100-watt ceiling lighting plus daylight entering the room through a window on one wall; due to the positioning of light sources the brooder boxes had variable illumination in addition to three of the boxes being covered with shade cloth. Lights were switched on in the brooder room at 8.00am and switched off again at 5.00pm, before and after which a small amount of light entered through the window. Kiwi were therefore exposed to a period of twilight each day that differed between brooders, with the brighter brooders having a slightly longer twilight period. The mean light intensities of their brooder boxes during the day were as follows:

***Table 4.1**: Light intensities during the day of the brooder boxes that nine kiwi were raised in with those boxes that were covered in shade cloth noted*

Name	Light intensity (lux)	
Tureiti	162.70	(covered)
Moriah	185.17	(covered)
Matua	185.17	(covered)
Jefferson	205.27	
Pimms	213.13	
Glamd	235.17	
Odbod	295.70	
Kotori	331.16	
Hianga	364.50	

The kiwi spent approximately 28 days in a brooder room or until their weight reached around 350 grams. They were then released at different times during a three month period between January and April to outdoor pens away from public viewing, and were housed and observed in five groups of between one and three in a range of pens. Jefferson and Hianga were housed together, as were Pimms and Kotori, and Matua, Moriah and Tureiti; Odbod and Glamd were housed individually. Kiwi were given an observation group number of between one and five based on who they were observed with. There were five different pens that housed kiwi and all enclosures had a similar amount of vegetative cover, but varied slightly in the proportion of edge to area. Additionally the sizes of the pens varied. When the kiwi shared a pen a leg band was placed on the hock of one of the kiwi's left legs, or in the case where there were three chicks a band was placed on one of the kiwi's right legs also, in order to distinguish them.

Observations occurred from early January until early April. These were aided by a night-vision monocular that was necessary to use for the duration of observations, and began at the New Zealand Metservice sunset time for that day with the official times of sunset and civil twilight recorded daily. Time of emergence from their roosting box was recorded for each kiwi as was the number of minutes that they were active, for the duration of the observations for that night. Observations occurred for approximately two hours per night or until park closing time, for a total of ten hours over five nights. There were an average of 120 minutes of observation per night. However, this varied from between 101 and 128 minutes but totalled 600 minutes. Observations commenced on the fourth night after the chicks were moved into the pens. This allowed a behavioural adjustment period. Kiwi were observed from outside of the pen over a low fence. All outdoor pens reached an illumination intensity that was below the level of detection (0.01 lux) by a light meter on all days of observation at which point kiwi needed to be observed with a night vision monocular. Weather conditions for each observation day were categorised as having three varying degrees of windiness and five varying degrees of

cloudiness and rain. This was done as weather has the potential to affect the behaviour of kiwi. The emergence times of kiwi that did not emerge during the daily observation period were recorded as being the time that I ended my observation period for that day; this enabled a representation of the fact that they had not emerged within the two hour time period that I was there and meant that their behavioural data were able to be included in the data set.

Emergence time (number of minutes after sunset) from the roost box was the dependant variable compared with the independent variables of mean brooder light intensity and observation group number. Time of activity was measured but was not a dependant variable tested as kiwi were active for most of the time after they emerged, so proportion of time had a 97% correlation with emergence time. The emergence times of kiwi were normally distributed in relation to their observation groups (Anderson-Darling; $p>0.05$), therefore an analysis of variance (ANOVA) test compared emergence times with mean brooder illumination. A post-hoc Bonferroni multiple comparison tested the extent of the differences between the emergence times of kiwi housed at different brooder illumination levels as well as a Pearson correlation measuring the relationship between brooder light intensity and mean emergence time. A Bonferroni multiple comparison was also completed on the emergence times of kiwi based on observation group number. Emergence time was compared with observation group using an ANOVA test, as well as weather category, to test whether variables other than brooder light intensity may explain the times of emergence. All significance tests were at the $\alpha = 0.05$ significance level.

4.3: Results

I wished to determine whether there was any behavioural effect on neonatal kiwi that were exposed to differing light intensities during their time spent in brooder boxes. I completed statistical tests on both individual and observation group data as well as testing the impact of weather conditions; this was done as the factors of observation groups and changing weather conditions may have impacted results. A power analysis found that I needed seven nights of observation for the nine kiwi in my experiment to detect the maximum mean difference in emergence times observed in my experiment at a 0.8 power level. This was calculated using a standard deviation of 24.92 and maximum difference in mean emergence times between kiwi of 55.6 minutes, both calculated using the statistical tests of my data described in the method section. As I completed five nights of observation for each kiwi as opposed to seven, my results may therefore need to be viewed with some caution, though they had reasonably good power to detect significance.

There was a significant relationship between the brooder light intensity and the emergence times of kiwi when data was combined (ANOVA; F(7,37)=2.70, *p*=0.023). However, the relationship between light intensity and emergence time was not linear when analysed as individuals; this can be seen in the boxplots of Figure 4.2. Three significant results were found in a post-hoc Bonferroni multiple comparison; Hianga, raised at 365 lux, emerged on average 54.4 minutes later than the kiwi raised at 163 lux (±15.57, *p*=0.035), 52.6 minutes later than the kiwi raised at 213 lux (±15.57, *p*=0.049) and 55.6 minutes later than the kiwi raised at 235 lux (±15.57, *p*=0.028). These results are reflected in Figure 4.2; according to this figure Kotori had a particularly wide range of emergence times and the overall range of emergence times of Hianga were later than five of the eight other kiwi reflecting the post-hoc test results.

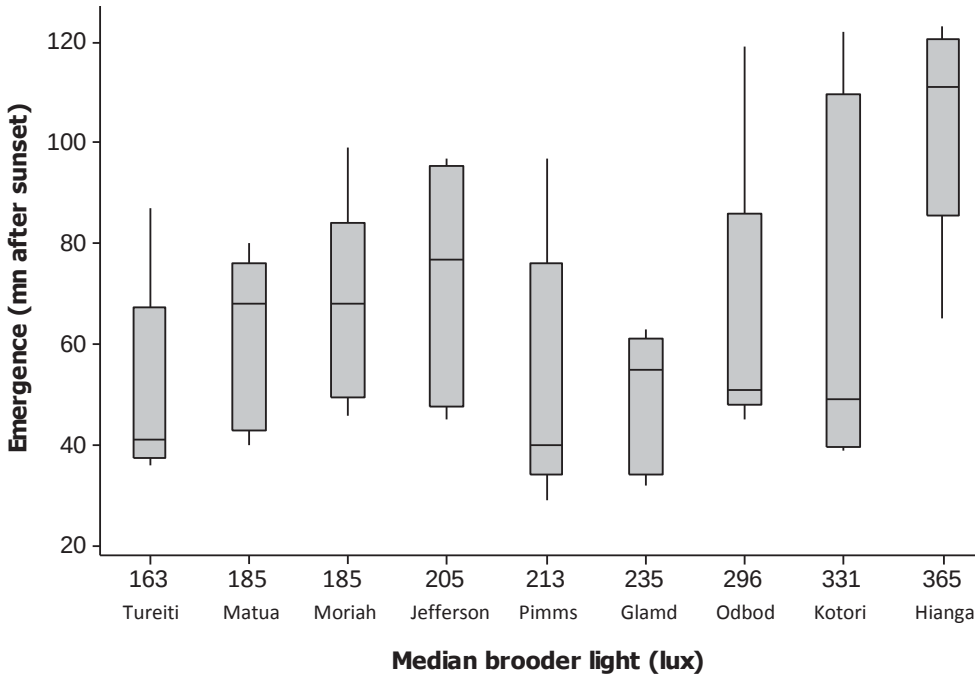


Figure 4.2: *Distribution of the emergence times after sunset from roosting boxes of nine kiwi juveniles raised under eight different light intensities. Individuals had significantly different emergence times, however median emergence times did not appear to have a strongly linear relationship with brooder light intensity.*

There was a significant positive correlation between the mean emergence times of kiwi and the mean brooder illumination that they were raised under, seen in Figure 4.3 (Pearson correlation; r(8)=0.67, *p*=0.03).

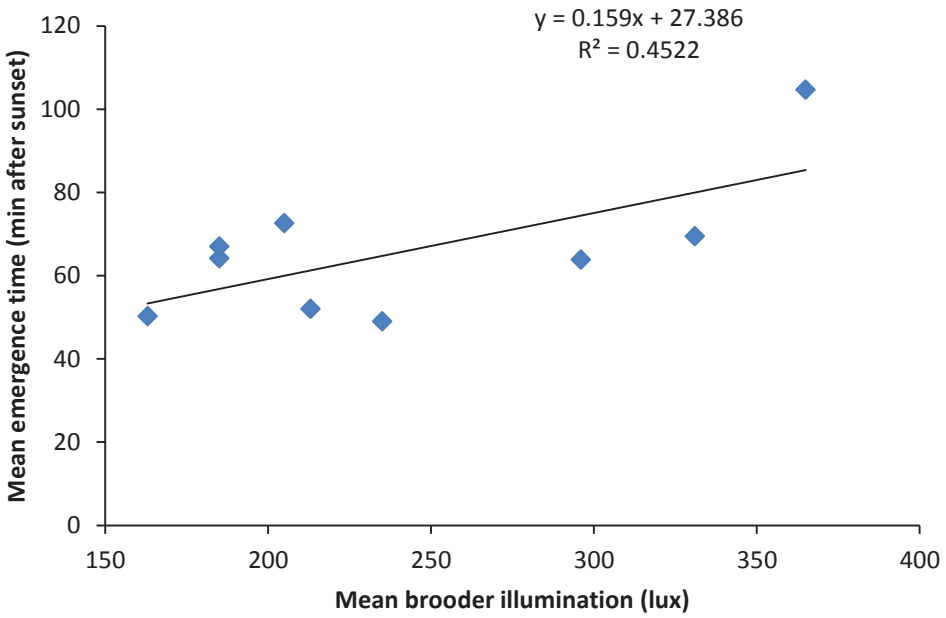


Figure 4.3: *The mean number of minutes after sunset before nine juvenile kiwi that were raised at different light intensities emerged from roosting boxes. A moderate, significant correlation was found between emergence time and light intensity during rearing (Pearson correlation; r(8)=0.67, p=0.03). All data points represent the mean emergence time after sunset over five nights of observations for each kiwi.*

Because kiwi were observed in groups, I investigated the potential impact of social grouping on the emergence time of kiwi. Observation groups had significantly different emergence times (ANOVA; $F(4, 40)=2.84$, $p=0.04$). It was not possible to determine how this was associated with brooder light intensity though. While significantly different emergence times were found between groups, this did not appear to be related to the number of kiwi being observed at once (Figure 4.4). Variation in emergence times within groups was less than variation in emergence times between groups; this suggests that kiwi housed in the same pens influenced the emergence time of each other. It is also possible that small differences in the outdoor pens and weather conditions may have increased the variance in emergence times between groups. However, post-hoc testing based on Bonferroni multiple comparison found that no single group was significantly different from another. Some variation in the median, upper and lower quartile and maximum and minimum emergence times was found between groups, as well as minor differences between groups in the range of emergence times observed.

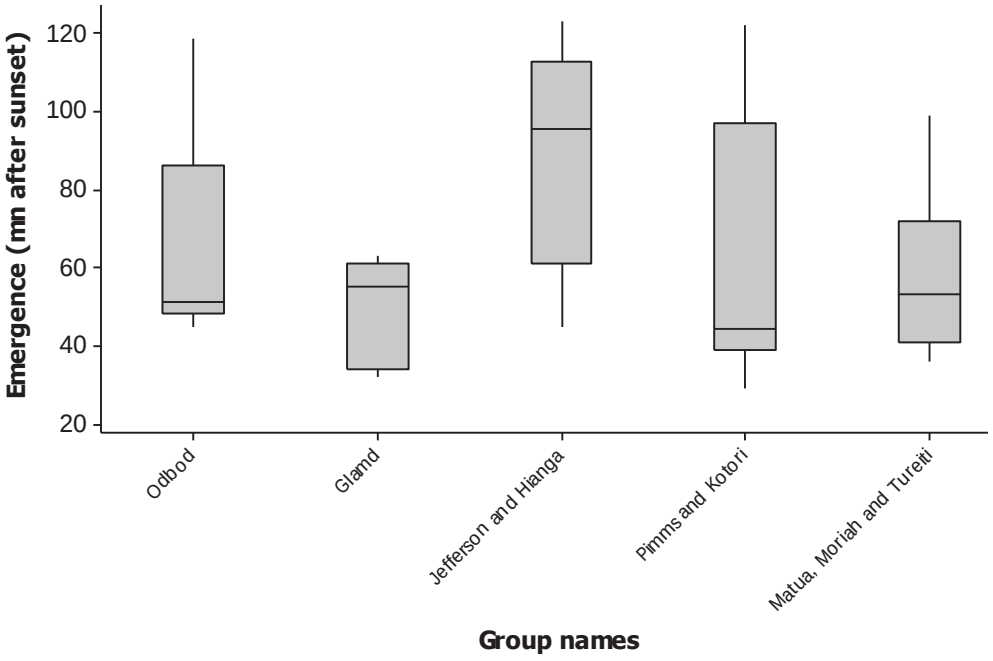
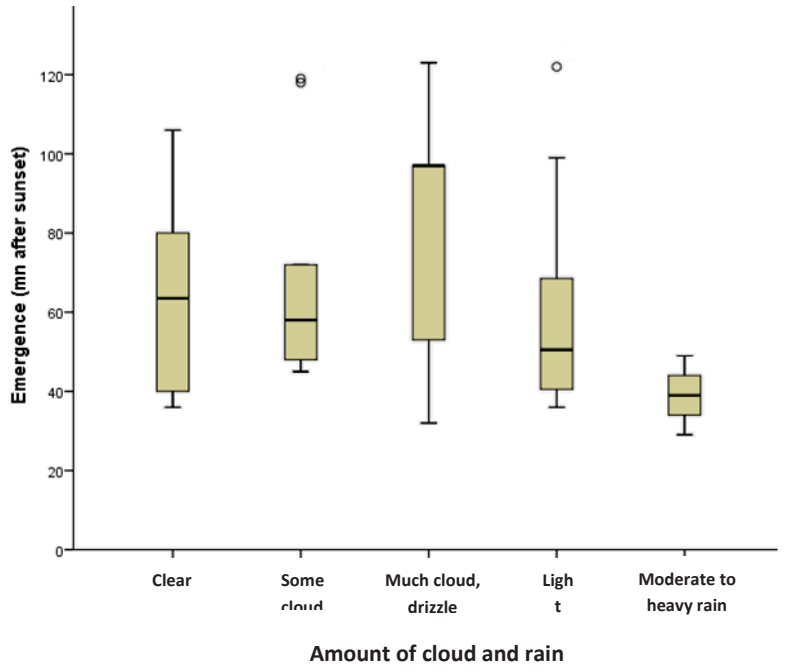


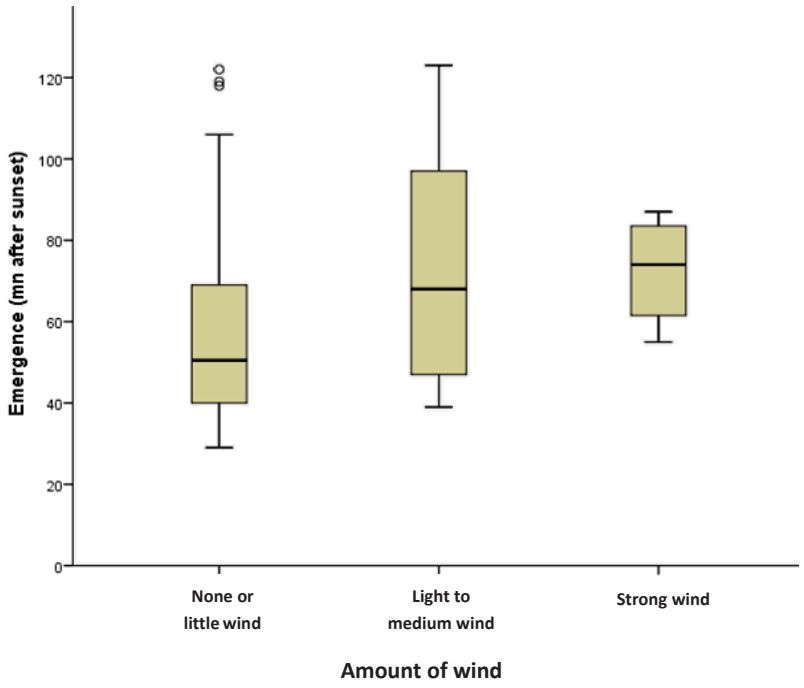
Figure 4.4: *Emergence times after sunset of nine young kiwi in different social groups from roosting boxes. Data of kiwi that were housed together is grouped together; groups of kiwi had significantly different emergence times but this did not appear to relate to the number of kiwi being observed at once.*

Finally, kiwi did not emerge at significantly different times as a result of rainfall (ANOVA; $F(4, 26)=1.29$, $p=0.30$) or wind (ANOVA; $F(2, 26)=1.34$, $p=0.28$) during observations. Weather conditions did seem to affect behaviour to a minor degree though, with kiwi emerging early on nights of heavy rain (Figure 4.5a and b). Light intensity is not likely to have factored into these results as on all nights nocturnal illumination was below 1 lux.

a)



b)



Figures 4.5a and b: *Distribution of emergence times of nine kiwi from roosting boxes after sunset in relation to amount of cloud/rain and wind. No significant relationship was found between weather conditions and emergence time.*

4.4: Discussion

Mixed results were found for emergence time of juvenile kiwi after sunset from outdoor roosting boxes. As predicted there appears to be a significant relationship between emergence time and the brooder illumination intensity to which these kiwi were previously exposed, however the relationship was the opposite to what was expected. Kiwi housed in the darkest brooder boxes emerged significantly earlier than kiwi housed in the brightest brooder boxes, though kiwi exposed to moderate illumination had mixed emergence times. These results suggest that the outdoor emergence times of brown kiwi may be impacted by the light intensities to which they were previously exposed. This may not occur after the juvenile kiwi have had an adjustment period to their outdoor setting, and further investigation is necessary to confirm this. Observation groups had significantly different emergence times which did not appear to relate to number of individuals in each group. It is possible that brooder light intensity may explain these differences; however, it is also possible that differences between groups may be explained by minor differences in twilight duration as groups were released over a three month period between January and April. This is unlikely though as the time period between sunset and end of civil twilight did not vary significantly during this time (see Appendix F).

Differences in illumination intensity of the brooders may explain the emergence time results. Operation Nest Egg kiwi are known to be exposed to diurnal light briefly every day during their time in the brooder room while being weighed and while feeding (Claire Travers, Personal communication, July 2012). ONE kiwi also regularly emerge during the day of their own accord particularly during their first 10 days of life, which may be used to sample the light levels of their surroundings (Claire Travers, Personal communication, July 2012); many nocturnal burrow-dwelling animals exhibit this “light-sampling behaviour” to assist the entrainment of the circadian and circannual rhythm, providing environmental information to their neural “pacemakers” (DeCoursey, 1986; White and Geluso, 2007; Sothern et al, 2009). Kiwi housed in the darkest brooder boxes were exposed to illumination levels during the day that were comparable with natural twilight illumination (normally ranging from 0 - 300 lux; Emborg, 1998). They may have therefore developed a willingness to spend more time out of the sleeping compartment of their brooder box before darkness and had more exposure to light levels above 0 lux during this time. It is possible that they became more willing to emerge before their brooders were completely dark which may have continued when they were released outdoors.

It is unlikely that the length of time between civil twilight and sunset affected the emergence times of the kiwi as the longest twilight length was 31 minutes and the shortest was 26 minutes (see Appendix F). However, the length of the twilight period experienced by kiwi in the brooder room may also have contributed towards the results. Juvenile kiwi were exposed to a small period of natural twilight at dawn and dusk through a window in their brooder room, with the kiwi housed in darker brooders experiencing a shorter twilight. Research suggests that twilight length affects emergence time; Welbergen (2008) found that the black flying-fox *Pteropus alecto* which experiences longer twilights than the closely related grey headed flying-fox *Pteropus poliocephalus* emerges later and has a larger variability in emergence times. Similarly, the kiwi housed in the three brightest brooders in this experiment also had later and larger ranges of emergence times than the three kiwi housed in the darkest brooders (Figure 4.2). This pattern of later emergence times after longer twilights has also been observed in three species of nocturnal *Dipodomys* kangaroo rats (White and Geluso, 2007). A possible explanation for this behaviour is that earlier emergence in spring and autumn when shorter twilights occur may allow for the early establishment of mates and territories during the former and allow more time for foraging before winter during the later (White and Geluso, 2007). In summer there is a higher predation risk and in winter there are reduced foraging opportunities for animals, therefore a later emergence time may be beneficial (White and Geluso, 2007).

These results may have implications for the Operation Nest Egg programme if lighting regimes in brooder rooms have a lasting effect on the behaviour of chicks that are released into the wild. If kiwi are fearful of emerging before it is fully dark, they may miss opportunities for feeding and finding mates and may have less activity time during the night. To resolve this, brooder room lighting may need to be dimmed during the day. However, the daytime illumination of the brooder boxes are dimmer than the daytime illumination levels reaching forest floors that wild kiwi chicks are exposed to; this can be between 150-1200 lux during the day dependent on the degree of canopy cover and amount of cloud (Emborg, 1998). Therefore it is not likely that the kiwi housed in the brooder boxes are being exposed to light levels that are significantly different from those that kiwi chicks in the wild are exposed to during the day. It would be necessary to complete long-term observations of kiwi to determine whether there is a lasting significant effect on the survival or reproductive success of released ONE kiwi. It is unlikely that this is the case; subadult ONE kiwi have the same survival probability until the first age of breeding as subadults raised in the wild that have survived infancy (Colbourne et al, 2005). It should be noted that all observed emergence times fell within the typical emergence

times of kiwi in the wild, as they have been observed to emerge between 26 minutes and 5.5 hours after sunset (McLennan, 1988).

There are several variables that may have impacted the validity of my experimental results. As previously discussed both the covered and uncovered brooder groups were exposed to darkness below the light level of equipment detection of 0.1 lux during the night, which meant that for some of the time that kiwi were active they had the same illumination levels. However, the light intensities of the covered and uncovered brooders during the daytime and crepuscular period were significantly different. Days when there was heavy rain had a very small spread of data with kiwi mostly emerging early, and there was also a small spread of emergence times on windy days with kiwi emerging around the middle range of emergence times. Environmental variables such as weather conditions and lunar illumination in the outdoor pen may have therefore impacted emergence time and/or activity levels to a minor degree, though weather did not significantly affect behavioural results and no kiwi emerged before outdoor illumination levels were below 0.1 lux. The size, shape and structural coverage of the outdoor pens had some variation which may have also affected how kiwi used their pen and subsequently the results of my observations. Repetition with a larger sample size in each of the two groups of kiwi would assist the robustness of the data, as would having darker nocturnal illumination of the brooders. Also the kiwi may have been able to sense my presence during observations as I was observing them from over a low fence, though I endeavoured to minimise movement. Finally, several of the kiwi were housed together and seemed to have influenced the emergence times of each other based on results.

4.5: Conclusions

The experimental results contradicted the prediction that juvenile kiwi initially exposed to darker light intensities would emerge from their outdoor pens significantly later. My results may have perhaps been caused by kiwi housed in darker brooders being more willing to emerge into their brooders at full or almost full lighting and thus having increased exposure to twilight-level lighting. It may also be that they had a shorter twilight than the kiwi housed in brighter brooders while in the brooder boxes. However, only the few kiwi housed in the darkest and the lightest brooders seemed to have significantly different emergence times; as with the previous chapters there was much individual variation seen in the results from the other kiwi. It is possible that environmental variables such as illumination intensity, weather conditions and differences in enclosure size and vegetative cover overshadowed the effect of brooder illumination to a degree. The results from this research have implications for the ONE program and for kiwi conservation if there is a significant, lasting effect of brooder light intensity on the time of emergence of kiwi once they are released into the wild. Future research could have a similar setup as this experiment but with a larger sample size in each group and a lighting schedule with significantly different brooder illumination levels during their night. It may also be valuable to observe the kiwi for a longer period of time both in captivity and once released into the wild to see whether there is a significant, lasting effect of brooder light regimes that may be impacting the reproduction and survival abilities of kiwi.

Chapter 5: Discussion of findings and implications for kiwi husbandry

I investigated how light regimes can impact the behaviour of captive brown kiwi. This topic was chosen as the light regimes of captive kiwi have the potential to affect their behaviour towards their nocturnal environment. Little is known about the general relationship between kiwi and light; kiwi probably have very good perception of light intensity but have poorly developed eyes compared with other nocturnal birds (Martin et al, 2007). In this way they are more similar to other nocturnal mammals that have adapted their senses to a dim forest floor environment (Martin et al, 2007). Light is an important determinant of the circannual and circadian cycles of animals, and most animals have a significant behavioural or physiological response to light intensity, duration and/or wavelength (Nash, 2006; Wikelski et al, 2008). Enclosure lighting has been shown to impact the behaviour of nocturnal and diurnal captive animals (Trent et al, 1977; Frederick and Fernandes, 1994). However, there are currently few guidelines for the light regimes of nocturnal houses displaying kiwi or the light regimes that juvenile Operation Nest Egg (ONE) kiwi are exposed to (Fraser and Johnson, 2011). Many kiwi are kept in captivity as part of a breeding program, on display for advocacy purposes or as part of ONE. Those on display are kept under reversed photoperiod in what can be unnatural light durations and wavelengths. My research provided an indication of how captive brown kiwi respond to their light regimes and whether adjustments to nocturnal house light regimes are necessary for the captive husbandry benefit and conservation of kiwi.

I observed mature brown kiwi on display in nocturnal houses to determine whether they had a preference for spending more time in areas lit by different colours or illumination levels. These parameters were chosen as I wanted an indication of how well kiwi can perceive light intensity and wavelength and to what extent this affects their behaviour. The activity patterns of kiwi seemed to vary from day to day, and varied between individuals with some kiwi spending much time in a few enclosure areas and others spending a small amount of time in many areas. There were largely differing responses to light also, suggesting that individual preferences may be a significant factor. The environmental factors of light, structural coverage and proximity to the enclosure edge appear to be interacting, and none of these variables alone explained where kiwi spent their time. The kiwi that was tested for response to coloured

lighting did not spend significantly more time in areas of the enclosure illuminated by a particular wavelength. However, more time was spent in areas that were darker and on the periphery of the enclosure. Eight kiwi were observed for how much time they spent in different areas of their nocturnal house depending on illumination levels. They spent significantly more time in darker enclosure areas when data was combined, though individual kiwi varied as to whether they spent more or equal amounts of time in lighter or darker areas. Kiwi also spent significantly more time in areas that were structurally complex and on the periphery of their enclosure.

The structural complexity of the nocturnal houses and illumination intensity seemed to be the two most significant variables that affect where captive kiwi spend their time. Kiwi spent the most time in darker areas of their enclosure that had at least moderate coverage. While both absolute and relative light levels are likely to be important, distribution of where kiwi spent time seemed to be explained more by absolute light levels than by relative light levels. Kiwi housed in enclosures with a wider range of light intensities did not seem to have different time proportion distributions from those housed in enclosures with a smaller distribution of relative light levels. Of those kiwi that had the option, more time was spent in enclosure areas dimmer than 10 lux and when data was combined kiwi spent at least 30% of time in grid squares that were 8 lux or dimmer, suggesting that absolute light levels were important. At dim light levels less than 10 lux visitors could still quite easily view the kiwi. At most of the nocturnal houses where I observed kiwi about half of the enclosure area contained moderate or full structural coverage; this mainly consisted of trees, stumps and low-lying vegetation such as flaxes, ferns and tussocks. These apparent behavioural preferences of kiwi for darker, more covered areas are likely to be a predator-avoidance instinct. In the past, kiwi would have been prey for birds with good vision (Holdaway, 1989). It is therefore unsurprising that they may have developed predator-avoidance behaviour, a theory that is supported by reports that kiwi naturally have “secretive” behaviour and are difficult to observe in the wild (Colbourne and Powlesland, 1988).

While nocturnal house lighting and structure may be important, other factors also contribute to where kiwi spend their time. Kiwi seemed to prefer spending much time around their enclosure edge which may have allowed enhanced perception of their surroundings as a result of thigmotaxis (Simon et al, 1994). Kiwi were apparently affected by the presence of other kiwi and visitors to various degrees based on their distribution. This again suggests personality differences and variable amounts of territoriality. Some kiwi were housed together and others were housed adjacent to each other over a low fence meaning that they could probably smell

each other; several of the adjacently housed kiwi, but particularly Pablo and Brackette, seemed to spend much time in opposite areas of their enclosure suggesting avoidance behaviour. Two kiwi that were housed together had similar distributions of where they spent time. Some kiwi spent more time away from where visitors walked, though this was not a significantly effect. It was expected that several factors in combination would determine where kiwi spend more time. This is because many variables have the potential to affect the behaviour of captive animals and a single variable would need to have a very strong impact to overshadow that of all other variables (Petren and Case, 1996; Evans et al, 2012).

My results suggest that brown kiwi may have reasonable perception of the light intensity of their environment as they showed a preference for darker light. The visual abilities of kiwi are likely to be limited to perception of light intensity though; their retina contains a thick layer of closely-packed rod photoreceptors that are probably very good receptors of photons, but do not allow good acuity or colour perception (Martin et al, 2007). The olfactory and vibratory senses used by kiwi to locate prey are highly developed and are likely to dominate their vision and hearing when assessing their environment (Cunningham, 2007). The increased amount of time spent by kiwi at the edges of their enclosure may have been an example of them using their developed olfactory and vibratory senses to their advantage. Some animals show thigmotaxis or a preference for spending time close to tactile stimuli to enhance the amount of information gathered from their environment (Simon et al, 1994). Additionally some kiwi demonstrated avoidance behaviour of other kiwi that they could probably smell from adjacent enclosures, suggesting that their olfaction ability may be powerful.

I expect that my nocturnal house behavioural observations would have led to different results had I been observing other nocturnal birds that are more reliant on vision. Kiwi probably have less of a reliance on vision than other nocturnal birds, for example owls and poorwills (Bowmaker and Martin, 1978; Brigham and Barclay, 1992). Birds that have highly developed vision are often more active during brighter moonlight to maximise time spent foraging during conditions where they can easily see (Nash, 2006). It is therefore difficult to generalise my results to other nocturnal birds. My results may be more applicable to other animals that have opted for more developed hearing, olfactory or tactile senses instead of having highly developed nocturnal vision that has a high energy cost (Martin et al, 2007). Examples of such animals are nocturnal primates and rodents, for example the potto *Perodicticus* and the kangaroo rat genus *Dipodomys*. However, as was found with brown kiwi I expect that most nocturnal animals vary in their reaction to environmental light intensity, and that multiple factors affect where they spend their time. It is important to note that only brown kiwi were

observed so results are not able to be generalised to other species of kiwi, though it is likely that other kiwi would respond to light similarly as they probably have very similar visual perception.

There are several aspects of my experimental design for the nocturnal house kiwi that limit the conclusions that may be drawn from my results. The biggest limitation was sample size; this particularly affected my first experiment involving coloured light manipulation where I had results for only one kiwi. Data was not independent as the location of kiwi affected the probability of their presence in surrounding grid squares, and some grid squares were smaller in size than others due to the shape of nocturnal houses, also impacting the probability of the kiwi being present in them. Kiwi were observed in enclosures that were different in size, amount of structural coverage and area of the enclosure that was on the periphery. In addition, some kiwi were housed and observed together while others were in enclosures close to each other and to visitors. These factors may have all contributed to where the kiwi chose to spend their time, and results would have been more comparable had the kiwi been housed in identical enclosures. Additionally, two of the kiwi that were housed together were incubating an egg for several of the days that I was observing them, though I chose to include their results as their activity levels were comparable with three of the other six experiment kiwi and with each other. The gender, age and amount of time that the kiwi had been in captivity were also variable. My results must therefore be viewed with a degree of caution.

I have several suggestions that may increase the amount of enclosure area that display kiwi use and benefit their captive husbandry. Kiwi may benefit from enclosures that are no brighter than 10 lux as kiwi appeared to prefer spending time in areas darker than this when given the option and are still quite visible at this light level to visitors of the nocturnal house. While in this regard absolute light levels may be important, further investigation under controlled conditions is necessary to confirm this, as relative light levels may be of equal importance. This could be tested by comparing the activity levels of kiwi exposed to identical ranges of light (i.e. same relative light levels) but different absolute light levels. Alternatively the enclosure use of kiwi could be examined if they were housed in enclosures that all had areas illuminated by 0 lux of light but with some kiwi having areas reaching a much higher light intensity (i.e. different relative light intensities). I also suggest that at least 50% of the area of nocturnal houses should be covered by low-lying vegetation such as flax, ferns and tussock (perhaps a suitable compromise between adequate visibility of kiwi by the public and an adequate amount of covered area for kiwi activity). Kiwi enclosures may benefit from having a high proportion of edge area or by being longer in shape; again this may assist visibility of the kiwi and the kiwi

preferred to spend more time around the edge. Dividing up enclosures to create more edge space instead of having large enclosures with kiwi housed together may be a suitable option, especially if territoriality is occurring. Having some low-lying vegetation around the enclosure edge may also enhance visibility of kiwi. The colour of nocturnal house lighting does not seem to need special consideration as the colour of lighting did not affect the behaviour of the kiwi that I observed. However, repetitions of my experiment with a larger sample size are necessary to confirm this.

My experiment results highlight the fact that the light regimes of nocturnal animals in general need consideration as little is known about the requirements of nocturnal house lighting and it can significantly impact the behaviour and well-being of animals. Most animals have some sensitivity to ambient light and if housed in enclosures that are inappropriately light or dark would be expected to negatively respond to this. Lighting regimes that are poorly suited can impact the activity levels of animals and cause stress, or may lead to the use of a limited area of an enclosure (Trent et al, 1977; Frederick and Fernandes, 1994; Petren and Case, 1996). The results from my experiment may have applications for other animals displayed in nocturnal houses; they are probably more applicable to animals that have reduced dependence on vision as with kiwi, and that display some predator-avoidance behaviour. Other animals that are displayed in nocturnal houses include owls, possums, bats, mice and rats, slow lorises, lizards, frogs and a number of marsupials such as bandicoots and bilibies. Of these animals my results are probably the most applicable to the slow loris, mice and rats, bandicoots and bilibies that are vulnerable to predators and do not have highly developed vision. The environmental conditions, including light regimes, that are the most suitable to captive animals may at times be at odds with the best viewing opportunities of these animals; solutions for helping visitors to view the animals may therefore have to be considered for each individual case. The distinct personalities of animals may also mean that enclosure needs vary to some extent between animals, as they seemed to with kiwi.

I believe that development of the experimental methods for my nocturnal house observations may yield very useful results that would further improve knowledge of the relationship that kiwi have with light, and knowledge of nocturnal house lighting in general. Investigation of whether kiwi are able to see red lighting specifically may be necessary as it is assumed but not known that this is the case, and my coloured light experiment did not specifically test this. Some facilities housing kiwi have based their light regimes on the likelihood that kiwi cannot see red lighting (Representatives from 10 New Zealand wildlife institutes, personal communication, June 2009). A study on the wavelength perception of kiwi may provide

valuable information, as would a behavioural study on the proportion of time that kiwi choose to spend in red lighting as opposed to the white or yellow lighting commonly used in nocturnal houses. I did not manipulate the lighting conditions of the kiwi that I observed for my second general observation experiment in Chapter 3; repetition of these observations with the duration and intensity of enclosure lights manipulated may add robustness to my data. For example, investigating the behavioural effect on kiwi of having different day lengths or of having complete darkness may help to determine how important photoperiod is to their endogenous circadian rhythm. It would also be useful to compare the activity patterns of kiwi exposed to different intensities of light to see whether different light levels are linked with different behaviours or activity levels.

I additionally researched the impact of brooder illumination levels on the emergence times of juvenile brown kiwi. Of nine kiwi juveniles that were exposed to varying light intensities during time in a brooder room, the kiwi housed in the brightest brooders emerged significantly later than the kiwi housed in the darkest brooders. Again individual variation was seen as there was a non-linear relationship and kiwi housed at moderate levels of illumination had variable emergence times. ONE kiwi are briefly exposed every day to daylight while in the brooder room during weighing, by having a food source in the open area of their brooder and by their own accord (Claire Travers, Personal communication, July 2012); this potentially "light-sampling" behaviour is commonly used by nocturnal animals (DeCoursey, 1986; White and Geluso, 2007; Sothern et al, 2009). It is possible that the kiwi living in darker brooders emerged more often during the day as their brooders were a similar light intensity to that of natural twilight (Emborg, 1998). The kiwi may have become habituated to twilight illumination levels and been more willing to emerge before complete darkness. Alternatively kiwi in darker brooders were likely exposed to a shorter twilight period, creating a behavioural pattern of emerging earlier. Such a pattern is seen in other nocturnal animals, for example the black flying-fox *Pteropus alecto* and at least three species of nocturnal *Dipodomys* kangaroo rat (White and Geluso, 2007; Welbergen, 2008).

Based on the results from juvenile kiwi I suggest that the light intensity of kiwi brooder housing may need to be dimmed during the day though there were several factors that may have impacted results, such as the time of year that kiwi were released. I also recommend long-term observations of ONE kiwi released back into the wild as these observations are necessary to confirm a significant long term behavioural effect. The open compartments of ONE brooders are no brighter than what most kiwi chicks would be exposed to in the wild, and adolescent kiwi raised in captivity have a similar survival probability as those that survived infancy in the

wild; it is therefore unlikely that any effect of brooder light is permanent (Emborg, 1998; Colbourne et al, 2005). These experiment results may be applicable to other animals, both nocturnal and diurnal, involved in captive recovery programs. Animals that are dependent on vision would probably have a more significant reaction to brooder light levels. As kiwi have poor vision in general their response to ambient brooder light may be reduced compared with other animals.

An ideal setup for the juvenile kiwi experiment would be to have at least 10 ONE chicks raised in brooder rooms with significantly different nocturnal illumination levels. This may increase the power of the results as the kiwi would be exposed to different light levels for a longer period of time and there would be a larger sample size than with my experiment. Ideally observations would start at the time that the kiwi are housed in brooders, occurring during the day and at least the first two hours of their night to determine how much light they are exposed to during this period. Observations once the kiwi are housed in outdoor pens would ideally occur at the same time for all kiwi with kiwi being housed individually in enclosures of identical size, shape, structure and light coverage. This would eliminate the potential impact of enclosure setup, changing environmental conditions and of behavioural interaction between kiwi housed together. Finally observations during this time in the outdoor enclosures would ideally occur for longer than two hours past sunset time for a period of at least a month to determine the short and long-term duration of any behaviour caused by brooder light regimes.

My results may have implications for the conservation of kiwi if the preferences for darker enclosure areas suggested by my results are significant enough to have a long term effect on their behaviour and/or physiology. It is possible that Operation Nest Egg kiwi may have nightly emergence times or other behaviours that are altered by their previous light regimes which may impact their future reproductive success; however, further support to my results is necessary before speculation can be made, and as previously stated their reproductive success once released into the wild seems to be no different at maturity from wild kiwi that have survived infancy. It is also possible that kiwi who are released into the wild after being on display at a captive facility may have more of a reluctance towards foraging in brightly lit areas or have later emergence times if previously exposed to bright nocturnal lighting. Their previous light regimes may also have impacted their nocturnal melatonin secretion levels, potentially impacting their circadian rhythm and gonadal development. Finally, the reproductive success of captive kiwi breeding pairs and any offspring may be affected if the lights of their enclosures are excessively bright; for example, they may exhibit reduced activity levels, they may restrict

the use of their enclosure to darker areas or their melatonin levels may be reduced. Again much behavioural and physiological research is necessary to confirm this.

I have answered my original question of whether captive kiwi have a significant reaction to different light regimes. Mature display kiwi spent more time in darker areas of their enclosure as predicted, and spent more time in structurally complex areas on the periphery of their enclosure. However, no effect of lighting colour was found. Young kiwi raised in darker brooders emerged earlier than those raised in brighter brooders. Light intensity and structural coverage seem to be the most important factors determining where kiwi spend their time. Nevertheless there was much individual variation and numerous environmental factors may have affected results. Based on the light intensity results, the light-perception abilities of kiwi may be reasonably developed. Kiwi vision is probably less important though compared with the highly developed tactile and olfactory senses that distinguish kiwi from most nocturnal birds. These results may be applicable to captive nocturnal mammals that naturally show much predator avoidance behaviour and do not rely on vision for feeding, and may have implications for the captive husbandry and conservation of brown kiwi.

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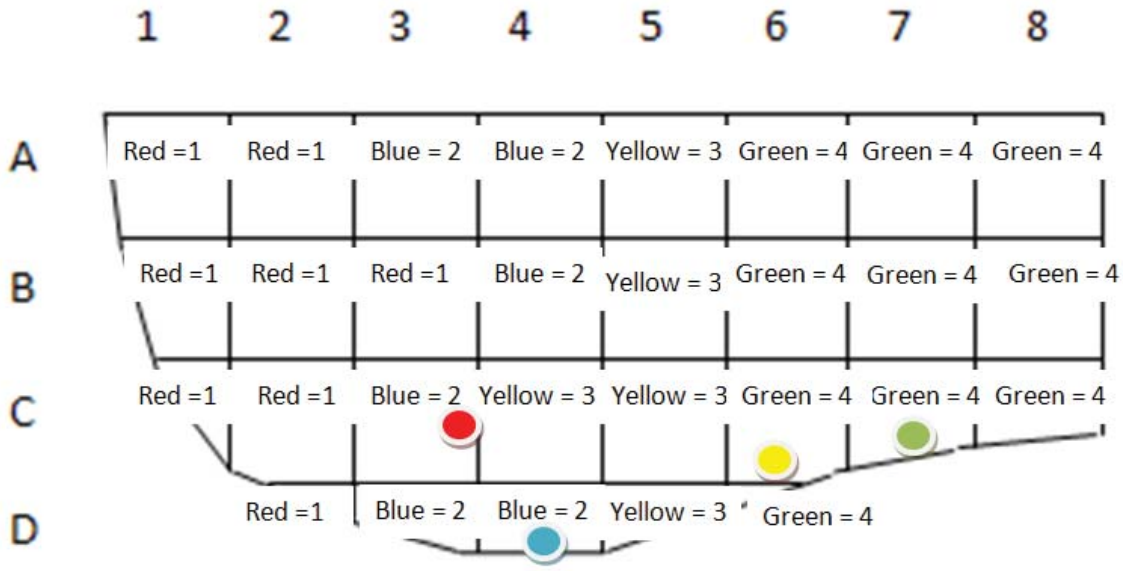
References

Appendices

Appendix A: Lighting setup for Chapter 2 experiment with position of coloured lights shown



Appendix B: Example of observation data for Chapters 2 and 3

Time	Action	Action	Action	A1	A2	A3	A4	A5	A6	A7	A8	B1	B2	B3	B4	B5	B6	B7	B8	C1	C2	C3	C4	C5	C6	C7	C8
10.37	PR	T		0.2								0.4								0.4							
10.38	PR	T		0.33								0.33								0.33							
10.38	SGA	M-Q																									
10.39	PR	T		0.33								0.33								0.33							
10.40	PR	T										0.33								0.66							
10.41	PR	T																		0.33	0.33						
10.42	PR	T		0.2								0.2								0.2	0.2						
10.43	PR	T		1																							
10.44	PR	T		0.5								0.5															
10.44	PR	T										0.5								0.5							
10.45	PR			0.33								0.33								0.33							
10.46	SGL																										
10.46	PR	T		0.4								0.4								0.2							
10.47	PR	T		0.4								0.4								0.2							
10.48	SG A & L	Q																									
10.49	PR	T		0.4								0.4								0.2							
10.50	PR	T		0.4								0.4								0.2							
10.51	PR	T		0.2								0.2								0.4	0.2						
10.52	PR	T					0.17							0.17	0.17					0.17	0.17	0.17					
10.53	PR	T					0.25	0.5	0.25																		
10.54	PR	T						0.5	0.5																		
10.55	PR	T						0.5	0.5																		
10.56	PR	T						0.2								0.2							0.2	0.2			
10.57	PR	T																		0.2	0.2	0.2					
10.58	PR	T																		1							
10.59	T	A																		1							
11.00	PR																			1							
11.01	PR																			0.5	0.5						
11.02	PR																			0.5	0.5						
11.03	PR	T																			1						
11.04	PR	T																			1						
11.04	SGL																										
11.05	PR																				1						
11.06	SGA	M																									
11.06	SGL																										
11.07	PR	F																		0.5	0.5						
11.08	F																			1							
11.09	F																			0.5	0.5						
11.10	F																				1						
11.11	F																				0.5						

Appendix C: Multivariate ANOVA of independent variables effect on proportion of time spent in grid squares

Source	Sum-of-squares	DF	Mean-square	F-ratio	P
Day	0.003	11	0.000	0.027	1.00
Edge	0.051	1	0.051	5.701	0.018
Structure	0.027	2	0.013	1.498	0.225
Light intensity	0.018	1	0.018	1.968	0.162
Colour	0.036	3	0.012	1.358	0.256
Error	2.940	329	0.009		

Appendix D: Tukey post-hoc results of Chapter 2

a) One-way ANOVA: Time proportion versus Quarter number

```
Source          DF      SS      MS     F      P
Quarter number   3  0.6142  0.2047  6.29  0.001
Error           44  1.4324  0.0326
Total           47  2.0467

S = 0.1804   R-Sq = 30.01%   R-Sq(adj) = 25.24%


                          Individual 95% CIs For Mean Based on
                          Pooled StDev
Level   N    Mean   StDev    +---------+---------+---------+---------
1      12  0.4242  0.2117                        (------*------)
2      12  0.2435  0.2197             (------*------)
3      12  0.2270  0.1813            (------*------)
4      12  0.1076  0.0653    (------*------)
                             +---------+---------+---------+---------
                          0.00      0.15      0.30      0.45
```

b) One-way ANOVA: Structure versus Quarter number

```
Source          DF      SS     MS      F      P
Quarter number   3  10.783  3.594  14.10  0.000
Error          344  87.700  0.255
Total          347  98.483

S = 0.5049   R-Sq = 10.95%   R-Sq(adj) = 10.17%


                          Individual 95% CIs For Mean Based on
                          Pooled StDev
Level    N    Mean   StDev    +---------+---------+---------+---------
1       96  1.3750  0.4867                 (----*----)
2       72  1.3333  0.4747               (-----*-----)
3       60  1.6000  0.8068                           (-----*-----)
4      120  1.1000  0.3013    (----*----)
                             +---------+---------+---------+---------
                          1.00      1.20      1.40      1.60
```

c) One-way ANOVA: Edge versus Quarter number

```
Source          DF      SS     MS      F      P
Quarter number   3   6.883  2.294  11.67  0.000
Error          344  67.600  0.197
Total          347  74.483

S = 0.4433   R-Sq = 9.24%   R-Sq(adj) = 8.45%


                          Individual 95% CIs For Mean Based on
                          Pooled StDev
Level    N    Mean   StDev   -+---------+---------+---------+--------
1       96  0.7500  0.4353                          (-----*-----)
2       72  0.6667  0.4747                      (-----*------)
3       60  0.4000  0.4940   (-------*------)
4      120  0.8000  0.4017                                  (----*-----)
                            -+---------+---------+---------+--------
                          0.30      0.45      0.60      0.75
```

Appendix E: Environmental characteristics of nocturnal house grids for Chapter 3

Kiwi	Indoor/ Outdoor	Total number of squares	Edge squares	Centre squares	Open squares	Mixed coverage squares	Covered squares	Light intensity range
Pablo	Indoor	50	29	21	40	9	2	0 – 41.6
Brackette	Indoor	41	21	20	25	16		0.1 – 64.8
Te Kaha	Indoor	29	20	9	21	7	1	1.5 - 86.2
Jules and Koru	Indoor	81	44	37	73	6	2	0 – 5.4
Koanga	Outdoor	70	32	44	46	23	1	0 – 6.4
Forest	Outdoor	51	24	27	36	14	1	0 – 9.3
Ruha	Outdoor	44	29	16	29	13	2	0 – 4.6

Appendix F: Civil twilight and sunset times during juvenile kiwi observations

Date	Sunset time	Civil twilight end time	Twilight length
9/01/2011	20.41	21.12	31
10/01/2011	20.41	21.12	31
11/01/2011	20.41	21.12	31
12/01/2011	20.41	21.11	30
13/01/2011	20.40	21.11	31
31/01/2011	20.30	20.59	29
1/02/2011	20.29	20.58	29
2/02/2011	20.28	20.57	29
3/02/2011	20.27	20.56	29
4/02/2011	20.26	20.55	29
13/02/2011	20.17	20.45	28
14/02/2011	20.16	20.44	28
15/02/2011	20.15	20.42	27
16/02/2011	20.13	20.41	28
17/02/2011	20.12	20.40	28
2/03/2011	19.55	20.21	26
3/03/2011	19.53	20.20	27
4/03/2011	19.52	20.19	27
5/03/2011	19.50	20.17	27
6/03/2011	19.49	20.16	27
29/03/2011	19.14	19.40	26
30/03/2011	19.12	19.39	27
31/03/2011	19.11	19.37	26
1/04/2011	19.09	19.36	27
2/04/2011	19.08	19.34	26