Nesting behaviour and development of New Zealand falcons (*Falco novaeseelandiae*) in a plantation forest

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Abstract The breeding behaviour and development of New Zealand falcons (*Falco novaeseelandiae*) were recorded at 2 nests in Kaingaroa Forest during a 4-month period up to 2 March 2007. This covered the later part of incubation, and the entire nestling and early post-fledging periods. Incubation was shared between parents; the male primarily incubated the eggs, during which time the female hunted. The male only provided occasional prey for the female. Brooding by both parents was intensive for the first 6 days and then gradually declined until the chicks reached 14 days old at which point it ceased. Assisted feeding of the chicks was almost always undertaken by the female. The male's primary role during the nestling period was prey delivery. During the early nestling period the female spent the majority of the time brooding chicks before shifting to hunting for the young.

INTRODUCTION

The New Zealand falcon (*Falco novaeseelandiae*) is New Zealand's only extant endemic bird of prey. It is currently recognised as a threatened species, largely as a result of predation by introduced mammalian predators, habitat destruction and illegal shooting (Fox 1977b; Hitchmough *et al.* 2007; Marchant & Higgins 1993). Falcons have been fully protected since 1970, however the species is probably still in decline (Gaze & Hutzler 2004). The New Zealand falcon is classified into 3 distinct forms: the "bush", "eastern", and "southern" falcons. The bush form has been reported to be the most at risk due to loss of breeding habitat (Fox 1977b). Recent reports, however, have found the bush form nesting on the ground in exotic plantation forests of the lower North Island, suggesting it may be able to adapt to some forms of habitat modification (Addison *et al.* 2006). Our research study site is the 190,000 ha Kaingaroa Forest in the central North Island. The forest is dissected into ~1,400 compartments of similar sizes, each averaging *c.*100 ha, but up to 363 ha (Caithness *et al.* 1989; Hyde & Stewart 2002). The forest is, therefore, a continuously changing mosaic of stands, ranging from clear-felled areas to mature 30-year-old trees with a diverse mix of native and exotic vegetation growing between most stands and road margins (Holland & McCutcheon 2007).

Studies undertaken by Massey University's Falcon Research Centre confirm the predilection of the New Zealand falcon for nesting in just-harvested up to 4-year old forest compartments (Seaton *et al.* 2013). However, little information is available on the breeding of falcons. In this study, we provide the first detailed reports of breeding behaviour of the bush form of New Zealand falcons in plantation forests during the incubation, nestling and post-fledging periods. Ground nesting within plantation forests provides an excellent opportunity to intensively study the breeding behaviour and development of the bush form in this modified habitat. The aim of this study was to better understand the behaviour and development of nesting New Zealand bush falcons in Kaingaroa Forest.

METHODS

Direct observations were made from a custom-built hide for part of the incubation and for the entire nestling and early post-fledging period. Occasional observations outside of the hide were made during the egg laying period and later stages of the post-fledging period at 2 nests. Both nest scrapes were located on the ground with minimal cover provided by a tree fern (*Dicksonia* sp.). They were in unplanted forest compartments with only slash remains from recent clear-fell harvesting of the mature trees. Nest observations were made over a 17-week period beginning from 5 November 2006.

Observations were made from a hide positioned *ca.* 30 m to the south of the nest. The 2 nests were observed using a 25 x 60 spotting scope and 10 x 50 binoculars. Each nest was observed continuously for *ca.* 6 hours per observation day. Nest 1 was observed between November and December, whereas nest 2 between January and March. 'Morning' observations generally started within an hour of sunrise and continued until around noon. 'Afternoon' observations generally started in the mid-afternoon and continued until after sunset when the light became too dim to observe nest activity at the nest using the spotting scope. Occasional observations were made from mid-morning until mid-afternoon as an overlap of the 2 main observation periods.

Both the adults and the young falcons appeared unperturbed by the presence of the hide near the nests. Indeed, potential prey species (*e.g.,* chaffinches and greenfinches) were observed feeding within 2 m of the hide and some prey was caught at the base of the hide by both parents hunting cooperatively. On one occasion a young fledgling tried unsuccessfully to land on the roof of the hide.

The sex of the falcons was distinguished by differences in size. The New Zealand falcon exhibits reverse sexual dimorphism, the female weighing about a third more than the male (Marchant & Higgins 1993). The female at Nest 1 and both parents at Nest 2 had been colour-banded previously. Identification of the chicks in and around the nest was based on size, pattern of down loss and coloured leg-band combinations.

Nest site 1 contained 3 eggs and the observation period included the last 6 days of the incubation, the entire nestling period and 15 days of the post-fledging period. Hide observations totaled 278 hours which spanned just over 9 weeks. Nest site 2 contained 4 eggs and hide observations included the last 18 days (*ca.* half) of the incubation period, the entire nestling period, and 3 days of the post-fledging period (calculated from the fledging date of the oldest nestling). Once the young were 39 days old no further observations were made of the fledglings. A total of 342 hours of observation were made from the hide at Nest 2. A single factor ANOVA was used to compare the feeding rate with ambient temperature during observations.
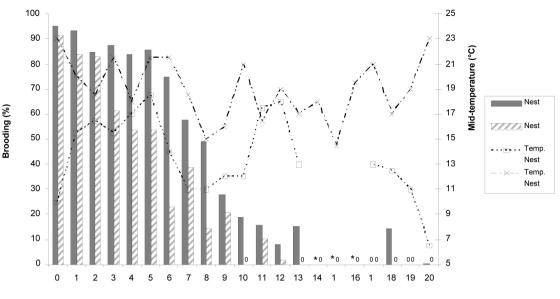
RESULTS

Incubation

Incubation is defined as the observed time that either parent spent sitting on the eggs during the incubation period. Incubation began on the day the last egg was laid and continued until the last chick hatched. Observed incubation attentiveness remained consistently high over the incubation period at both nests (range = 90.3 - 99.2%). The highest level of attentiveness was made on the day prior to hatching at Nest 2. This was a very windy day and attentiveness may have increased as a response. Incubation rates remained high during the whole incubation period with the exception of 2 events. Overall, the females provided 2/3 of the total diurnal incubation. Females also spent longer per incubating bout and undertook more incubation bouts than the males. In contrast, the male at Nest 2 contributed slightly more incubation than the female during 3 observation days.

Brooding of the nestlings

Observed brooding events were defined as the time spent by either parent sitting or otherwise covering at least half of the full brood of chicks (Dykstra *et al.* 2003). The nestling period in this study began on the day of hatch of the first chick and continued until the first flight was observed by one of the chicks. The amount of time spent brooding per day showed a general downward trend from hatch date until the chicks were 13 days old (Fig. 1). Time spent brooding remained consistently above 80% until the chicks were 5 and 2 days old at Nests 2 and 1, respectively. From day 6 the chicks were unattended for short periods each day. Unattended time increased

Fig. 1. Percent of observed time brooding the chicks per day. Observations lasted on average 6 hours per day. Age 0 = hatch date (12 November 2006 in Nest 1 and 22 January 2007 in Nest 2). * = missing data. 0 = no brooding observed. Mid-temperature represents the mid-point between the minimum and maximum temperature recorded during observation bout. Data represents daytime observations from *ca.* 0520 h to 2050 h for Nest 1 and *ca.* 0600 h to 2030 h for Nest 2. From Day 16 female parent in Nest 1 absent (presumed dead).

steadily and by day 10 the chicks were unattended for more than 4 hours at a time. After day 13, additional brooding was termed "stress-brooding" and occurred only when environmental conditions were particularly adverse. Time of day appeared to affect the amount of brooding undertaken by the falcons. Once the chicks were 6 days old they were left unattended for just under an hour. All observed brooding of the chicks greater than 10 days old occurred before 0800 h.

The females did most of the brooding of the chicks, especially on the hatch date. The longest observed brooding bout (3.5 h) was undertaken by the Nest 1 female when the chicks were 1 day old. Almost all male brooding occurred before the chicks reached 7 days old. The involvement of males in chick brooding varied considerably between nests. The male's contribution to brooding at Nest 1 was *ca.* 20% of that provided by the male at Nest 2. The male at Nest 2 provided considerable brooding from the day of hatching until day 5, after which he undertook no further brooding. The female at Nest 1 disappeared from day 17 and was presumed dead. On the following day the male spent much more time brooding than earlier in the nestling period. Adverse weather conditions were recorded on both days 18 and 20 at Nest 1. With the exception of these 2 days, weather conditions during the brooding stage (hatch to day 20) of the

nestling period were relatively mild at both nest sites.

Prey delivery and feeding of the young
Prey delivery in this study refers to the passing of captured prey items by the adult falcon near to or at the nest area. Prey deliveries were assumed to be deliveries of recently killed items brought to the nest (Palmer *et al.* 2004; Vekasy *et al.* 1996). The rate of prey deliveries increased from the day of hatch to about day 16, after which it leveled off and remained similar for the remainder of the nestling and early post-fledging periods. The peak in prey delivery occurred several days sooner in Nest 2 than Nest 1 (Fig. 2). Prey delivery rates to each nest was similar (Nest 1 = 1 prey item per 72 minutes; mean delivery rate Nest 2 = 1 prey item per 75 minutes) although there was substantial daily variation to each nest. A high prey delivery rate was recorded at Nest 1 on Day 20, when over 2 prey items per hour were delivered to the nest area.

Low prey delivery rates were recorded on the day prior to fledging of the male chicks (Fig. 2). Birds made up the majority of the delivered prey items at both nests, with the remaining proportion being made up by both mammals and insects. Nest 2 had a slightly higher proportion of prey deliveries that could not be identified to prey class (unknown prey class at Nest 1 = 22.3%; Nest 2 = 31.0%).
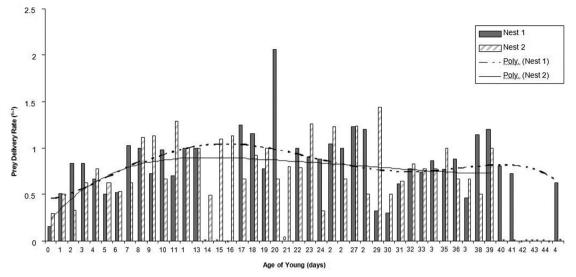
Fig. 2. Observed hourly delivery rate of prey items to the nest area throughout the nestling and early post-fledgling period. * = missing data. 0 = observation days in which no prey deliveries was observed. "Poly" refers to polynomial trend line. Observations were only made during daylight and cover *ca.* 0508 h to 2100 h at Nest 1 and *ca.* 0600 h to 2031 h at Nest 2. The female parent was absent from Day 17 (presumed dead) at Nest 1. Both male chicks at Nest 1 fledged at 31 days of age. The male chick at Nest 2 fledged at 31 days and the female at 36 days of age.

During the early nestling period all prey items delivered by the male were passed to the female parent before they were fed to the young. Half way through the nestling period the male began to pass prey items directly to the chicks. The females at both nests were recorded delivering prey items that they had caught from day 12. During the first 14 days of the nestling period at Nest 1, before the female disappeared, the prey delivery rate averaged one item every 80 minutes. After the female disappeared from Nest 1, the prey delivery rate by the solo male was higher than the combined rate provided by both parents at Nest 2.

Allocation of prey deliveries between the 2 young in each nest was quite variable between observation days. "Yellow", one of the 2 male young at Nest 1, received 10% more of the observed prey deliveries than "Red". At Nest 1, between day 22 and 30, both young received similar daily allocation of whole prey items. However, from days 31 onwards, Yellow generally received more than his sibling Red. "Pale", the female from the Nest 2 brood, received 6% more of whole prey items than her male sibling "Dark".

Feeding rates increased steadily from the day of hatch and peaked at day 25 after which feeding rates declined. The overall mean feeding rate was slightly higher at Nest 1 than at Nest 2 (Fig. 3). However, the self-feeding by the young on prey remains occurred twice as frequently at Nest 1 than Nest 2.

The female parent at Nest 1 provided all of the assisted feedings of the chicks prior to her disappearance somewhere between the ages of 13 and 16 days old after which the male assisted with most feeding events at 17 and 18 days of age, by which time no further assisted feeding events were observed. The first self-feeding event by a young bird was observed when the chicks were 17 days old at Nest 1 and 15 days old at Nest 2. Both male chicks at Nest 1 fledged at 31 days of age and the male chick at Nest 2 fledged at 31 days and the female at 36 days of age.

Chaffinches (*Fringilla coelebs*) made up the majority of prey items fed to the young at both nests and greenfinches (*Carduelis chloris*) and blackbirds (*Turdus merula*) were also occasionally fed to the young at both nest compartments. North Island robins (*Petroica australis longipes*) were a minor component of the young falcons diet at Nest 2. Yellowhammers (*Emberiza citrinella*) were also a minor prey species at Nest 1. Only one species of mammal and insect were fed to the young, a weasel (*Mustela nivalis*) and a huhu beetle (*Prionoplus reticularis*).

DISCUSSION
Incubation
In this study, the incubation period could only be calculated at one nest and the recorded 25 days is considerably shorter than that reported by Fox (1977a) of 29 to 35 days. One possible reason for the shorter incubation period may be the combination of nearly constant attentiveness by the parents
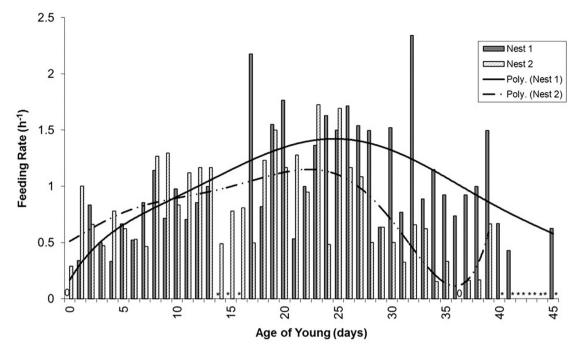
Fig. 3. Observed hourly feeding rate of the young throughout the nestling and early post-fledgling period. R^2 = 0.45 for Nest 1 and R^2 = 0.52 for Nest 2. * = missing data. 0 = no feeding of the young was observed. "Poly" refers to polynomial trend line. Observations were only made during daylight and cover from *ca.* 0508 h to 2100 h at Nest 1 and *ca.* 0600 h to 2031h at Nest 2. From Day 16 female parent at Nest 1 was absent (presumed dead).

and warm ambient temperatures recorded during the incubation period for Nest 2 (Ratcliffe 1980). Ratcliffe (1980) reports that some of the variation in incubation periods of peregrine falcons was related to ambient temperature.

The eggs in this study were generally left unattended for periods of up to 1 minute. With the exception of 2 disturbance events, near continuous incubation was undertaken by the parents after the last egg of the clutch was laid. Although both parents incubated the eggs, the female was more attentive, with males providing only 1/3 of diurnal incubation. Enderson *et al.* (1972) found consistent levels of male involvement in the diurnal incubation of peregrine falcons (*Falco peregrinus*). The males' incubation in this study was within the range (30-50%) reported by Nelson (1970) for male peregrine falcons. The amount of incubation contributed by the male at Nest 2 was quite variable between days. Similar variation has also been reported in studies of peregrines and captive New Zealand falcons (Murray 1998; Ratcliffe 1980). During the final week of incubation for 3 observation days, the male from Nest 2 provided 56% of the total observed incubation. Murray (1998) made no recordings of greater than 44% of diurnal incubation by a captive male New Zealand falcon.

Brooding

The New Zealand falcon is semi-altricial; the chicks hatch with a thin covering of white natal down and their eyes only partially open (Burnham 1983; Deeming 2002; Newton 1979a; Starck & Ricklefs 1998). The young require parental brooding until they develop the ability to thermoregulate, however, if weather conditions are particularly adverse then stress brooding can occur intermittently. After the day of hatch, brooding remained high for the first few days before progressively dropping off. Brooding remained near-continuous until the chicks reached between 3 and 6 days old. This is in contrast to the continuous brooding of eastern falcons (Fox 1977b) until the chicks reached 10 days of age. Our results suggest that the New Zealand falcon chicks gradually developed the ability to self-regulate their own body temperature during this period of declining brooding.

The amount of time spent brooding by the parents at Nest 2 declined after the chicks were only 3 days old. The chicks at this age are still only sparsely covered by white natal down and appear similar to recently hatched chicks. Fox (1977b) reported that captive New Zealand falcon chicks at 3 days of age appeared relaxed at a temperature 1°C lower than on hatch date. Day old captive chicks

of the bush form have been reported to survive a single period of up to 3 hours without brooding (D. Stewart, *pers. comm.* 2008). This, however, appeared to represent the upper extreme of tolerance for a chick at this age.

In contrast with Nest 2, the decrease in brooding in Nest 1 was not seen until the chicks had reached 6 days of age. In another study on the New Zealand falcon, brooding remained constant even at 7 days (Fox 1977b). Jenkins (2000) reported significant differences between the point of decline in brooding between different populations of peregrine falcons. In this species, the thicker grey down grows through the natal down between the age of 9 and 11 days and is considered the point at which partial thermoregulation by the chicks is achieved (Fox 1995; Potapov & Sale 2005; Stewart 2007). Data from this study suggest that partial thermoregulation may be achieved as early as 6 days of age, at which time the chicks were only brooded for about 60% of the day (Nest 2 only). This is consistent with partial thermo-regulation by captive New Zealand falcon young (Stewart-Badger 1997).

The recorded ambient temperature at Nest 2 was considerably warmer than Nest 1 during the first 20 days of the nestling period. Ambient temperature has also been reported by Ratcliffe (1980) to influence the brooding of young peregrine falcons. The lower level of brooding observed at Nest 2 when the chicks were 6 days old, may have been as a result of the observation from the hide being made in the afternoon when the ambient temperatures were several degrees above average. Once the chicks reached 10 days of age, morning brooding only occurred before 0800 h. This data suggests that the New Zealand falcon chicks had at least some control of their body temperature from 10 days of age. At 10 days, the grey down starts to grow through the natal down, aiding in the chicks ability to maintain their body temperature. Also, by day 10, the chicks were able to leave the nest scrape and seek shade from the sun. From about the age of 14 days, the chicks were only brooded occasionally when weather conditions were particularly inclement.

The female provided the majority of the brooding of the chicks at both nests. The female was always present on the eggs when they hatched and was likely able to anticipate the hatching of the chicks, as they make cheeping noises within the egg over 24 hours prior to hatching (Fox 1995). The male's contribution to brooding at Nest 1 was negligible (3%). This was very different from the Nest 2 male, who provided nearly 20% of the total brooding.

Prey delivery and feeding of the young
Prey delivery rates to both compartments increased steadily till day 17 and day 11 in Nest 1 and Nest 2,

respectively, and coincided with the major growth stage of the chicks – an observation also reported by Fox (1977b) and Stewart-Badger (1997). The males at both nests provided most of the prey items for chicks. After day 12, the females began to hunt for the young, however, their prey deliveries comprised a small proportion of the food delivered during the early post-fledgling period. We observed that between brooding bouts the female parent generally remained close to the nest during the early nestling period and only a small proportion of her time was spent hunting prey and this was relatively close to the nest site. Ratcliffe (1980) observed similar behaviour with peregrine falcon females. When the female was not visible from the hide, frequent begging calls suggested that she generally remained close to the nest. This was also supported by virtually all prey deliveries by the male first being passed to the female before being fed to the young. The female provided all of the assisted feeding of the young. The exception to this was observed at Nest 1 when the female disappeared and the male started feeding the chicks until they were able to self-feed. Once the chicks were able to self-feed at Nest 1 the male began to hunt further from the nest and spent less time guarding the young.

The male at Nest 1 started delivering prey items directly to the nest on the same day the chicks began self-feeding and around about the time the female ended her intense brooding phase. The male provided food for the female during the early stages of the nestling period before she began to self-hunt. This is consistent with Herbert & Herbert's (1965) findings who reported the male peregrine falcon provides most of the prey during the nestling period. Olsen *et al.* (1998) found that male peregrine falcons provide over 90% of the prey deliveries from hatch until chicks reach their adult weight.

We observed that *kekking* calls almost always announced the arrival of the male to the nest area. As the male approached the female would make begging calls prior to food being passed to her. Prey delivery rates dropped markedly at both nest sites the day prior to the fledging of the male chicks. This supports Brown's observations (1955) who suggested the parents actively reduce the prey deliveries in an attempt to induce the fledging of the young.

The investment by the male to the nestlings at Nest 1 increased after the female's disappearance from the nest. In fact, his delivery rate exceeded that of the combine prey deliveries of both parent birds at Nest 2. This behaviour corroborates the findings of a kestrel (*Falco tunnunculus*) study (Meijer *et al.*, 1989) where males made more strikes at prey when energy requirements at the nest were increased. At the same time that the Nest 1 male was providing more prey deliveries, his nest defence behaviour

Table 1. Summary of the previous understanding of New Zealand falcon breeding behaviour, major areas for improvement, and the significance of results found in this study.

Behaviour	Prior understanding & anecdotal observations	Understanding gained from this study	Significance & recommendations
Incubation behaviour			
Period of incubation	29 to 35 days but few estimates	As short as 25 days	Requires further estimates & investigation of influential factors
Parental involvement	Shared incubation by parents	Confirmed, but variable between days	Further understanding of investment in incubation
Male role	40% of diurnal incubation in captive birds	Male can contribute over half diurnal incubation	Male role in diurnal incubation important
Egg turning rate	Based on overseas species of raptors	Found to be consistent with other raptors	Improved understanding of egg turning rate
Egg turning technique	Lack of detailed observations	Suggest feet play role in egg turning	Dummy eggs with tilt switches could be used to determine role of parents
Brooding			
Thermo-regulation	Abrupt change in brooding from 9 days as secondary down grows; captive young thermo-regulate at 10 days	Gradual transition from as early as 3 days old; only brief brooding from 10 days	Gradually gain ability to thermo-regulate, starting prior to growth of secondary down; wild young develop as quickly as captive ones
Prey delivery			
Prey delivery rate	Poorly understood; only anecdotal reports	Increased to peak then remained high	Feeding of captive young should follow this pattern
Parental role	Male provides most prey deliveries	Confirmed but females can have a minor role; male capable of providing all prey to young	Female's role in late nestling period is to supplement male prey deliveries & feeding young
Allocation between young	Largely unknown	Possible competitive advantage develops between young	Competitive advantages can develop in brood even when food availability high but requires further study
Feeding of the young			
Feeding rate	Anecdotal reports in the nestling or post-fledging periods	Increases to peak then declines at a similar rate	Feeding of captive young should follow this trend
Parental assistance	Female provides all food to young	Consistent, but male capable of assisting with feeding	Female controls male's access to young
Diet fed to young	Exotic passerines most common prey in plantation forests	Consistent findings	Diet analyses using pellet & prey remains are accurate methods

increased and he was observed providing more time brooding the young.

Competition between the young for food was aggressive and occurred prior to receipt and post receipt of food. On several occasions after whole prey items were passed to the chicks, a sibling stole or fought for the item. Most parent-assisted feeding events involved the partitioning of single prey items between the siblings in the brood thereby ensuring a more equitable distribution of food. There appeared to be some competitive advantage of the female nestling at Nest 2. This was especially noticeable during the assisted feeding events on day 25 when the female nestling received more of the food portions from the adult female than the male sibling. In the American kestrel (*Falco sparverius*), female nestlings are larger and require *ca.* 7% more food resources than the male to reach adult weight (Anderson *et al*. 1993). This value is similar to the 6% greater number of whole prey items allocated to the female nestling than the male in this study. The female nestlings are likely to develop more strength than the male siblings late in the nestling period, yet the males may make up for this by increased agility and flight abilities (Anderson *et al*. 1993; Beebe 1960; Newton 1979a; Newton 1979b). When very small items were delivered, the larger females gain an

advantage over the male young as they were able to swallow larger portions whole (Anderson *et al.* 1993). Observations during this study suggest this was occurring between the young of New Zealand falcons. Although the size of the sexes are considerably different, food requirements of the nestlings to reach adult weight may be less than proportional to their body mass (McDonald *et al.* 2005). In the New Zealand falcon, the larger females continue to build up body mass for several days after the male young have already reached their adult weight (Fox 1977b).

Feeding rates form a somewhat bell-shaped distribution with respect to the age of the young. This is consistent with the pattern described by Poole & Boag (1988) for gyrfalcon (*Falco rusticolus*). During the first few days, young require only a small amount of food as they are still gaining nutrition from metabolising their yolk sac (Fox 1995). Once the chicks reach adult weight (about 18-22 days old), feeding rates slow after day 25 when most of the chicks' energetic demands are put into feather growth and they become adept at self-feeding (Fox 1977b; Stewart-Badger 1997). The observed feeding rates in this study concur with Fitzgerald's (1965) observations of New Zealand falcon chicks that were three-quarters developed.

The majority of the prey deliveries at both nests were birds in conjunction with the small numbers of insects and mammals. Chaffinches made up the majority of the prey items fed to the young New Zealand falcon nesting in plantation forests. This supports the findings of a number of previous studies on the diet of this species in other parts of its range (Barea 1995; Barea *et al.* 1999; Fitzgerald 1965; Fox 1977b; Guthrie-Smith 1927; Lawrence & Gay 1991; Seaton 2007).

CONCLUSIONS

In this research the details of the development of New Zealand bush falcon chicks and associated parent bird attendance behaviour in plantation forests were studied. Findings from this study generally support the incubation observations made on captive New Zealand bush falcon and wild eastern form birds (Fox 1977b; Murray 1998) thereby supporting the notion that captive birds express relatively natural behaviours during the breeding cycle. The patterns of behavioural development were very similar to those found in overseas studies on other species of falcon. The exact timing of different developmental stages, however, was not as consistent. Even within the same species, behaviours such as self-feeding did not appear to be related exclusively to the age of the young. A summary of observations from this study and selected recommendations for future research are presented in Table 1.

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