

**Factors affecting breeding success in the
Peregrine Falcon (*Falco peregrinus macropus*)
across Victoria 1991 - 2012**

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**Submitted in fulfillment of the requirements for the degree of
Doctor of Philosophy**

Deakin University

August, 2013



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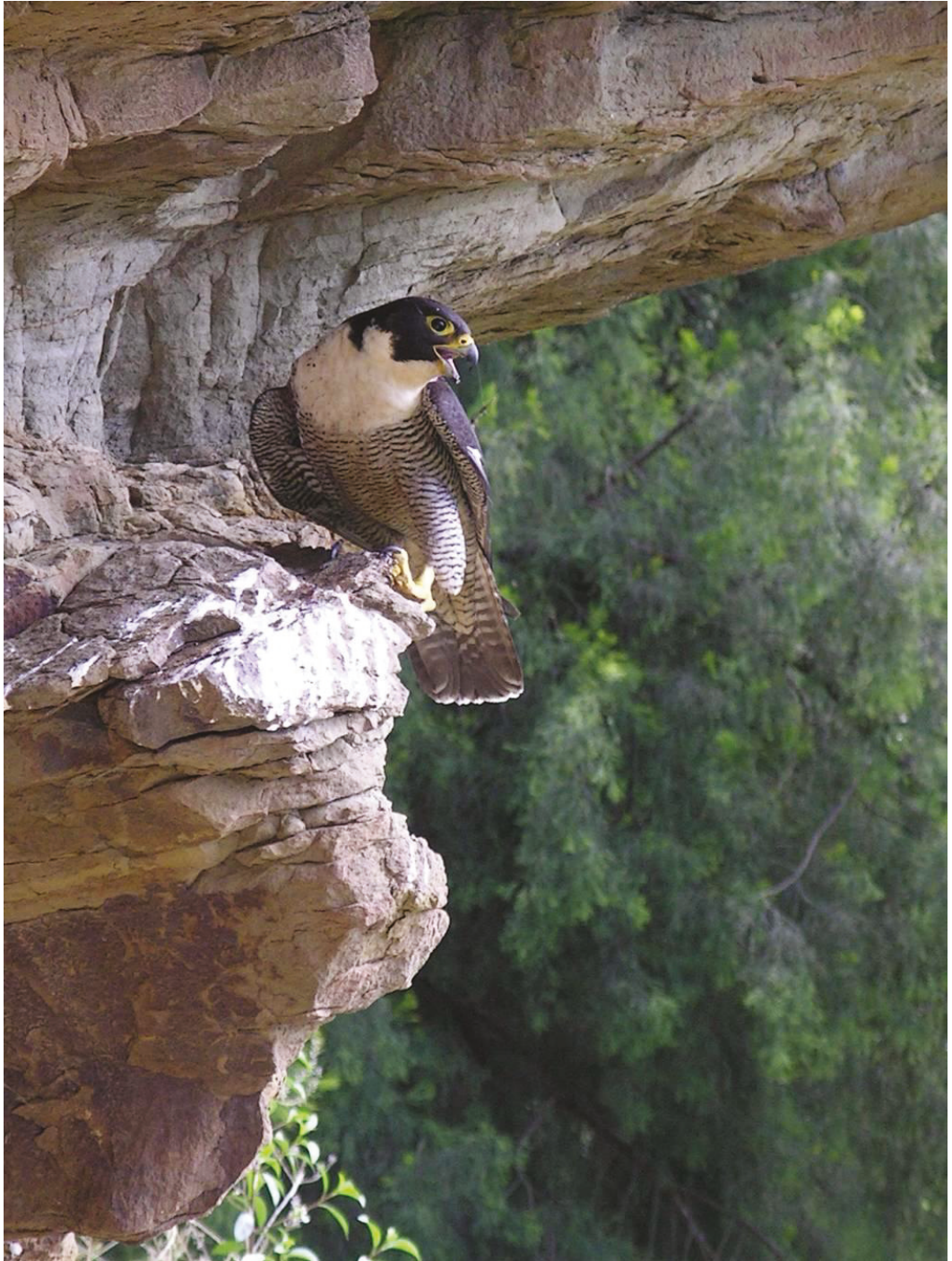
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Frontispiece



"Mother" Peregrine Falcon – Otway Ranges, Victoria, 2006.

*"There are some who can live without wild things, and some who cannot.
These essays are the delights and dilemmas of one who cannot."*

Aldo Leopold

Preface

This thesis is a compilation of my own work spanning 22 years, where I designed all of the methods and field techniques for the study. I conducted all of the field work, collected and analysed all of the data, and conducted all the statistical analysis for this research. I have conducted all of the statistical data analysis presented and prepared all of the maps. The preparation of the thesis has been undertaken with guidance from Dr Raylene Cooke, Associate Professor John White and Professor Andrew Bennett. The genetic analysis in Chapter two was conducted in collaboration with Dr Fiona Hogan. I drafted and revised all of the manuscripts and took all of the photographs included in the thesis except where otherwise photographic credit has been given.

The reader is advised that this thesis has been written in Australian English as per the Australian Macquarie Dictionary. So words such as colour and behaviour do not have the 'u' missing.

All data chapters (2, 3, 4, 5 and 6) have been written and submitted as manuscripts for publication. Each chapter is therefore self-contained and some repetition occurs, especially in the methods sections. The abstracts to some chapters may be in different formats to suit style guides of the chosen journal for publication. All references have been placed at the end of the thesis not at the conclusion of each chapter (manuscript). Two chapters (2 and 3) have been published, whilst chapters 4, 5 and 6 have been submitted for publication. These manuscripts have been co-authored with the above mentioned supervisory panel and they have therefore contributed to the ideas presented in each. In Chapters 2 and 3, which have been published prior to this thesis, I have used the personal pronoun of 'we' as per the published texts. Elsewhere throughout the thesis the singular personal pronoun 'I' is used. The thesis publications are as follows:-

Chapter 2:

Hurley, V.G., Hogan, F., White, J.G. and Cooke, R., (2007). "A morphological model for sexing nestling Peregrine Falcons (*Falco peregrinus macropus*) verified by genetic analysis". *Wildlife Research* **34:1**, pp 54-58.

Chapter 3:

Hurley, V.G., Cooke, R., and White, J.G., (2013). “Methods for improving the efficiencies of banding Peregrine Falcon nestlings: climb hard, band fast. *Wildlife Research* **40:4**, pp 269-280.

Chapter 4:

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Chapter 5:

Hurley, V.G., Bennett, A., Cooke, R., and White, J.G., (in prep.). “Longevity legacy: lifetime reproductive output by the Peregrine Falcon (*Falco peregrinus macropus*) is enhanced by lifespan and nest choice rather than landscape level influences.” (In preparation for submission to a relevant journal).

Chapter 6:

Hurley, V.G., White, J.G., and Cooke, R. “Interventions for improving the breeding success of the Peregrine Falcon (*Falco peregrinus macropus*) at anthropogenic nest sites: plugging an attractive sink”. (Submitted to *Biological Conservation*).

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This thesis is dedicated to the memory of W.B. 'Bill' Emison

"In science, publication is your legacy."

One of nature's gentlemen, sadly missed.

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Finally, this research was conducted under the A-Class banding Authority (1705) issued by the Australian Bird and Bat Banding Scheme and colour banding approvals were received to undertake colour marking (leg-bands).

Permission was granted to conduct scientific research on wildlife in Victoria under permits BB-90-032; BB-91-020; BB-92-007; RP-93-132; BB-93-007; RP-94-164; RP-95-160; 10001095; 10001578; 10002965; 10003428; 10002120; 10000640; and 10006046 issued under the *Wildlife Act* 1975 by the Victorian Department of Environment and Primary Industries

Permission was granted to conduct scientific research on wildlife in National Parks in Victoria under the following Scientific permits 912/126; 934/031; 956/061; and 934/035; issued under the *National Parks Act* 1975 Parks Victoria.

This research dates back to 1991. Approval for bird banding from a registered Animal Ethics Committee has only been a requirement in recent years. Approval was applied for and granted by the Department of Primary Industries – Wildlife and Small Institutions Animal Ethics Committee under approval numbers 01/08 & 09/11.

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Abstract

Birds of prey (raptors) are a useful indicator of environmental health. Due to their trophic level in food webs, raptors are particularly sensitive to bioaccumulation of toxic chemicals. The bioaccumulation of certain anthropogenic chemicals has been linked to the production of thin shelled eggs (egg shell thinning) which caused widespread reproductive failure among some raptor species. Thus, the monitoring of breeding performance of raptors can also inform us of the health of their environment and their ecology and resource requirements. Whether they form part of a healthy population, one in a state of decline or recovery, monitoring can inform conservation biologists through each of these stages.

This thesis investigated factors effecting the breeding success of the Peregrine Falcon (*Falco peregrinus macropus*) following the banning of the use of persistent organochloride pesticides in Victoria in south eastern Australia in 1987. The field work for this thesis is based on a 22 year dataset (1991 to 2012). A total of 1,504 nest site years (hereafter referred to as breeding events) were monitored (68.36 ± 5.80 , mean $\pm$ s.e., range 10-111 year⁻¹). Sites were monitored for an average of 7.78 , ± 0.44 s.e., breeding events (range 1-22) across an area of approximately 227,000 km². A total of 2,325 nestlings were colour banded with metal visual identification (VID) bands (111.14 ± 9.50 , mean $\pm$ s.e., range 14-179 nestlings year⁻¹).

To undertake this level of monitoring and in the planning of this thesis two broad research themes were developed. The first involved enhancing field techniques in order to conduct the field work most efficiently and the second the monitoring and management of breeding success.

New field techniques were developed, based on morphometrics verified through genetic analysis, for determining the sex of nestlings with 98.6% accuracy. This allowed banding of nestlings from the youngest age possible (15 days post hatching) and so provided the largest window of opportunity for banding at each nest. This technique coupled with using recent breeding phenology of active Peregrine Falcon nest sites provided *a priori* knowledge to accurately predict when to band nestlings at each nest. Targeting nestlings of 25 days post hatching using this predictive method increased the proportion of whole broods banded from 67.4% to 97.4%. This is compared to a more traditional approach of banding nestlings at or past asymptotic weight following multiple site visits. These field techniques formed the basis of the capture-mark-re-sight (CMR) applied in the second theme of this thesis.

These innovations in field techniques were critical to generating sufficient numbers of breeding adults of known age and origin as identified by the VID bands placed on them as nestlings. These ‘known’ adults then provided the study subjects for monitoring patterns of dispersal, age at first breeding, nest territory fidelity, nest selection choices and lifetime attributes such as lifetime reproductive output and lifespan. Nest site occupancy and breeding performance data was also collected for territories where adults were not wearing bands. There were three primary questions under investigation:

- 1) patterns of natal dispersal, nest site imprinting and consequences of nest site selection;
- 2) effects of landscape features, levels of nest site protection and longevity on the total number of fledglings produced in a lifetime; and

- 3) the efficacy of nest site interventions at poorly performing nests on anthropogenic structures.

The Peregrine Falcon is considered to be a cliff nesting specialist, however, in Victoria Australia they also use stick nests of other birds, tree hollows and building ledges. These atypical nests accounted for 39.7% of 237 known nests in Victoria. Using CMR techniques the type of nest birds fledged from and the nest type adopted for breeding was recorded for 102 individuals. In addition to nest selection choices, the effect of search effort (dispersal distance) and search time (age at first breeding) on lifespan and lifetime reproductive output were examined. Females dispersed further than males ($t = -4.983$, $P < 0.001$), ($\text{♀} 61.2 \pm 6.4$ km: $\text{♂} 24.4 \pm 5.8$ km; mean $\pm$ s.e.). No bias in dispersal direction was recorded. Novel dispersals (i.e. natal dispersals from one nest type to another) accounted for 30.4% of dispersals with no sex bias and dispersed shorter distances also with no sex bias ($F_{(1,98)} = 13.818$, $P < 0.001$). Breeding success was lowest on building ledges and greatest in tree stick nests or hollow (cavities). The level of novel dispersals recorded strongly suggests that once traditional nest sites (i.e. cliffs) are saturated, Peregrine Falcons will spontaneously adopt atypical (non-cliff) nest sites. This was initiated among individuals that disperse significantly shorter distances, suggesting novel dispersals are due less to a lack of the natal nest type but maybe more due to a fidelity to a familiar and available prey resource.

Lifetime reproductive output (LRO; the total number of young produced) was recorded for a total of 66 individuals. For each of these 66 breeding adults, landscape features within 5 km of the nest site were measured to contribute to an information-theoretic approach to comparing linear models to investigate factors effecting LRO. These models

were developed to investigate the relative influence of nest site level and landscape level factors on the LRO of these Peregrine Falcons.

There is no difference in lifespan between the sexes of breeding Peregrine Falcons ($t=0.768$, $df=64$, $P=0.446$). Years spent breeding and lifetime production of nestlings were all positively correlated. Landscape features did not influence LRO, however, the level of protection of a nest site did. Peregrine Falcons mate for life and display strong nest site fidelity. Moving to an occupied higher quality territory risks mortal combat with one or both of the resident pair. A safer strategy to overcome poor quality (less protected) site is longevity to increase LRO.

The use of anthropogenic sites for nesting by Peregrine Falcons has grown without any captive breeding and release programmes in Victoria from 7.5% in 1987 to 36.4% by 2012. During this study breeding performance was monitored at 127 nests, for at least five years each, from 1991 to 2012 and anthropogenic sites tended to have lower breeding success than natural sites (72.4% and 88.0% respectively). We tested whether this lower breeding success was the result of unsuitable physical features of the nests, exposing the eggs to the effects of temperature or rainfall. Nest boxes were installed at 18 poorly performing anthropogenic sites (eight quarry cliffs, 10 buildings) where egg hatch rates were particularly low (average 25.6%; ± 5.63 s.e.) compared to 63.25% (± 3.65 s.e.) for 18 nearby reference cliff sites. At the 18 treatment sites, where nest boxes were installed, egg hatch rates increased significantly (Tukey, $P = 0.010$) to 76.64% (± 2.74 s.e.).

Urban growth projections globally suggest that nesting opportunities for Peregrine Falcons on anthropogenic structures are likely to continue to increase. To inform both site managers and biologists, a decision matrix was developed outlining the strategies available for the management of Peregrine Falcons attempting to breed at anthropogenic sites. Appropriate management of these sites will become increasingly important in the context of Victoria's urban growth projections.

Since the removal of the key threatening process (persistent organochloride pesticides) in 1987 the Victorian Peregrine Falcon population has been recovering and continues to grow. Much of this population growth has been through the adoption of anthropogenic structures for breeding. Given the generally poor nest substrates provided by anthropogenic sites the significant ongoing increase in the proportion of anthropogenic nest sites being adopted by this species warrants careful monitoring. Nest site interventions to improve the quality of the site can overcome this and result in significant improvement in the breeding performance of Peregrine Falcons at these sites. This approach can include relocating nest sites to cater for land management requirements and so promotes a 'living with wildlife' message with management and staff in addition to improving the breeding performance of Peregrine Falcons. The large scale recovery of Peregrine Falcon populations in the northern hemisphere (primarily due to banning the key threatening process and captive breeding and release programmes) is a welcome conservation success story. Monitoring and managing nests on anthropogenic structures in the face of increasing urbanisation will assist in securing the future of the Victorian Peregrine Falcon population.

1.

Introduction and thesis overview



A Peregrine Falcon “lining up another would be climber”. (Image by Chris Field ©)

“No Peregrine Falcon would ever pass a college physics exam.
Instead they live it, every day!”

VG Hurley

(Advice to students, regarding how the Peregrine Falcon can dive so fast)

1.1. Introduction

The scale of the environmental changes brought on by the Anthropocene has had significant consequences for global biodiversity, with reduced areas of habitat and substantial impacts to natural systems (Crutzen, 2002; Garden *et al.*, 2006). For these reasons, there is an increasing focus in environmental research on the impacts of anthropogenic change on biodiversity (Sinclair *et al.*, 2007; Leu *et al.*, 2008; Rodewald *et al.*, 2011; Glennon & Kretser, 2013). A key to understanding how anthropogenic changes influence species is the long-term monitoring of species, including non-threatened species (Lindenmayer *et al.*, 2011). Longitudinal studies that monitor known individuals provide more robust datasets than space-for-time substitution studies, when attempting to untangle the relative roles of natural fluctuations and anthropogenic change in the environment (Clutton-Brock & Sheldon, 2010).

Anthropogenic impacts on biodiversity tend to have a trophic level bias with higher order (predator) species disproportionately at risk of extinction than lower order consumers or producers (Duffy, 2002). Whilst debated in the literature, one reason that top order predators have been monitored in long-term studies is due to the role they play in the healthy functioning of ecosystems (Sergio *et al.*, 2008). Due to their high trophic level, in most environmental systems they are influenced by distant changes throughout the food web and therefore are often regarded as strategic indicators of environmental health (Smits & Fernie, 2012). The loss of higher order predators has also been shown to have far reaching consequences in communities, such as the effects of meso-predator release or unexpected trophic cascades (Ritchie & Johnson, 2009; Ripple & Beschta, 2012).

Raptors, as with most top-order predators, tend to be under greater anthropogenic pressure than lower order consumers (Martínez-Abraín *et al.*, 2009; Amar *et al.*, 2012). As such, they have been used as a priority group in environmental monitoring programmes and are also the recipients of considerable conservation efforts (Duffy, 2002; Cade *et al.*, 2009; Sielicki & Mizera, 2009). Anthropogenic pressure on raptors occurs in a variety of forms ranging from alteration in prey abundance and direct persecution, to habitat modification and loss, to agricultural intensification, through to urbanisation; the latter not only destroys suitable habitat but replaces it with a more hostile environment containing novel threats (Hager (2009); Appendices I, II & VIII). These include increased risk of strikes due to overhead electricity wires and wire fences, more windows and the wind shear forces developed amongst high rise buildings, increased exposure to a range of exotic toxic chemicals and increased threat of direct persecution (Newton, 1979b; Hager, 2009; Park *et al.*, 2011).

The use of raptors as model species to investigate environmental change appears to be a valuable and efficient undertaking. This is because these species tend to mate for life, display strong site fidelity, generally have a predictable breeding season, and are readily visible with vocal territorial defense (aiding in locating an active nest), thus making them well-suited for monitoring (Newton, 1979a; Steenhof & Newton, 2007; Kovács *et al.*, 2008). The advantages of monitoring raptors, however, also have numerous biological and technical challenges. Raptors tend to be long lived, are often slow to reach reproductive age, disperse over considerable distances, breed at low densities and often nest in remote or difficult to access locations, therefore reducing their appeal as targets for long-term monitoring programmes (Newton, 1979a; Bednarz, 2007).

Logistical and budgetary constraints seldom align with the timelines required for undertaking long-term monitoring-based research (Lindenmayer *et al.*, 2012); and this is particularly manifest with raptors (Bednarz, 2007). Unfortunately, these challenges have led to a distinct bias, particularly in the southern hemisphere, toward intensive research on birds that breed colonially or co-operatively, compared with non-passerines such as raptors (Clarke, 1997). To overcome this bias, it is critical that the challenges associated with long-term research on raptors are addressed, and efficient approaches for their use in environmental monitoring are developed. As such, one of the major themes of this thesis is focused on developing techniques and approaches for improving the efficiency, planning and conduct of fieldwork on raptors (**Chapters 2 & 3**). Which is an essential component of long-term monitoring.

The second major theme of this thesis concerns the factors that affect breeding success in a raptor population in a state of recovery. The term ‘breeding success’, as applied in this study, extends beyond the basic metric of nest success or failure (Thompson *et al.*, 2001). Data on the number of eggs laid, the number hatched, the hatch rate, and the number of nestlings that survive to fledging per breeding event, are different aspects of and are clearly defined and applied separately within the broad term of ‘breeding success’ in this thesis. A history of crushed thin-shelled eggs causing reproductive failure by this species due to pesticide bioaccumulation warrants singling-out this aspect when monitoring the breeding success of this Peregrine Falcon population (Olsen *et al.*, 1992; Ratcliffe, 1993). When these parameters are recorded over the entire breeding life of adult birds, they provide a measure of lifetime reproductive output and a broader perspective on reproduction (Clutton-Brock, 1988; Newton, 1989). How each of these parameters is related to variables such as dispersal distance, nest type and quality, age at first breeding

and landscape features in the breeding territory, can combine to provide a meaningful assessment of the reproductive condition of a population (**Chapters 4, 5 & 6**).

Monitoring the reproduction of a population of a species in recovery from impaired reproduction, such as for the Peregrine Falcon (*Falco peregrinus*), is critically important to its persistence. With the cause of the decline removed it is important to confirm, through monitoring, that reproduction rates have recovered and that no new threat has emerged to restrict the species recovery.

This thesis on aspects of the ecology and breeding performance of the Peregrine Falcon, builds on earlier studies (1975-1984) that monitored this species in Victoria, led by the late W.B. “Bill” Emison (Cowling, 1981). Those studies were motivated, in part, by a concern for the conservation status of the species after 30 years of exposure to the agricultural use of DDT and Deildrin (Emison, 1979). However, these studies also represented the gathering of baseline data on the breeding biology and distribution of the Peregrine Falcon in Victoria (White *et al.*, 1981). The research in this thesis was initiated and undertaken entirely as a private monitoring project by the author. The Victorian Peregrine Project (VPP) was established as part of this research, thus distinguishing it from the previous government-based studies. Data for this thesis is based on a 22 year dataset (1991-2012) spread over ~227,000 km² in which 143 active nest sites were “discovered”. Breeding was monitored at 200 nest sites across Victoria. A total of 1,504 breeding events were monitored (68.36 ± 5.80 ; mean $\pm$ s.e., range 10-111 year⁻¹). Sites were monitored for an average of $7.78 (\pm 0.44 \text{ s.e.})$ breeding events (range 1-22) and a total of 2,325 nestlings were colour banded (111.14 ± 9.50 ; mean $\pm$ s.e., range 14-179 nestlings year⁻¹).

1.2. Ecology of Falcons

Globally, the composition of the Order Falconiformes (comprising 39 species of falcons) and their relationships with other avian Orders remains controversial and is not completely resolved (Ferguson-Lees & Christie, 2005; Christidis & Boles, 2008). For the purposes of this study, I have followed the systematics and taxonomy of Australian birds adopted by Christidis and Boles (2008).

Falcons have an almost global distribution, with species recorded on every continent and large island group except Antarctica (Cade, 1982). They are small to medium-sized diurnal raptors that are highly predatory and seldom eat carrion (Brown & Amadon, 1989). They represent a diverse genus and have in common a number of features that, combined, distinguish them from other raptors and these features include:

- i) Falcons do not construct nests *per se* but rather dig a scrape in a suitable substrate or adopt a variety of pre-existing structures in which to nest. These include stick nests of other birds (or mammals), tree hollows, ledges on cliffs or near the entrance of caves and on buildings, or even on the ground in low lying treeless habitats or underground near the entrances of caves.
- ii) They seldom kill their prey by penetration with their talons; instead they kill their prey by neck biting or disarticulating cervical vertebrae. The tominal teeth on the cutting edge of the upper jaw and corresponding notches on the lower mandible contribute to this killing mechanism.
- iii) Unlike members of the hawk family, perching falcons will head-bob when scrutinising an object intently.
- iv) They display strong reversed sexual dimorphism (i.e. females are larger).

- v) The nostrils (nares) contain a central bony tubercle, which is an extension of the septum, which leads to a whirled passage in the anterior nasal cavity. An exact function for these structures is yet to be confirmed.
- vi) Falcons have a distinctive molt sequence of flight and tail feathers from other raptors. In falcons the primaries are molted in both the ascent (towards to outermost) and the descent (toward the innermost) directions beginning with P₄. The tail molt begins with the central retrices progressing outwards, except that the outer pair R₆ fall out before R₅.
- vii) Falcons do not display nestling siblicide and have limited sibling aggression within the nest.

These features are reported variously in the following references; Cade (1982); Brown and Amadon (1989); Ferguson-Lees and Christie (2005); and Ollila (2009).

Falcons, however, share a number of ecological attributes in common with most raptor species. These include a relatively slow rate of reproduction, they are generally long-lived, they have a tendency to maintain lifetime pair bonds and they are usually fiercely territorial (at least during the breeding season; Ferguson-Lees and Christie (2005)).

1.3. Falcon fauna of Australia

As an island continent, Australia has six falcon species of which five are wholly endemic. The endemic falcon species of Australia are the Brown Falcon (*F. berigora*; Vigors and Horsfield (1827)), Nankeen Kestrel (*F. cenchroides*; Vigors and Horsfield (1827)), Little Falcon (*F. longipennis*; Swainson (1837)), Grey Falcon (*F. hypoleucos*; Gould (1841)), and the Black Falcon (*F. subniger*; G.R. Gray (1843)). The sixth species, the Peregrine Falcon (*F. peregrinus macropus*; Swainson (1837)) is an endemic

subspecies to Australia. There are 19 subspecies of Peregrine Falcon worldwide with a natural breeding distribution covering almost every zone of latitude, climate and ecosystem except waterless and treeless deserts (White *et al.*, 2013). They nest from sea level up to the snow line on every continent and large island group except for Antarctica and New Zealand (White & Boyce, 1988).

1.4. Peregrine Falcon ecology

The natural breeding distribution of the Peregrine Falcon (*Falco peregrinus*) is arguably, second only to that of humans (Santana *et al.*, 2006; White *et al.*, 2013). Despite this flexibility in habitats occupied, Peregrine Falcons exhibit three ecological specialisations: namely, they i) prefer to hunt birds in flight, ii) do not exhibit any nest building capabilities beyond digging a shallow scrape (usually on a rocky or sandy cliff ledge), and iii) they tend to occupy a single nest territory over a lifetime (Cade, 1982).

1.4.1. Diet

Across its cosmopolitan distribution the Peregrine Falcon is adapted to hunting and feeding on birds (Ratcliffe, 1993). With few exceptions dietary studies have found this species to feed almost exclusively on birds and feeds heavily on those species most commonly found in a particular area (Court *et al.*, 1988; Rosenfield *et al.*, 1995; Jenkins & Avery, 1999; Palmer *et al.*, 2004; Dekker & Taylor, 2005; Zuberogitia *et al.*, 2013). Further, the Peregrine Falcon prefers flocking species that are quite aerial tending towards more open country (Pruett-Jones *et al.*, 1981b; Ellis *et al.*, 2004; Drewitt & Dixon, 2008; López-López *et al.*, 2009). Brightly coloured species or those with conspicuous habits are also favoured (Cade, 1982). Recent intensive dietary studies

using compositional analyses of prey species have recorded Peregrine Falcons to be selective predators along the Yukon River, Canada (Dawson *et al.*, 2011). Prey remains collected over 13 years at 37 nest sites totaling 320 breeding events included 2,832 prey from 128 different species in the Bay of Biscay, Spain (Zuberogitia *et al.*, 2013). These prey differed greatly in size from the Firecrest (*Regulus ignicapilla*) (6 g) to the Northern Gannet (*Morus bassanus*) (2,800 g). However, just four species comprised 52.3% of the diet by biomass and these were: (7.3%) Yellow-legged Gull (*Larus michahellis*) (816 g), (9.1%) Whimbrel (*Numenius phaeopus*) (425 g), (25%) Rock Dove (300 g) and (11%) Common Blackbird (*Turdus merula*) (100 g).

As with other studies, dietary studies of the Peregrine Falcon in Australia have consistently recorded an almost exclusively avian diet (Pruett-Jones *et al.*, 1981b; Olsen & Georges, 1993; Olsen *et al.*, 1993; Cogley, 1995; Olsen *et al.*, 1998; MacKinnon, 2011). During the field work for this thesis a total of 1,504 breeding events were monitored and cursory inspections of each nest during each monitoring event revealed avian prey remains in all but two nests in different years. These non-avian remains were a hind foot from a European Rabbit (*Oryctolagus cuniculus*) and the tail from a Shingleback Lizard (*Tiliqua rugosa*) both of which were dried out and uneaten. It is presumed these two items may have been pirated from another raptor and most likely a Brown Falcon.

The range of avian prey species taken by the Peregrine Falcon in Victoria varies in weight from the European Gold Finch (*Carduelis carduelis*) (17 g) up to the Sulphur-crested Cockatoo (*Cacatua galerita*) (890 g) (Olsen *et al.*, 1993) and even the Australian

White Ibis (*Threskiornis molucca*) (2.5 kg) (in this study). Typically the Peregrine Falcon, from the published Australian studies, preys heavily upon flocking, open country birds such as Galahs (*Eolophus roseicapillus*) (335 g), feral Pigeons or Rock Doves (*Columba livia*) (465 g) and European Starlings (*Sturnus vulgaris*) (75 g). These three species comprised 42.9% of prey items and 49.8% of diet by biomass among prey remains collected at 53 nest sites across Victoria in spring 2010 (MacKinnon, 2011). So the dietary approach of the Peregrine Falcon in Australia and in particular Victoria is similar to that of Peregrine Falcons globally. That is, being predominantly a diurnal hunting specialist of avian species taking a wide range of prey but tending to focus on a small range of preferred open country flocking prey species.

1.4.2. Dietary adaptations

Despite being identified as an avian hunting specialist the Peregrine Falcon has demonstrated a high degree of flexibility in hunting strategies; for example, to the point of switching from diurnal to nocturnal hunting in some urban environments (DeCandido & Allen, 2006; Drewitt & Dixon, 2008). Detailed longitudinal monitoring of hunting and diet at one site in Canada recorded Peregrine Falcons modifying their diet to improve hunting efficiency over time (Dekker & Taylor, 2005). Another population has adapted from exclusively hunting birds to including a high proportion of mammals during microtine rodent population peaks in an Arctic environment of the Keewatin District, Canada (Court *et al.*, 1988) and Rankin Inlet, Canada (Bradley & Oliphant, 1991). Peregrine Falcons have also been recorded hawking for insects in tropical grasslands during fires in Fiji (White & Brimm, 1990). The resident pair, to fend off starvation during severe drought, on Hongdo island south of South Korea, preyed heavily upon migrating dragonflies, most commonly the Lesser Emperor (*Anax parthenope*) and Globe

Skimmer (*Pantala flavescens*) (Choi & Nam, 2012). Opportunistic catching of fish has been documented (White & Roseneau, 1970), and one female in Alaska was recorded regularly taking fish (namely: Rainbow Trout (*Oncorhynchus mykiss*)) to raise three young (Hetzler, 2013). These examples all point to the Peregrine Falcon having an unexpected degree of flexibility in its diet, which no doubt has assisted it attaining a near global distribution.

1.4.3. *Nest selection*

Primarily the Peregrine Falcon is considered to be a cliff nesting species (Cade, 1982; Ratcliffe, 1993). Nest construction is limited to digging a shallow depression called a ‘scrape’ on a rocky, gravelly or sandy cliff ledge or cave and laying the eggs in the scrape. No material is added to line the nest with the eggs lying on the bare substrate. During incubation the female will roll the eggs so each egg rests between two toes and is thus supported as she sits with her abdomen covering them.

1.4.4. *Nest selection adaptations*

A lack of nest-building instinct has not restricted the Peregrine Falcon to nesting on cliff ledges alone. A poorly protected nest ledge, however, can negatively impact on breeding success through reduced egg hatching rates due to exposure to the elements and nest inundation from rainfall (Olsen & Olsen, 1989b; Bradley *et al.*, 1997) (Figure 1.1_{A&B}). A large stick-nesting population (~500 pairs) occurred across the extensive forests of northern Europe, and became extinct after 1972 primarily due to organochloride pesticide bioaccumulation coupled, in their final years, with direct persecution (Kirmse, 2001). In addition to the use of stick nests of other birds, nesting in tree cavities has been recorded

in Australia (Emison *et al.*, 1997). Nesting has been recorded in grass tussocks on the ground in boreal bogs of Finland and Russia (Karyakin & Pazhenov, 2009; Ollila, 2009). Peregrine Falcons have also adopted a large range of built structures, from high rise city buildings to grain silos, power station chimneys and rail and road bridges (Bird *et al.*, 1996; Tordoff *et al.*, 1998). In Australia, they display the highest level of plasticity in selection of nest types, including cliffs, the stick nests of other birds, tree hollows (cavities) and buildings (Emison *et al.*, 1997) (Figure 1.2).



Figure 1.1 Clutches of Peregrine Falcon eggs at two sites. A = healthy Peregrine Falcon eggs on a well-protected ledge, B = Peregrine Falcon eggs dead due to inundation of the nest ledge. This same ledge (B) was occupied the year before and after this photo was taken, and four young fledged in each of those years. C = ♀ Peregrine Falcon trying to shield eggs from radiant heat ($\sim 54^{\circ}\text{C}$). This clutch did not hatch. D = failed eggs from two separate years. The metal beam acted as a heat sink to chill the eggs.

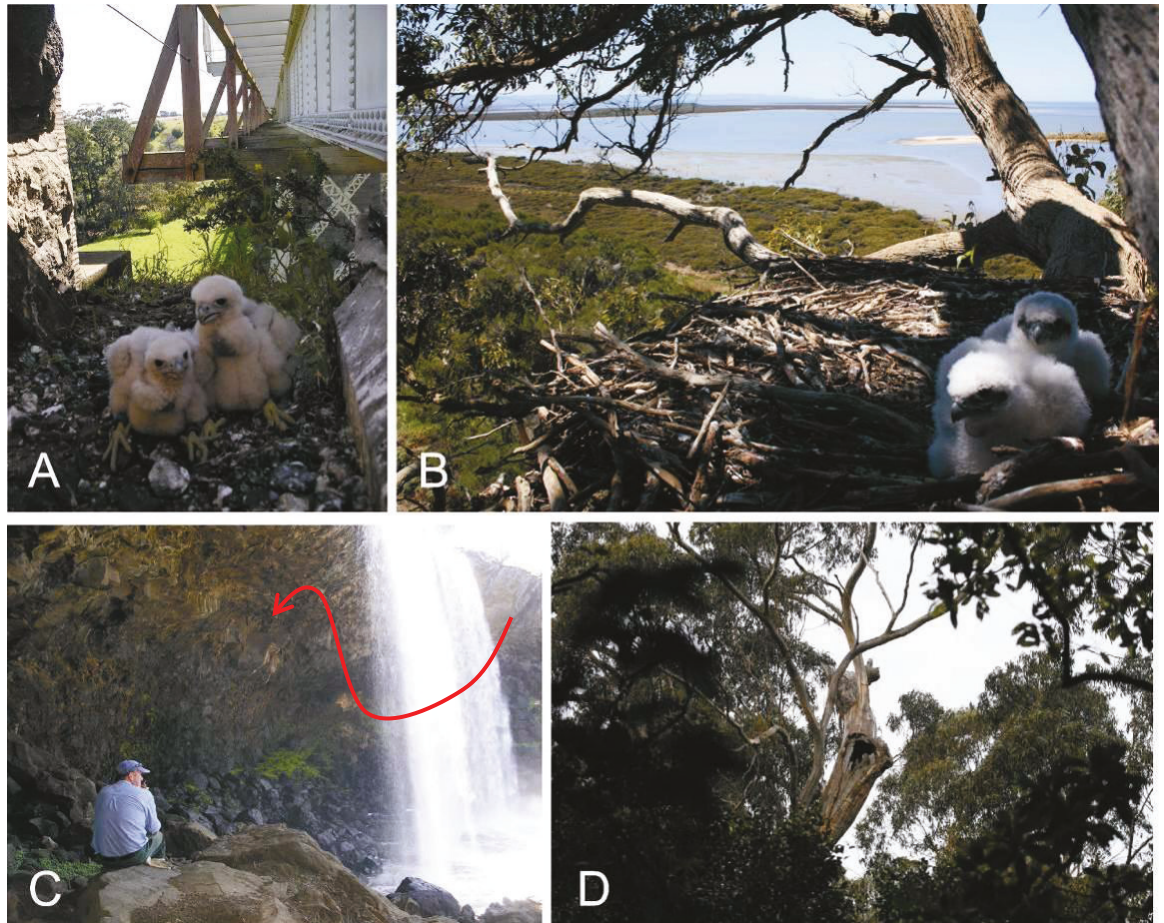


Figure 1.2 The four distinct nest types used by Peregrine Falcons in Victoria. A = ‘Building’ (a stone railway bridge); B = Stick nest (disused White-bellied Sea Eagle (*Haliaeetus leucogaster*) nest; Photo. M. MacKinnon); C = ‘Cliff’ (an unusual nest behind a water fall. Red arrow indicates flight path to nest; photo. S. King); and D = tree cavity (entrance is 12 m off the ground and the cavity is 1 m deep; photo. R. Bilney).

1.5. The Peregrine Falcon in Australia

Peregrine Falcons are distributed throughout mainland Australia and the southern island state of Tasmania, tending to avoid the arid interior where it is replaced by the Grey Falcon (*Falco hypoleucos*) in much of this region (Schoenjahn, 2012). The Peregrine Falcon in Australia is sedentary, not undertaking annual migrations unlike those of the northern hemisphere (Norris *et al.*, 1977; Fuller *et al.*, 1998). From a distributional view point, the strong hold for the species on mainland Australia is along the Great Dividing

Range, running down the eastern seaboard of Australia. The fertile alluvial plains that extend either side of the Great Dividing Range from south east Queensland through eastern New South Wales and across Victoria appear to support the largest populations of the species' distribution (Barrett *et al.*, 2003) (Figure 1.3).

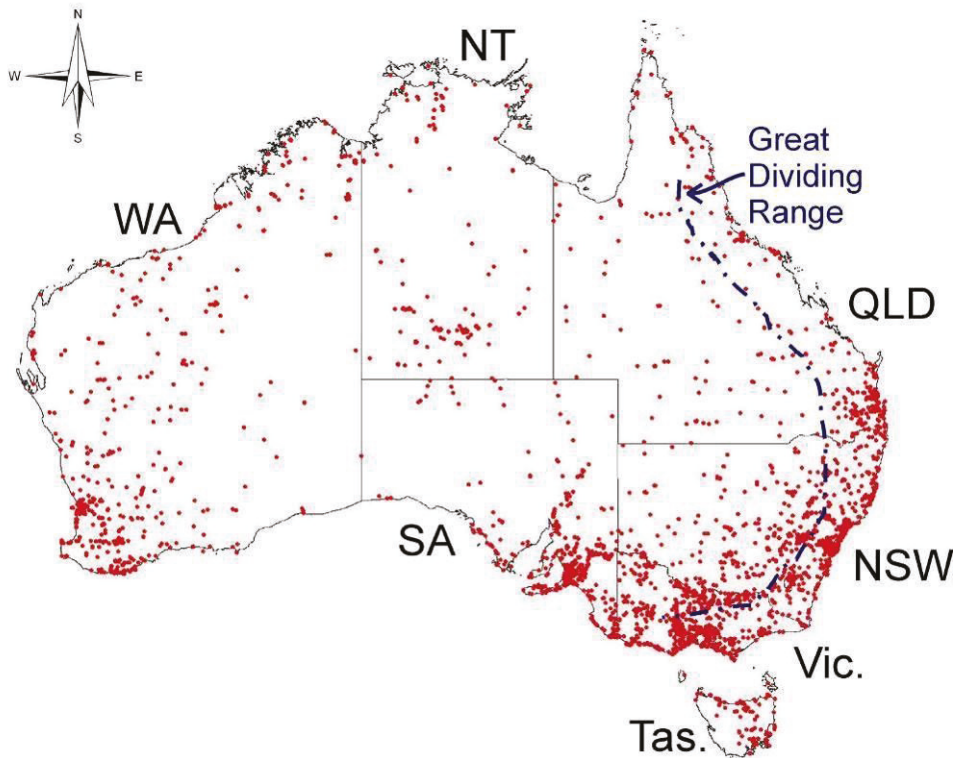


Figure 1.3 Distribution map of the Peregrine Falcon in Australia. ● = sighting record. Sourced from Birdlife Australia Bird Data database©.

The Peregrine Falcon occupies a diverse range of ecosystems in Victoria, that are representative of those it occupies across the continent (White *et al.*, 1981; Emison *et al.*, 1997). Breeding records have been recorded from the low lying semi-arid north west (40 m above sea level (asl)), the basalt and sandstone cliffs along the southern coast, rural landscapes throughout Victoria, to the highest nest recorded at 1,180 m asl on a cliff topped with Snow Gums (*Eucalyptus pauciflora*) and in the artificial canyons of Melbourne's central business district with a human population of 4.25 M (Pruett-Jones *et al.*, 1981b; Emison *et al.*, 1997; ABS, 2011) (Figure 1.4).



Figure 1.4 A diversity of ecosystems occupied by the Peregrine Falcon in Victoria. All pictures are of or near active nest sites. A = coastal cliffs (Otway coast); B = Snow Gum forests above 1,200 m (Dandongedale Falls, ne Vic.); C = Urban environment, (Altona looking east towards Melbourne); D = farmland with treed riparian zone; E = Mountain Ash (*Eucalyptus regnans*) forest, (Gembrook, east of Melbourne; white circle signifies climber); F = Gippsland Forest Red Gum (*Eucalyptus tereticornis subsp. mediana*) ring barked in 1930s in now cleared grazing land (Gippsland Plains, east Vic.); and G = Treed Mallee vegetation in the semi-arid north west.

1.6. Recent history of the Peregrine Falcon

1.6.1. Globally

Any comprehensive account of the breeding performance of the Peregrine Falcon in the past 60 years would not be complete without some reference to the effects of persistent organochloride pesticides (Ratcliffe, 1993). The serious collapse in Peregrine Falcon populations across its northern hemisphere range and the many international captive breeding and release conservation programmes to re-establish the species has made the species a globally recognised bird of prey (Cade *et al.*, 1988; Frank, 1994; Sielicki & Mizera, 2009). The results of these programmes have led to the Peregrine Falcon as being an icon of successful reintroduction biology (Cade *et al.*, 2009). It is out of concern for the conservation of this species over this time that has also raised the Peregrine Falcon to the status of environmental sentinel, due to their susceptibility to the toxic effects of certain anthropogenic chemicals.

Bioaccumulation of persistent organochloride pesticides (i.e. DDT, dieldrin and cyclodiene), introduced into agricultural systems as a seed dressing after 1946, interfered with calcium uptake and deposition on the eggshell membrane causing female Peregrine Falcons to lay thin-shelled eggs. These eggs collapsed under the weight of the incubating female late in the incubation period, crushing the embryo inside (Grier, 1982; Peakall & Kiff, 1988; Newton *et al.*, 1989; Ratcliffe, 1993). This effect of the pesticides had significant global impacts on Peregrine Falcon populations, resulting in its extinction from several countries in Europe and large tracts of north America (Hickey, 1969; Cade *et al.*, 1988). Parallel declines were also detected in populations of other raptor species, most notably the Sparrowhawk (*Accipiter nisus*), Common Kestrel (*Falco tinnunculus*), Barn Owl (*Tyto alba*) and Bald Eagle (*Haliaeetus leucocephalus*) (Prestt, 1965; Grier,

1982). The timing of breeding failures (i.e. late in the incubation period) often meant that a second clutch was not attempted that year, thus significantly reducing the fecundity of those populations of Peregrine Falcons affected by these toxins (Pruett-Jones *et al.*, 1981a). Furthermore, increased concentrations of these chemicals also killed embryos outright and still higher concentrations in the adults proved lethal and led to increased adult mortality and further acceleration in population declines (Ratcliffe, 1993).

Large-scale captive breeding programmes for Peregrine Falcons in many countries throughout Europe and North America up until the mid-1990s, coupled with the gradual removal of the legal use of organochloride pesticides in agriculture in many developed countries in the '70s and '80s, led to a reversal in population decline across much of the species' range (Cade *et al.*, 2009; Sielicki & Mizera, 2009). Much of the recovery and population growth has been by captive bred Peregrine Falcons nesting on anthropogenic structures in urban and non-urban environments (Cade *et al.*, 1996). Many of these early urban-breeding birds are considered to be the result of captive bred birds released near fledging into urban nest boxes and fed until fledging (a process called 'hacking'; Sherrod *et al.* (1982)); resulting in the successful adoption of an urban nesting habit in Europe and North America (White, 2009).

1.6.2. Australia

The Peregrine Falcon population in Australia also experienced a significant decline, but not as disastrous as that recorded in the northern hemisphere (Pruett-Jones *et al.*, 1981a; Olsen & Olsen, 1988b; Emison & Hurley, 1995). Peregrine Falcon eggs in Victoria, south eastern Australia, recorded the highest levels of shell thinning and concentrations of dieldrin and DDE (the metabolite of DDT) of any region in Australia (Olsen *et al.*,

1992). The levels in Victoria, the highest recorded anywhere in Australia, were comparable with those from northern hemisphere countries where population declines had occurred (Pruett-Jones *et al.*, 1981a). In addition to toxic chemicals the Peregrine Falcon has been subject to continual persecution. The first band recovery in Australia was recorded in Hamilton in south west Victoria in 1958 of a Peregrine Falcon that had been shot (Appendix I). Persecution, particularly by Pigeon fanciers, remains a constant pressure on this population (Appendix II & VIII) as it does elsewhere (Hager, 2009).

1.6.3. Victoria

Due to concerns for the conservation of this species in Victoria following 30 years of exposure to the use of DDT in local agriculture, several investigations were undertaken by the Victorian Government's conservation department (1975-1977) (Emison & Bren, 1981; Pruett-Jones *et al.*, 1981b; Pruett-Jones *et al.*, 1981a; White *et al.*, 1981; Emison & White, 1988). These were the first studies of the species in Victoria and provided baseline data and the location of 110 nest sites (of which 57 were subsequently monitored as part of the research presented in this thesis). A reduced level of banding and monitoring continued until 1984 (Emison *et al.*, 1993). During these studies (1975-1984) there appeared to be a steady decline in the occupancy rate of 20 regularly monitored Peregrine Falcon nests within a 100 km radius of Melbourne, Victoria (Emison 1988). A subsequent survey in 1992 established that occupancy at those 20 nest sites had recovered to 86% of the 1976 levels (Emison & Hurley, 1995). The 1976 occupancy rates, however, represented a population that had potentially been subject to a 30 year exposure to damaging persistent organochloride pesticides (Pruett-Jones *et al.*, 1981a), and so is not necessarily a reliable benchmark for a healthy population. Following the banning of these chemicals in Australian agriculture, not out of

environmental or human health concerns but due to threats of trade bans on Australian beef (Ford, 1987), it seemed timely to begin a new long-term, large-scale monitoring project of this species in 1991.

1.6.4. *The Victorian Peregrine Project*

The Victorian Peregrine Project (VPP) is a private initiative established by the author to conduct a long-term monitoring study of the Peregrine Falcon across Victoria. In the appendices of this thesis copies of banding, monitoring and egg measurement field data sheets, a copy of the 2013 edition of the banding manual developed for this project, and an example of a completed public band recovery report are included (Appendix III, IV, V, VI, VII & VIII). While this information (e.g. the data sheets and manuals) do not warrant publication in the scientific literature, they complement the data chapters of this thesis. Appending these to this thesis provides a more detailed reference to the practical aspects of undertaking this project in a single volume. Information in the appendices is the product of 22 years of development and refinement and will remain a valuable resource to anybody wishing to undertake some component of this project in the future. Including such items in the appendices of a thesis has been shown to have real practical application to facilitate follow-up monitoring programmes (Lindenmayer *et al.*, 2012). Unfortunately due to the ongoing persecution of this species it was not considered appropriate to provide the grid references or location details of the nest sites. These are available to interested conservation biologists through the Victorian Government's Biodiversity Atlas databases or by contacting the author directly.

1.7. Thesis aims and structure

The overall aim of this research (when it began in 1991) was to monitor the breeding performance of the Peregrine Falcon at a large temporal and spatial scale following the banning of the use of persistent organochloride pesticides in Australia in 1987 (Ford, 1987). This work builds on the pioneering research (1975-1984) lead by W.B. ‘Bill’ Emison (deceased) of the Fisheries and Wildlife Division in Victoria, Australia. Key questions unresolved in the previous studies are investigated in this research. These include, but are not restricted to; nest site selection and the consequences of adopting non-cliff nest sites (White & Jones, 1977), natal dispersal distances, age at first breeding, lifespan, years spent breeding (Emison & Bren, 1981) and influences on lifetime reproductive output (Emison *et al.*, 1993). Many of these questions could only be answered through a long-term study using some form of capture-mark-re-sight or recapture (CMR) procedure conducted at temporal and spatial scales reflective of the longevity and dispersal capabilities of the Peregrine Falcon.

Most detailed studies of dispersal patterns and lifetime reproduction in birds have focused on short lived species that breed in discrete (Cooper & Walters, 2002), or island populations (Pärn *et al.*, 2009), or are colonial breeders (Calabuig *et al.*, 2008). Targeting such species makes the studies logistically and financially more viable (Clarke, 1997). In this study, the integration of data on natal dispersal with that on lifetime reproduction for a long-lived raptor over a large spatial scale, means that this thesis is distinctive in its field. The data chapters in this thesis follow two, broadly complementary themes: (1) enhancing field techniques for long-term raptor research (**Chapters 2 & 3**), and (2) understanding the factors influencing breeding success and management of the Peregrine Falcon (**Chapters 4 – 6**; Figure 1.5).

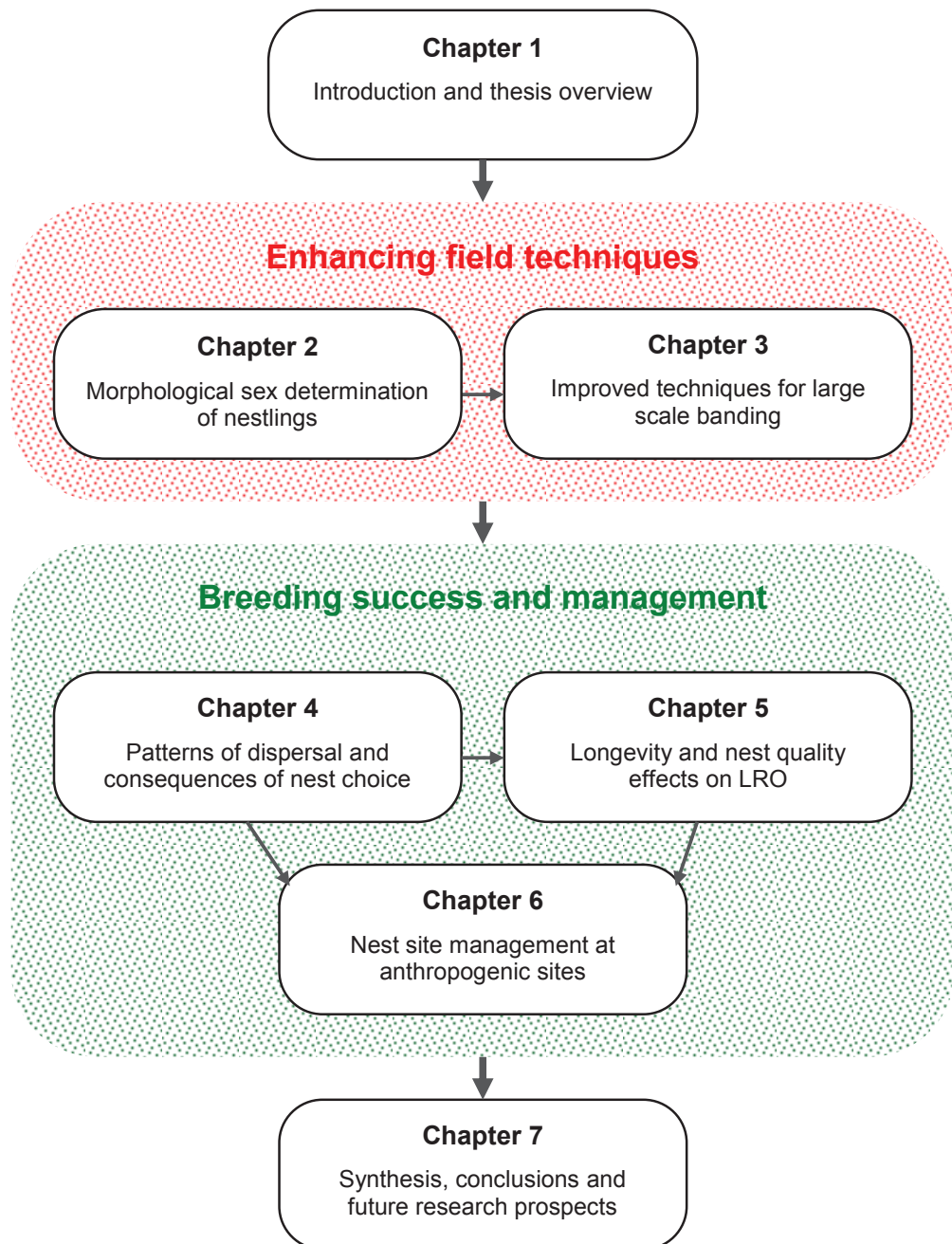


Figure 1.5 Overview of the structure of this thesis.

Because females require larger tarsus bands than males, it is critical to accurately determine nestling sex prior to banding. Prior to this study there was no field based technique available to reliably determine the sex of nestling Peregrine Falcons smaller than asymptotic weight (i.e. ≤ 10 days pre-fledging). **Chapter 2** details a field-based technique developed to accurately determine the sex of nestlings from the earliest safe

banding age. This approach was established using genetic sexing of individuals and validated in the field on a large sample set of nestlings. Through the implementation of this field-based method for sexing nestlings, it was possible to increase the window of opportunity in which safe banding of nestlings could occur. This was fundamental to being able to successfully monitor, and band nestlings in more nests each year.

This study was initiated to establish long-term monitoring of a species during its recovery from a human facilitated decline. The intent was to develop approaches and protocols to marking animals and banding as many individual nestlings in the population as possible. To facilitate the long-term viability of this research, field protocols and approaches needed to be developed that made the study more time and cost-effective. **Chapter 3** develops methods to further improve the efficiencies of conducting capture-mark-re-sight (CMR) studies at a large temporal and spatial scale. With the improved field techniques (from Chapters 2 & 3), it became possible to then investigate the ecology and conservation of breeding Peregrine Falcons.

The influence of biogeographic features on the distribution of the various nest types (i.e. cliff, building, stick nest and tree cavity) used by Peregrine Falcons in Victoria has been well described by Emison *et al.* (1997). Natural cliff nests tend to occur in the uplands (> 200 m above sea level) or along the coast. Tree nests, in stick nests and tree cavities, were considered restricted primarily to the distribution of River Red Gum (*Eucalyptus camaldulensis*) and Belah (*Casuarina pauper*) (Emison *et al.*, 1997). White and Jones (1977) first raised the question of whether populations were behaviourally isolated by natal nest site imprinting that subsequently influenced nest type selection. **Chapter 4** investigates patterns of dispersal; in particular, from fledge site to breeding site, to

determine to what degree nest site selection is influenced by natal site imprinting. This chapter then compares the lifetime reproductive consequences of dispersal distance and nest site choice.

Levels of nest site protection from the elements (referred to as nest quality) have been linked to variations in breeding success (Olsen & Olsen, 1989b; Emison *et al.*, 1993). Despite this, Peregrine Falcons show a strong lifetime fidelity to a mate and nest territory (Mooney & Brothers, 1993; Ratcliffe, 1993). **Chapter 5** seeks to establish the relative influence of attributes of nest sites and the surrounding landscape on the lifetime reproductive output of Peregrine Falcons. Specifically, this chapter seeks to determine whether site and landscape level factors influence lifetime reproductive output (LRO) beyond that which can be attributed to the number of years in which an animal attempts to breed.

Globally there has been a growing trend of Peregrine Falcons adopting anthropogenic structures for nesting (Bird *et al.*, 1996). The first nesting by the Peregrine Falcon in Victoria on anthropogenic structures was identified in 1981 (White *et al.*, 1981).

Chapter 6 compares the level of use and the breeding performance of natural versus anthropogenic derived nest sites. This chapter also then assesses the efficacy of nest site interventions for improving breeding performance of previously poorly performing nest sites.

Finally, **Chapter 7** presents a synthesis of the key findings of the preceding chapters and discusses the conservation prospects and management actions for the Peregrine Falcon in Victoria. Recommendations for future research are also presented.

2.

A morphological model for sexing nestling Peregrine Falcons (*Falco peregrinus macropus*) verified by genetic analysis

This chapter has been published as:

Hurley, V.G., Hogan, F., White, J.G. and Cooke, R., (2007). "A morphological model for sexing nestling Peregrine Falcons (*Falco peregrinus macropus*) verified by genetic analysis". *Wildlife Research* **34:1**, pp 54-58.



Three male nestling Peregrine Falcons banded at 20-22 days old. Otway coast, 2008.

"Nature does nothing needlessly."

Aristotle

2.1. Abstract

In Australia, adult Peregrine Falcons (*Falco peregrinus macropus*) have monotypic plumage and display strong reversed sexual dimorphism (RSD), with females significantly larger than males. RSD is measurable amongst nestlings in the latter stages of their development and can therefore be used to differentiate between sexes. In the early stages of development, however, nestlings cannot be sexed with any degree of certainty as morphological differentiation between the sexes is not well developed.

During this study we developed a model for sexing younger nestlings based on genetic analysis and morphometric data collected as part of a long-term banding study of this species. A discriminant function model based on morphological characteristics was developed for determining the sex of nestlings in the field and was shown to be 96.0% accurate. This predictive model was further tested against an independent morphometric data set taken from a second group of nestlings ($n = 131$). The model correctly allocated sex to 96.2% of this second group of nestlings. Sex can reliably be determined (98.6% accurate) for nestlings which have a wing length of 9cm or greater using this model.

Application of this model permits the banding of younger nestlings, and as such significantly increases the period of time over which banding can occur.

2.2. Introduction

The Peregrine Falcon (*Falco peregrinus*) has a wider geographic distribution than any other bird species (Kiff, 1988). This has led to morphological variation across the species' near global range (White & Boyce, 1988; Brown & Amadon, 1989), generating 20 subspecies based on distinct colouration and sizes (White, 1987). Many studies have been undertaken on Peregrine Falcons, particularly in relation to the impacts of pesticides such as DDT and Dieldrin (Porter *et al.*, 1987; Cade *et al.*, 1988). No studies to date, however, have developed accurate field based methods for sexing nestlings prior to attaining asymptotic weights (Nisbet, 1988; Olsen, 1995).

Within Australia, adult Peregrine Falcons (*Falco peregrinus macropus*) are considered monotypic in plumage (Marchant & Higgins, 1993; Olsen, 1995), however, they do display a high level of reversed sexual size dimorphism (RSD), with females significantly larger than males (Baker-Gabb, 1984). Male and female adults of this species display virtually no overlap between commonly measured morphometric characteristics such as weight, wing length and culmen length (Baker-Gabb, 1984). RSD is so significant in Peregrine Falcons that females warrant a larger sized leg band than males (Lowe, 1989).

RSD is also clearly measurable amongst nestlings in the latter stages of their 35-40 day nestling period (Olsen, 1995). Nestlings in the earlier stages of development, however, cannot be sexed with any level of certainty as RSD is not discernible. Banding nestlings of unknown gender poses a number of risks, with the most obvious relating to band size and subsequent injuries (Berggren & Low, 2004) or band loss if the incorrect sized band is applied (Emison & Bren, 1981).

To reduce the risk of birds being incorrectly sexed a field based model needs to be developed. This model needs to be accurate and easy to use to ensure that researchers adopt the model, especially when banding younger nestlings which display little or no size dimorphism. This study aims, therefore, to use genetically validated morphometric data to develop a model for determining the sex of nestling Peregrine Falcons and secondly, establish the minimum size/age at which this model can accurately be applied.

2.3. Methods

2.3.1. Study area

This study was conducted at 64 eyries covering ~118,577 km² (52.1%) of Victoria, Australia (2.1). Sites surveyed were from each of the five geographical regions of Victoria as described in Emison *et al.* (1997). The altitude of sites ranged from 18 to 528 m above sea level and rainfall varied from 250 to 2,600 mm per year. The average maximum winter (initiation of breeding) temperatures range from < 10° C at the higher elevations to 13° C along the coast and 17° C in the semi arid north-west.

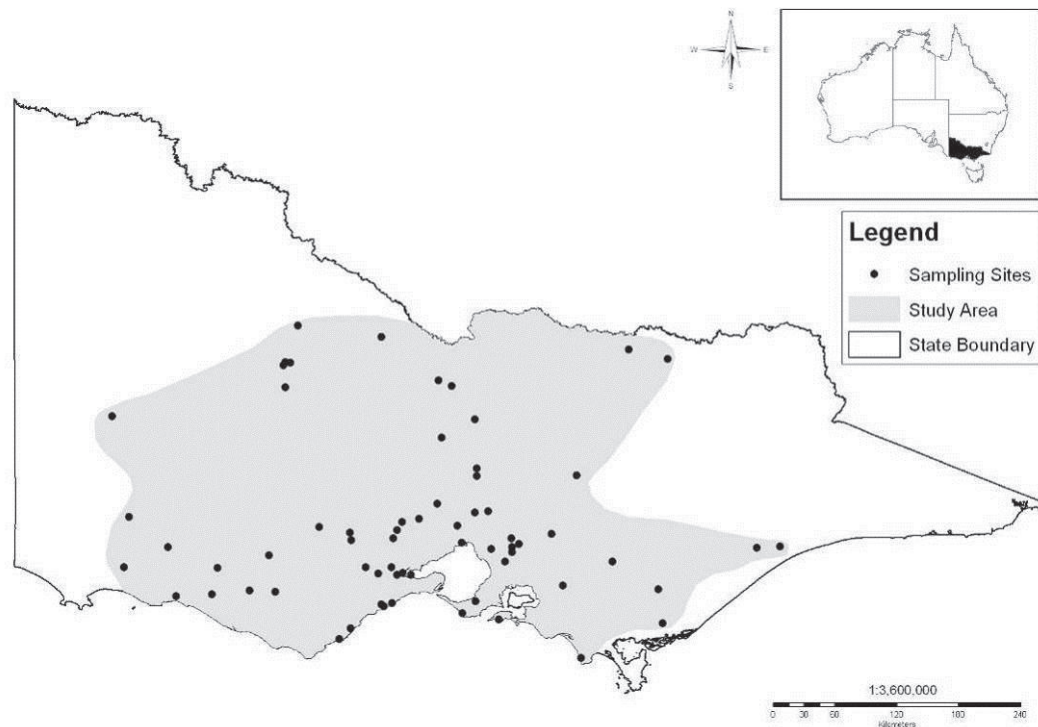


Figure 2.1 Study sites where DNA and morphometric data were collected (2003 and 2004). Shaded area represents study area. Black dots represent nest sample sites.

This study involved taking blood samples, morphometric measurements and leg banding 150 Peregrine Falcon nestlings prior to fledging. This was undertaken over a two year period (2003-2004). Nestlings sampled ranged in age from 10 to 43 days post hatching. This range in age was selected to generate nestling growth curves commencing at pre-banding age and ceasing at fledging. Nestlings younger than 10 days were excluded as they were considered too small to retain the recommended adult sized bands.

2.3.2. *Morphometric data collection*

Eleven morphometric features were measured for each nestling, however, only five of these were useful for determining gender. The five features measured were body mass, wing chord length, culmen chord length, tarsus length and head-bill length.

Body mass was measured using spring Pesola balances accurate to ± 1 g, ± 5 g and ± 10 g for nestlings weighing up to 600, 1,000 and over 1,000 g respectively (nestling body masses recorded ranged from 40 - 1,153 g).

Wing chord was taken as a straight line between the carpal joint and the tip of the 9th (longest) primary laid, not flattened or straightened along a stainless steel butted rule (Lowe, 1989). Wing length increases linearly with age, at a steady rate, consistent for both sexes regardless of nutritional status (Olsen & Olsen, 1987b). Wing chord length has therefore been utilized as a surrogate for absolute age in this study.

The culmen, tarsus and head measurements were each taken to the nearest 0.1 mm with Mitutoyo Digimatic (model number CD-6") digital callipers (± 0.01 mm, max. 150 mm).

Culmen chord was taken as the chord from the tip of the upper mandible to the front of the feather line toward the rear of the cere. Tarsus length was measured from the posterior notch between the tibia-fibula and the tarso-metatarsus to the anterior notch between the tarso-metatarsus and third toe joint. This measurement was taken by gently holding the tibia and tarsus in a right angle and holding the metatarsi flexed in a right angle. The combined head and bill measurement was taken from the tip of the upper mandible to the rear of the occipital condyles at the rear and base of the skull.

2.3.3. Molecular sexing

Blood samples were taken from the brachial vein of 150 nestlings using a 26-gauge syringe; 50 µL of whole blood was preserved in 99% ethanol (1 mL). Samples were then stored at -20° C until analysis. DNA was extracted from blood samples using Proteinase K digestion followed by extraction with ammonium acetate (Nicholls *et al.*, 2000). DNA was also extracted (ammonium acetate extraction) from muscle tissue of Peregrine Falcons of known sex via dissection (Museum of Victoria tissue collection). One male and two females were used to validate the genetic sexing protocol.

PCR amplicons were prepared using the 2550F and 2718R primers (Fridolfsson & Ellegren, 1999). These primers provide a universal method for molecular sexing of non-ratite birds which is based on the detection of a constant size difference between the chromo-helicase-DNA binding protein CHD1W and CHD1Z (Fridolfsson & Ellegren, 1999).

PCR reactions were performed in 12.5 µL volumes on a Palmer Cyclyer (Corbett Research) Thermal Cyclyer using 0.05 U/µl Hot Star Taq (Qiagen), 0.1 mM dNTP's, 1.5 mM MgCl₂ (Qiagen), 0.6 µM of primers 2550F (5'-GTTACTGATTCGTCT ACGAGA-3') and 2718R (5'- ATTGAAATGATCCAGTGCTTG-3') and 1µL DNA template. The thermal profile comprised an initial denaturing step of 95° C (15 min), followed by 40 cycles of 30 s denaturation at 95° C, 30 s annealing at 40° C, 30 s extension at 72° C, followed by a final extension 72° C (5 min). PCR products were separated on 1.2% agarose gels, run in standard TBE buffer and visualised by ethidium bromide staining

2.3.4. *Analysis and model development*

Discriminant function analysis was used to develop a model for predicting the sex of nestling Peregrine Falcons based on the morphometric data and genetically derived sexes. The final model was validated against the data used to derive the model and tested against a separate set of morphometric data from Peregrine Falcons of known sex which were not used to derive the model.

2.4. Results

2.4.1. *Molecular sexing*

The universal method for molecular sexing developed by Fridolfsson and Ellegren (1999) provides a robust and simple PCR protocol for sexing birds. The technique involves using a pair of highly conserved primers which consistently amplify a different-sized intron of CHD1 (W) and CHD1 (Z) in birds throughout the whole avian phylogeny, with the exception of ratites (Fridolfsson & Ellegren, 1999). Male birds can be recognised by a single fragment Z, while females show two fragments Z and W.

Preferential amplification of the shorter CHD1 (W) intron led to no detectable CHD1 (Z) production in females in the case of *F.p. macropus*. The single female product was due to CHD1 (W) amplification out competing that of the CHD1 (Z) when both templates are present as targets for PCR (Fridolfsson & Ellegren, 1999). Amplification of the CHD1 (W) and CHD1 (Z) genes revealed a size difference of 150 bp, which was clearly detectable when run on a 1.2% agarose gel and stained with ethidium bromide (Figure 2.2).

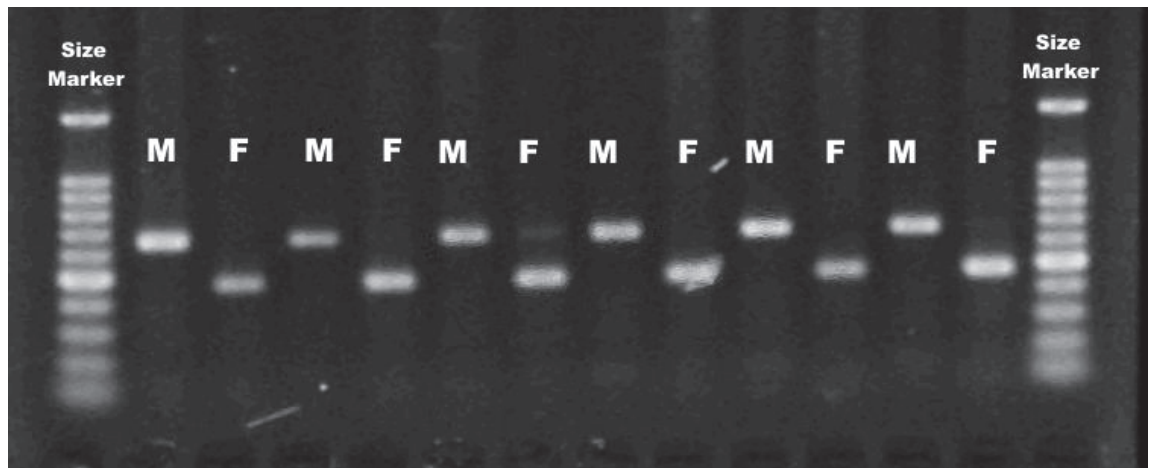


Figure 2.2 Molecular sexing of *Falco Peregrinus macropus* using PCR amplification of the CHD1 (W) and CHD1 (Z) genes separated on 1.2% agarose stained with ethidium bromide. The molecular weight standard is 100bp ladder (promega).

The molecular sexing technique accurately sexed all three museum samples. This technique was then used to sex the blood samples taken from Peregrine Falcon nestlings and the results found that of the 150 nestlings sampled and tested 79 were female and 71 were male.

2.4.2. Model development

Morphometric data from the 79 female and 71 male Peregrine Falcon nestlings that were sexed using genetic techniques were used to develop a predictive model for determining sex using discriminant function analysis. The morphometric measurements used in the model were wing chord ($\log_{10}$ cm), weight ($\log_{10}$ g), tarsus length (mm), head plus bill length (mm) and culmen chord (mm). These variables were selected because they are frequently measured by field researchers (Olendorf, 1972; Arroyo *et al.*, 2000; Balbontín *et al.*, 2001) and they are likely to differ between sexes (Baker-Gabb, 1984; Olsen, 1995). Overall, body mass (weight), tarsus length, head plus bill length and culmen chord length all differed significantly between the sexes, with nestling females tending to have larger

measurements than males of the same age (Table 2.1). Wing length did not differ significantly between the sexes (Table 2.1), however, it was maintained in the model as it is an indicator of and is directly proportional to the age of the nestlings (Olsen & Olsen, 1987b; Olsen, 1995).

Table 2.1 Morphometric characters and total body mass (means $\pm$ 1 s.d.) for nestling Peregrine Falcons, and statistical comparisons between sexes. $n = 150$ (71 ♂, 79 ♀).

Character	female	male	t	P
Wing chord ($\log_{10}$ cm)	1.16 $\pm$ 0.14	1.13 $\pm$ 0.15	1.38	0.171
Body weight ($\log_{10}$ g)	2.86 $\pm$ 0.09	2.73 $\pm$ 0.09	8.90	<0.001
Tarsus length (mm)	48.12 $\pm$ 3.60	43.22 $\pm$ 3.22	8.74	<0.001
Head+bill length (mm)	63.15 $\pm$ 4.42	58.59 $\pm$ 3.78	6.76	<0.001
Culmen chord (mm)	24.60 $\pm$ 1.71	22.15 $\pm$ 1.47	9.38	<0.001

The model discriminated between male and female groupings of Peregrine Falcons (Pillai's trace = 0.750, $df = 5, 144$, F-Ratio = 86.519, $P < 0.001$). The mean discriminant score for males was -1.791 (s.e. = 0.107) and for females was 1.657 (s.e. = 0.121) (Figure 2.3). The function that best discriminated between male and female Peregrine Falcon nestlings was:

$$D_i = -39.930 - 16.830 (\text{wing chord } (\log_{10} \text{ cm})) + 12.128 (\text{weight } (\log_{10} \text{ g})) + 0.124 (\text{head+bill length (mm)}) + 0.130 (\text{tarsus length (mm)}) + 0.502 (\text{culmen chord (mm)})$$

Scores greater than zero were assigned as females and scores less than zero were allocated as males (Figure 2.3).

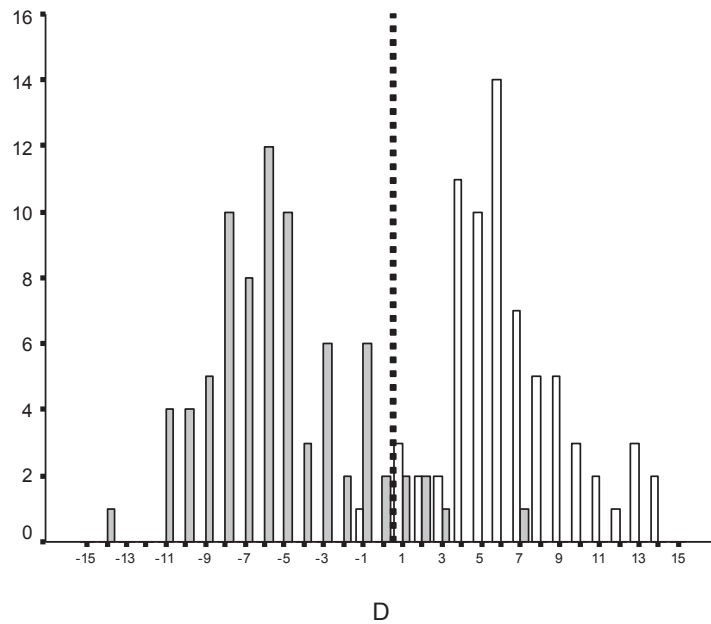


Figure 2.3 Discriminant scores for male and female Peregrine Falcon *F.p. macropus* nestlings. Grey bars represent males and white bars represent females as determined by genetic analysis (71♂, 79♀). The reference line is at zero to indicate the pivot point between male and female classification.

2.4.3. Validation of model

The above formula was tested on 150 birds that were sexed by molecular techniques and used in the original model development. Overall, the model was able to correctly allocate the sex of 96.2% of this sample of birds (Figure 2.4). Applying the model to females with wing chord lengths less than 9 cm was extremely inefficient with only 20% (1 in 5 birds) correctly identified as a female. Females over 9 cm in wing length were correctly allocated 98.6% (73/74) of the time. Overall, the model worked extremely well for males with 98.6% (70/71) of all males correctly sexed (Figure 2.4).

This model was further tested by applying it to 131 birds (66 females and 65 males) which had their sex confirmed by band recoveries later in life (via post-mortem of

individuals recovered injured, deceased or observed as breeding adults that had been banded and measured as nestlings). The model correctly sexed 96.2% (126/131) of these birds. Overall the model was 98.5% (64/65) accurate for males and 93.9% (62/66) accurate for females. There was only one female with a wing length less than 9 cm, which was incorrectly classified by the model. If this bird is excluded from the results females with a wing length greater than 9 cm were correctly classified 95.4% (63/66) of the time.

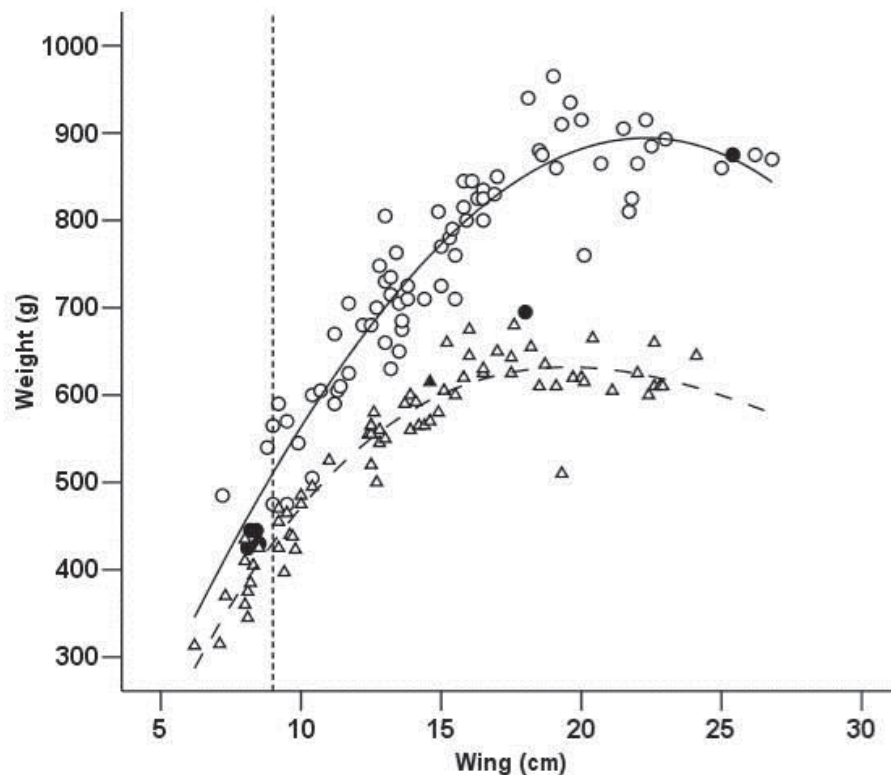


Figure 2.4 Relationship between wing chord length and body mass in nestling Peregrine Falcons *F. p. macropus* as sexed by genetic analysis. Triangles represent males and circles represent females. Open symbols represent correct classification by the model whereas solid symbols represent incorrect classification. The vertical dotted line represents a wing length of 9 cm. The solid curved line represents cubic regression model of nestling growth for females (using data from open circles). The lower dotted curved line represents the male growth cubic regression using data from open triangles.

2.5. Discussion

Correctly identifying the sex of a raptor nestling is an essential component of any banding project and especially with dimorphic species where band sizes differ between the sexes. This is often a difficult task as younger nestlings show very limited, if any, sexual size dimorphism. During this study we successfully developed a field model to reliably sex nestling Peregrine Falcons. This model has been genetically validated and correctly sexed 96.2% of field samples used.

Previous Australian studies on Peregrine Falcon nestlings have relied on determining sex with older nestlings (i.e. larger individuals) as RSD is more pronounced in larger nestlings where sex can be determined through morphometric features such as body weight or tarsus length compared to wing length (Emison & Bren, 1981; Olsen *et al.*, 1982; Olsen & Cockburn, 1991; Mooney & Brothers, 1993).

Wing length is directly proportional to age in nestling diurnal raptor species and formulae have been developed predicting age on wing length for nine raptor species in Australia (Olsen & Olsen, 1987b). As egg hatching is rarely monitored during most raptor banding studies, wing length can be used as a surrogate for the age (in days since hatching) of raptor nestlings. Our study set out to determine the minimum age (wing length) at which nestlings could be sexed in order to increase the number of days available for banding prior to fledging. The model developed here predicted sex most accurately when nestlings had a wing length of 9 cm or greater. When applied to the formula developed by Olsen and Olsen (1987b) this translates to 15 days post hatching and allows for 20 days or 63% of the nestling period to accurately sex and band Peregrine Falcon nestlings at each nest.

Most studies on dimorphic raptors rely on morphometric measurements, in particular weight and wing length of adults and free flying juveniles, to accurately determine sex (Baker-Gabb, 1984; Hartley & Mundy, 2003; Delgado & Penteriani, 2004). The use of a single feature, however, has been found to provide limited accuracy for some species even amongst adults, as was reported with footpad length in Northern spotted owls (*Strix occidentalis caurina*) (Fleming *et al.*, 1991). Further, the use of a single feature such as wing chord alone has been challenged on statistical grounds and the degree of overlap of this feature between the sexes of adult saw-whet owls (*Aegolius acadicus*) (Mueller, 1990). Although these features may become apparent in older nestlings, they are extremely difficult to distinguish in very young nestlings. As a result, most studies attempting to sex nestling raptors have relied on using morphometric measurements of older nestlings approaching fledging. These were successfully developed for nestling bald eagles (*Haliaeetus leucocephalus*) (Bortolotti, 1984a, b), Brown Falcons (*Falco berigora*) (McDonald, 2003), short-eared owls (*Asio flammeus*) (Arroyo *et al.*, 2000) and brown goshawks (*Accipiter fasciatus*) (Olsen *et al.*, 1982).

(Bortolotti, 1984b) was able to allocate the sex of nestling bald-eagles using size measurements (foot-pad length and bill depth) at 51.2% of nestling period when growth was almost complete. Arroyo *et al.* (2000) in their study on the dimorphic short-eared owl were able to sex nestlings ($n = 16$) on plumage features when the nestlings reached 12 days of age. The nestling period for this species is 30 days and therefore sex could be correctly assigned after 40% of the nestling period. A study on the growth of nestling brown goshawks found weight plotted against age, derived from wing length, showed a clear size separation (not genetically tested) amongst nestlings from 20 days of age or by as late as 65.6% of the nestling period (Olsen *et al.*, 1982). Our study on Peregrine

Falcons was able to predict the sex of nestlings at 36% of the nestling period. Correctly sexing raptor nestlings at 36% of the nestling period is a vast improvement on past studies as this provides a much greater time period to band nestlings with confidence.

3.

Techniques for optimising long-term, large-scale capture-mark-re-sighting raptor studies: Climb hard, band fast.

This chapter has been published as:

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The author ascending a coastal cliff.
(Photo by M. MacKinnon ©)

"To band a bird is to hold a ticket in a great lottery."

Aldo Leopold



Banding on top of a petro-chemical plant, 2006.

3.1. Abstract

Context. Efficiency of large-scale capture–mark–recapture (CMR) studies can be improved by developing accurate methods for predicting the window of opportunity in which banding can occur.

Aims. This research aimed to investigate potential efficiency improvements in a long-term CMR raptor study. The research focused on (1) developing selection processes for adopting CMR protocols; (2) testing methods for increasing the number of nestlings successfully banded and (3) assessing the efficacy of visual identification (VID) bands for collecting re-sight data.

Methods. Ten selection criteria were developed into a robust CMR-technique selection process and used to assess marking techniques commonly applied to birds. Optimising banding effort by predicting banding dates using two different techniques *a priori* and *a posteriori* were tested against a traditional approach to the timing of banding. The cost (in time) to collect re-sight data at an active nest site was also measured.

Key results. The CMR selection criteria and parameters provided a transparent selection process and scored metal VID bands the highest for the study design. This provided individual recognition of marked birds up to the expected life-span of 14 years. Both techniques for predicting banding dates improved the proportion of whole clutches banded by 40%. The average time to identify both Peregrine Falcon adults of a breeding pair wearing VID bands was 30 min.

Conclusions. The two methods described here for predicting preferred banding dates are of particular value as efficient approaches to banding large numbers of nestlings are key to the success of CMR studies. All of the methods developed in this research can be applied to CMR studies of almost any bird species with a predictable seasonal breeding system.

Implications. Optimisation and cost effectiveness of CMR studies for seasonal breeding birds can be significantly improved by accurately predicting the window of opportunity in which banding of nestlings can be carried out, and also utilising VID colour bands for rapid collection of recapture data.

3.2. Introduction

Longitudinal studies are critical for increasing knowledge of ecological or evolutionary processes (Hobbie *et al.*, 2003; Robertson *et al.*, 2012). Whether it be charting the levels of carbon dioxide in the atmosphere (Keeling, 1998), assessing change in ecological communities through time (Nichols & Williams, 2006; Sinclair *et al.*, 2007) or collecting data on lifetime reproductive success (hereafter LRS; (Newton, 1989; Brommer *et al.*, 2002), longitudinal studies provide more robust datasets than do space-for-time substitution studies (Clutton-Brock & Sheldon, 2010). The importance of improving the quality and efficiency of long-term studies has been recognised by numerous authors, with three key areas of focus being improved monitoring design (Black & Groombridge, 2010; Lindenmayer *et al.*, 2012), more efficient (Nichols & Williams, 2006) and targeted monitoring (McDonald-Madden *et al.*, 2010) and greater rigor in archiving published data (Whitlock, 2011). Inherent, if not explicitly stated, is the requirement for greater efficiency in data collection to make continuing long-term monitoring sustainable.

An important area of faunal population research dependant on longitudinal monitoring is the estimation of individual fitness (Brommer *et al.*, 2002). The collection of data to determine LRS requires knowledge of breeding success of marked individuals throughout their entire life and broad-scale surveying for their offspring, to determine survivorship and subsequent breeding (Newton, 1989). Although conducting LRS studies overcomes many of the limitations in short-term cross-sectional studies (Clutton-Brock & Sheldon, 2010), the logistical and budgetary constraints seldom align with the timeframes for undertaking such research (Lindenmayer *et al.*, 2012). The challenges associated with establishing and maintaining long-term research have led to a distinct bias, particularly in the southern hemisphere, toward intensive research on birds that

breed colonially or co-operatively compared with non-passerines such as raptors (Clarke, 1997). This is, no doubt, partly because of raptor's tendency to live longer and breed at lower densities than do lower-order consumers (Newton, 2003; Korpimäki *et al.*, 2005) and often breed in difficult-to-access nests in remote locations (Bednarz, 2007). To overcome these challenges, techniques for improving efficiencies in the planning and conduct of fieldwork are essential to ensure that long-term raptor-research projects remain viable.

There is a variety of CMR techniques available for collecting LRS data (Silvy *et al.*, 2012). For the purpose of the present paper, CMR is defined as follows: animals are marked as nestlings (i.e. still in the nest) and re-identified later in life without physically re-trapping. Animals re-encountered are therefore of known age and origin. In CMR studies where molecular techniques are not being employed, and individuals are difficult to distinguish, it is vital that the study animals and their offspring are marked for future identification. When animals are marked, it is critical that the markers remain attached and readable for the lifespan of the animal, and have no impact on their behaviour (Newton, 2001). Selecting the most appropriate method for a large-scale and long-term CMR study involves balancing competing financial, technical (Thomas *et al.*, 2011), operational (Silvy *et al.*, 2012) and ethical and or legal (Boal *et al.*, 2010) constraints. In addition, consideration must also be given to public concerns that can lead to political pressure influencing whether government agencies will allow the use of certain marking techniques (Varland *et al.*, 2007; Boal *et al.*, 2010).

Taking into account these requirements, there is a diverse array of marking techniques available (Silvy *et al.*, 2012), ranging from passive integrated transponder (PIT) tags

(Smith & McGrady, 2009), and non-invasive DNA sampling (Waits & Paetkau, 2005; Hogan *et al.*, 2008), to the more traditional methods such as leg bands (Varland *et al.*, 2007). Given the range of markers available, careful planning is essential to ensure that the CMR protocol selected is the most appropriate and efficient for the species and questions being investigated (Garton *et al.*, 2012; Lindenmayer *et al.*, 2012).

After selecting a CMR protocol, the next challenge is obtaining sufficient sample sizes to ensure that they are representative of the study population (Bednarz, 2007). In LRS studies, it is vital to collect full sets of LRS data (i.e. marking all young produced from marked individuals) without any gaps in the data (Newton, 1989). When investigating birds, this is most efficiently undertaken on nestlings old enough to carry the marker but not yet fledged from the nest (Silvy *et al.*, 2005; Garton *et al.*, 2012). This presents a very small window of opportunity at each nest (Bednarz, 2007) and, in seasonal breeding species, this window will overlap for many pairs. Consequently, the timing of field surveys to mark all nestlings at every nest, over several years, can be extremely challenging, especially when breeding pairs are spread over large geographic areas. In these situations, field methods that require multiple site visits are rarely sustainable and ideally a system is required whereby predictions can be made as to the most appropriate time to mark nestlings at each site.

Peregrine Falcons (*Falco peregrinus*) possess life-history traits suitable for longitudinal studies, including occupancy of traditional nest sites over many generations (Mooney & Brothers, 1993; Ratcliffe, 1993), high levels of mate fidelity (Mooney & Brothers, 1993; Olsen, 1995), nest-site fidelity (Mearns & Newton, 1984, 1988; Newton, 1989; Frank, 1994), vocal territorial defense (which assists in locating an active nest site) and a

predictable annual breeding season (Mooney & Brothers, 1993; Ratcliffe, 1993; Olsen, 1995). They are, however, a relatively long-lived species (15.3 years in Australia; (Environment Australia, 2012)), rendering the collection of complete LRS datasets more challenging. Also, in Victoria, Peregrine Falcons breed at low densities (mean distance between nests 16 km, range 5–36 km; (White *et al.*, 1981)) and the breeding season is reasonably short (Pruett-Jones *et al.*, 1981b), with 91% of clutches initiated between 17 August and 14 September, a span of 29 days ($n = 779$ breeding events between 1991 and 2010; V. G. Hurley, unpubl. data).

Few CMR raptor studies have reported on the approaches taken to increase the proportion of nestlings banded across large study areas (Mooney & Brothers, 1993; Tordoff & Redig, 1997; Restani & Mattox, 2000). This represents a significant knowledge gap for researchers establishing new long-term programmes. As part of a 20-year LRS study on Australian Peregrine Falcons (referred to as the Victorian Peregrine Project (VPP) in the present paper), methods to improve the efficiencies of undertaking a CMR study on a large number of active eyries were evaluated. Three key areas of the VPP planning and operations were examined and improvements implemented. These key areas, in the order in which they occur in the development and implementation of any CMR study, were as follows: (1) development of selection criteria whereby the most appropriate marking technique for large-scale, long-term mark–re-encounter research could be determined, (2) development of techniques to increase the number of breeding events where all nestlings are marked and (3) measuring the efficiency (time taken) to collect re-sight data.

The present study was privy to the original field notes of an earlier long-term banding study (Emison & Bren, 1981) of Peregrine Falcons in Victoria (W. B. Emison, deceased.). From these notes, the overall success rate of banding complete broods of nestlings was 67.4% ($n = 253$ monitored breeding attempts between 1975 and 1985). This figure was used as a benchmark for what we termed a ‘traditional’ approach to the timing of banding nestlings. Our aim was to determine the best method for improving on this benchmark figure for banding complete broods of Peregrine Falcons at a large number of eyries across a large geographic area in a long-term study.

3.3. Methods

3.3.1. Study Area

The present study was undertaken in Victoria, south-eastern Australia, and covered an area of ~226, 923 km². The geographic range of the study area included a latitudinal span of four degrees north to south (from 34°30’S to 38°45’S) and seven degrees of longitude west to east (from 141°E to 148°E). In total, 188 eyries were monitored across Victoria (Figure 3.1) with maximum distances between monitored eyries being 589 km west to east and 521 km north to south.

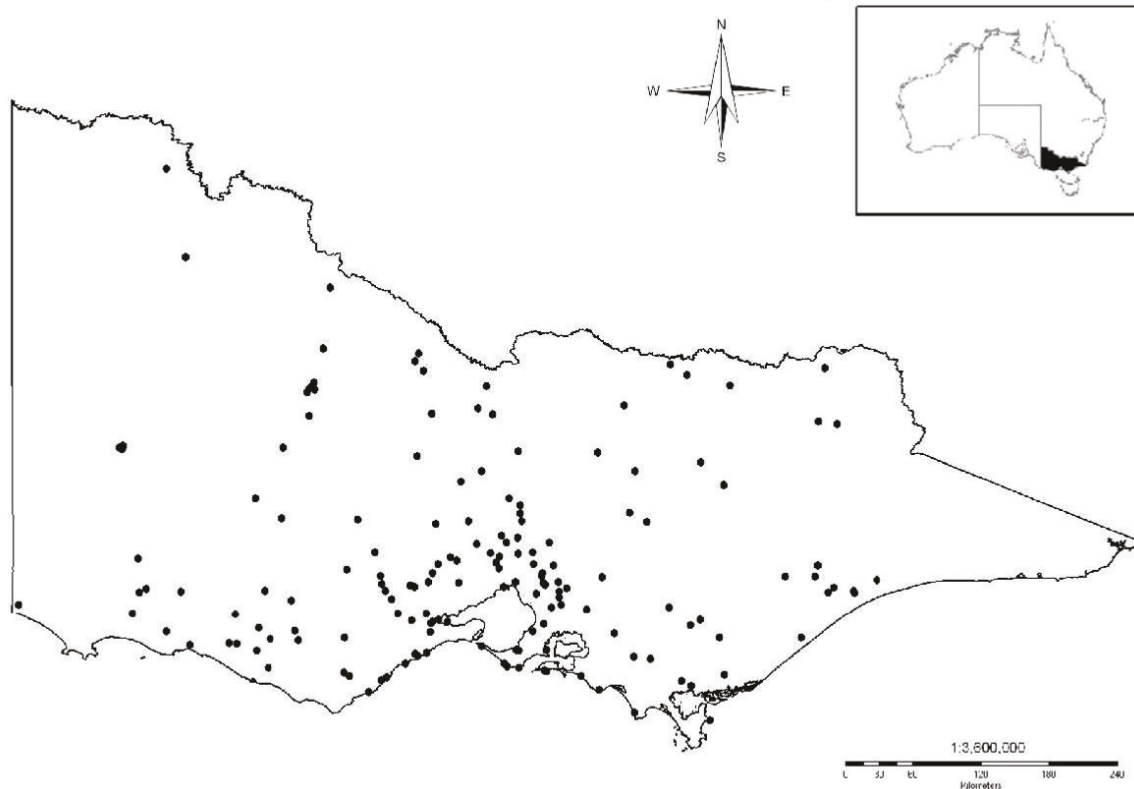


Figure 3.1 Map of Victoria showing the locations of Peregrine Falcon nests (•). Each nest was monitored at least once during this study between 1991 and 2010 ($n = 188$ sites).

3.3.2. *Determining the most appropriate CMR technique*

The six most commonly used marking techniques for raptors (Bednarz, 2007) were assessed against each of the 10 selection criteria and scored either one or zero, with one being suitable and zero unsuitable (Table 3.1). Marking techniques that failed any of the selection criteria were deemed unsuitable, with the exception of ‘mark redundancies’ (Criterion 3), which was not possible for all marking techniques. A graded score for each selection criterion was not implemented because it added a level of complexity that did not improve the robustness of the selection process. No radio-transmitter or satellite locator systems were assessed because these techniques were excluded because of the cost and the requirement for physical recapture of the animal for removal of the tracking device.

Half of the six CMR marking techniques failed three or more of the selection criteria. Metal VID bands ranked highest, fulfilling all 10 of the selection criteria. The second-highest ranked technique was coloured plastic bands. The durability and colourfastness of plastic bands has, however, been found to be inadequate from reports on other studies of this species (Emison & Bren, 1981; Mooney & Brothers, 1993) and many other bird species, including bald eagles, *Haliaeetus leucocephalus* (McCulloch, 1990), fulmars, *Fulmarus g. glacialis* (Anderson, 1980), welcome swallows, *Hirundo neoxena* (Park, 1981), and a range of 60 passerine species in Hawaii (Lindsey *et al.*, 1995).

Table 3.1 These 10 selection criteria were used to assess six capture–mark–recapture (CMR) techniques listed as follows: VID = visual-identification metal band; plastic = coloured plastic band (may include alpha and or numeric characters); metal = national banding-scheme metal band; PIT = passive integrated transponder (tag); wing = patagial (wing) tag; and DNA = molecular analysis using DNA from caste feathers from adults to be compared with whole blood samples taken from nestlings. Each marking technique was assessed and scored against each selection criterion, with 1 = yes, 0 = no. The total selection score was used to rank the CMR protocols

Selection Criteria	Parameters	VID	Plastic	PIT	Metal	Wing	DNA
1 Longevity	Durability of mark and VID features (up to 15 years)	1	0	1	1	0	1
2 Individual recognition	Individual recognition per mark (for 2,000+ individuals)	1	1	1	1	1	1
3 Mark redundancies	Partial colour and or code provides useable data	1	1	1	0	1	1
4 Remote readability	Individual identification in the field without the need for re-trapping	1	1	1	0	1	1
5 Expense	Cost per mark (for 1,000s of marks)	1	1	1	1	1	0
6 Application	Ease of application in the field	1	1	1	1	0	0
7 Animal welfare	No negative impact on the animal	1	1	1	1	0	1
8 Politics	Acceptable to ethics committee	1	1	1	1	0	1
9 Monitoring - cost	Cost per datum	1	1	0	1	1	0
10 Monitoring - time	Collection time per datum	1	1	0	0	1	0
Selection score:		10	9	8	7	6	6

3.3.3. Preferred marking technique

Peregrine Falcons were banded as nestlings, using two different types of metal leg bands (cohort bands and VID bands) attached to the tarsus, one on each leg (Figure 3.2).

Cohort bands are conventional open- or split-ring (Bird & Bildstein, 2007) stainless-steel bands issued by the Australian Bird and Bat Banding Schemes office (ABBBS) (Lowe, 1989) (Figure 3.2A). These bands have a unique, eight-digit identifier code which is extremely difficult to read on birds in the field at distances greater than 20 m. To make these bands more effective for use on Peregrine Falcons, we powder-coated each band with a single colour to represent the year of banding, which for nestlings equals the year of hatching and fledging (or the cohort year). Eight distinguishable colours were used (singularly) on these bands. In order of preference for readability these colours were blue, black, white, red, dark green, light green, pink and orange. Powder coating of these coloured bands to identify cohorts commenced in 1991, and to the best of our knowledge, this is the first time powder coating has been used on stainless-steel bands for use on wild birds. This is in essence a modification of the metal-marking technique listed in (Table 3.1). The colouring allows these bands to be used for visual identification.

VID bands are open aluminium bands made by Acraft Sign and Nameplates, Edmonton, Alberta, Canada (Figure 3.2B). Up to two colours anodised per band were used and the colours were a combination of black, dark blue, dark green, red, orange and mauve (purple). This style of band has been made to order for use on Peregrine Falcons in Australia and variations have been used on a wide range of species from the small (45 g) orange-bellied parrot, *Neophema chrysogaster*, in Australia (Holdsworth *et al.*, 2011) to the large (≤ 6.8 kg) harpy eagle, *Harpia harpyja*, in Panama and Belise (Campbell-

Thompson *et al.*, 2012). Each VID band had two alpha and or numeric characters routed into the metal surface, one above the other three times around the band. The characters appeared silver or white against the darker anodised colours when viewed with a spotting scope. Each VID-band colour combination provided for 2,983 unique dual alpha and or numeric codes. In Sweden, it has been reported that VID-band colours can be distinguished on Peregrine Falcons at a distance up to 300 m and the VID characters read up to 200 m (Lindberg, 2009).

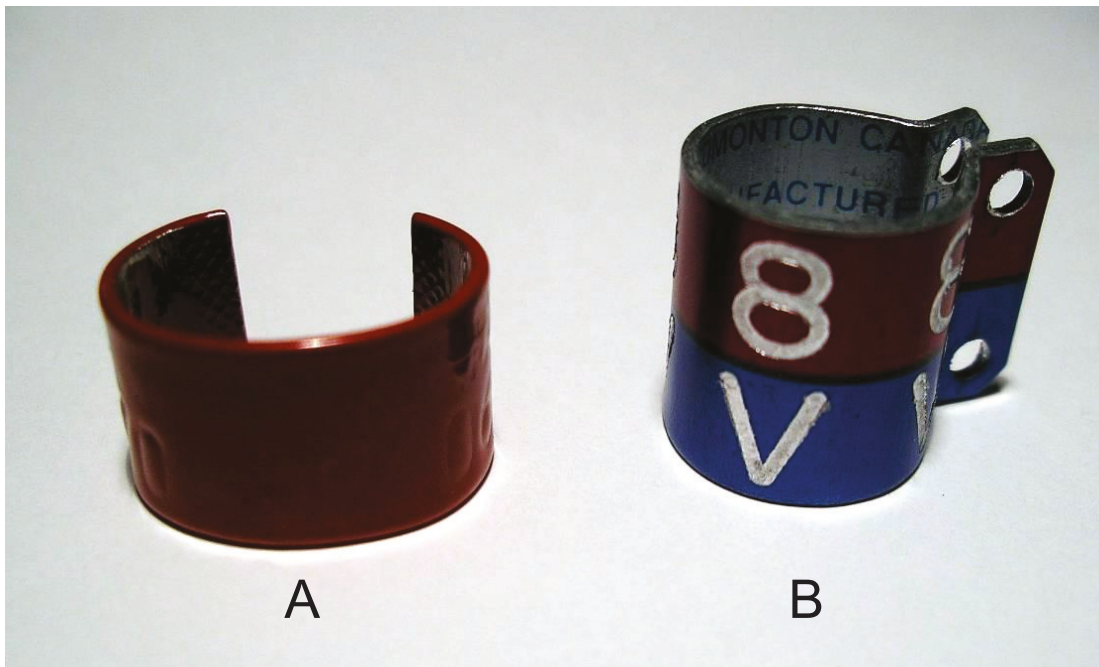


Figure 3.2 Two coloured metal band types used on Peregrine Falcons. A = cohort band issued by the national banding authority (ABBBS) and is made from stainless steel and was commercially powder-coated red. B = the VID band purchased from Acraft©, Canada.

Placing a metal band on each leg ensured that only one leg had to be seen to determine whether the adult was banded (Howitz, 1981). VID bands were placed on the left leg of females and the right leg of males, allowing sex and age to be determined even if the

individual could not be identified via the VID-readable characters. The trouser feathers of Peregrine Falcons hang down and can obscure the top portion of the VID bands. This makes the lower character more likely to be read first. By keeping the top character constant as the lower characters changed between bands in alpha and or numeric sequence reduced the range of characters to identify for each cohort of banded Peregrine Falcons. These are the redundancies referred to in Criterion 3 (table 3.1).

3.3.4. *Efficient broad scale marking*

Having selected the CMR technique, the next step was to determine how to mark the maximum number of nestlings at as many sites per year as possible. This became critical as banded birds entered the breeding population over time, as it was imperative to the success of the LRS study that all nestlings produced throughout each individual breeding-adult's lifetime were banded (Newton, 1989; Clutton-Brock & Sheldon, 2010).

Banding was targeted at nestlings of ~25 days post-hatching because the reversed sexual dimorphism is well developed in this species by this age and allows accurate determination of sex (Hurley *et al.*, 2007). Morphometric measurements of nestlings were 98.6% accurate in sex determination of nestlings from as young as 15 days post-hatching (Hurley *et al.*, 2007). Additionally, wing chord length (measured to ± 1 mm with a flat rule) allows age estimation as it is directly proportional to the age of the nestling (Olsen & Olsen, 1987b).

3.3.5. *Predicting banding dates within the safe banding period*

When attempting to band nestlings, they must be large enough to retain a leg band but not so large that they are already flying or at risk of prematurely fledging (Bednarz, 2007). Timing banding trips to coincide with the window of opportunity between these

situations is critical to the success of large-scale banding for CMR studies. The first task was determining how many days this window of opportunity was for Peregrine Falcons. As mentioned above, nestlings could be sexed and banded from as young as 15 days post-hatching and are known to fledge at ~35 days (for males) and 42 days (for females) (Olsen & Olsen, 1987b). Although it is technically possible to band nestlings just before fledging, because of the risk of premature fledging causing death or injury to the nestlings, we recommend not banding males older than 30 days or females older than 37 days. By subtracting the minimum banding age (15 days) from each of these maxima ages provided a banding window of 15 days for males and 22 days for females. Because Peregrine Falcon clutches have asynchronous hatching, which leads to differences in the age of the nestlings in each brood (Olsen, 1982), some caution must be used when scheduling banding so that all nestlings can be banded. We investigated the age difference of 39 broods containing four nestlings (maximum clutch size) by using wing length as per Olsen and Olsen (1987b) and found that the modal age difference between the first and last hatched nestlings was 4 days (28% of $n = 39$ clutches, range 2–12 days, mean = 5.2, median = 5, s.d. ± 2.19). Taking the median of a 5 day age difference within broods of four nestlings, the banding window of opportunity is only 10 days in an all-male brood and 17 days in an all-female brood. The operational focus of the field work was to band complete broods of nestlings at as many eyries as possible. To maximise these banding outputs, within the above constraints, we allowed no more than a 10 day window of opportunity for banding at each eyrie.

3.3.5.1. Method A – traditional

A traditional approach to banding (Emison & Bren, 1981) involved multiple *ad hoc* visits to active eyries to observe the size and feather development of nestlings and band at or post-asymptotic development (≥ 30 days (Boulet *et al.*, 2001)) to aid in gender

determination. Another study of this species (Restani & Mattox, 2000) used a photographic guide for ageing nestling prairie falcons, *Falco mexicanus* (Moritsch, 1983), to assist in scheduling banding of nestling Peregrine Falcons at 15–20 days post-hatching in Greenland. Neither study reported using *a priori* knowledge to predict the date of the first monitoring visit to each site. In contrast to the traditional approach to banding, accurately predicting the phenology (e.g. timing; Moussus *et al.* (2009) of egg laying or hatching dates provides the opportunity to select the optimal date for banding nestlings. The following two methods provided such opportunities.

3.3.5.2. Method B – *a priori* aging eggs

An *a priori* approach to predicting banding dates was developed by ageing eggs to calculate hatch dates and, from these, preferred banding dates later in the same season. This is possible because bird eggs lose weight at a constant rate throughout the incubation period (Hoyt, 1976, 1979). This weight loss is primarily via water evaporation through the egg shell. The rate of weight loss and the total percentage weight loss varies among species, but is constant within a species (Saunders & Smith, 1981; Burnham, 1983; Olsen, 1997). For Peregrine Falcons the net egg-weight loss from laying to hatching has been calculated as 18% (Burnham *et al.*, 1988) for the incubation period of 33 days (Saunders *et al.*, 1984; Burnham *et al.*, 1988). Because the recommended age for banding nestling Peregrine Falcons is 25 days after hatching (Olsen & Olsen, 1987b). It was possible to measure eggs to calculate hatch dates and add 25 days to predict preferred banding dates for that site later in the same breeding season (Figure 3.3).

There were three key formulae to age eggs (Formulae 1–3, Figure 3.3), derived from other studies, and two additional formulae developed in the present study to calculate

preferred banding dates (Formulae 4, 5, Figure 3.3). Results from these formulae also provide clutch-initiation dates, the spread of egg laying dates and hatch order across the clutch. The process of predicting banding dates through egg measurements required a minimum of two site visits for the banding at each site, including one visit to weigh and measure the eggs and a second, some weeks later, to band the nestlings. During the first visit, we recorded the site name and date, and measured egg length and maximum width to the nearest 0.01 mm with digital Vernier callipers (Model CD-6', Mitutoyo Digimatic, Kawasaki, Kanagawa, Japan) and weighed eggs with a small battery-powered digital scales (accuracy 0.1 g).

- | | |
|--|-------------------------|
| 1. $W_{Lay} = (L \times B^2) \times K_w$ | (Hoyt, 1979) |
| 2. $W_{Hatch} = W_{Lay} \times 0.82$ | (Burnham, 1983) |
| 3. $Age_{Measure} = \frac{(W_{Lay} - W_{Measure})}{(W_{Lay} - W_{Hatch})} \times 33$ | (Saunders et al., 1984) |
| 4. $Date_{Hatch} = (Date_{Measure} - Age_{Measure}) + 33$ | |
| 5. $Date_{Band} = Date_{Hatch} + 25$ | |

Figure 3.3 Formulae for calculating the age of Peregrine Falcon eggs and then the preferred banding date when the nestling is 25 days post-hatching. W_{lay} = egg weight at laying, L = egg length, B = maximum egg width, $K_w = 0.0005474$, $W_{Measure}$ = egg weight on date of measurements, W_{Hatch} = egg hatch weight, $Age_{Measure}$ = egg age on date of measurements, $Date_{Hatch}$ = egg hatch date, $Date_{Measure}$ = date of egg measurements, $Date_{Band}$ = preferred banding date.

3.3.5.3. Method C – *a posteriori* breeding Phenology

Although Australian Peregrine Falcons have a restricted breeding season (Pruett-Jones *et al.*, 1981b), clutch-initiation dates are known to vary by latitude and mean September temperatures (Olsen, 1982). These variances may lead to local patterns in clutch-initiation dates that could assist in predicting site-based banding dates using *a posteriori* knowledge gained from the age of nestlings at banding in previous years. If successful, this process could remove the need for two site visits as required by the egg-measurement method (Method B), further optimising fieldwork effort.

Three years of nestling wing-chord measurements with banding dates were collated for several sites (Figure 3.4). These were converted to give an age for each nestling at banding, using the formula:

$$\text{Age (in days)} = \frac{(WL + 0.84)}{0.69},$$

where WL = wing-chord length (Olsen & Olsen, 1987b). Nestling age was subtracted from the date at banding, to give the date of hatching and, to this, 25 was added to give the preferred date of banding for each nestling. For each breeding event, the median preferred banding date was calculated for the brood and assigned to the eyrie for that breeding event (year). Preferred banding dates from the previous 3 years were collated and a single preferred banding date was assigned to the eyrie for the next season. Banding sites were then grouped by dates and geographic area to aid in field efficiency. If nestlings were successfully banded (and wing chord measured), these data were incorporated into the assessment process of the following year and the data from the oldest year were removed, to give a rolling 3 year sample for each future year (Figure 3.4).

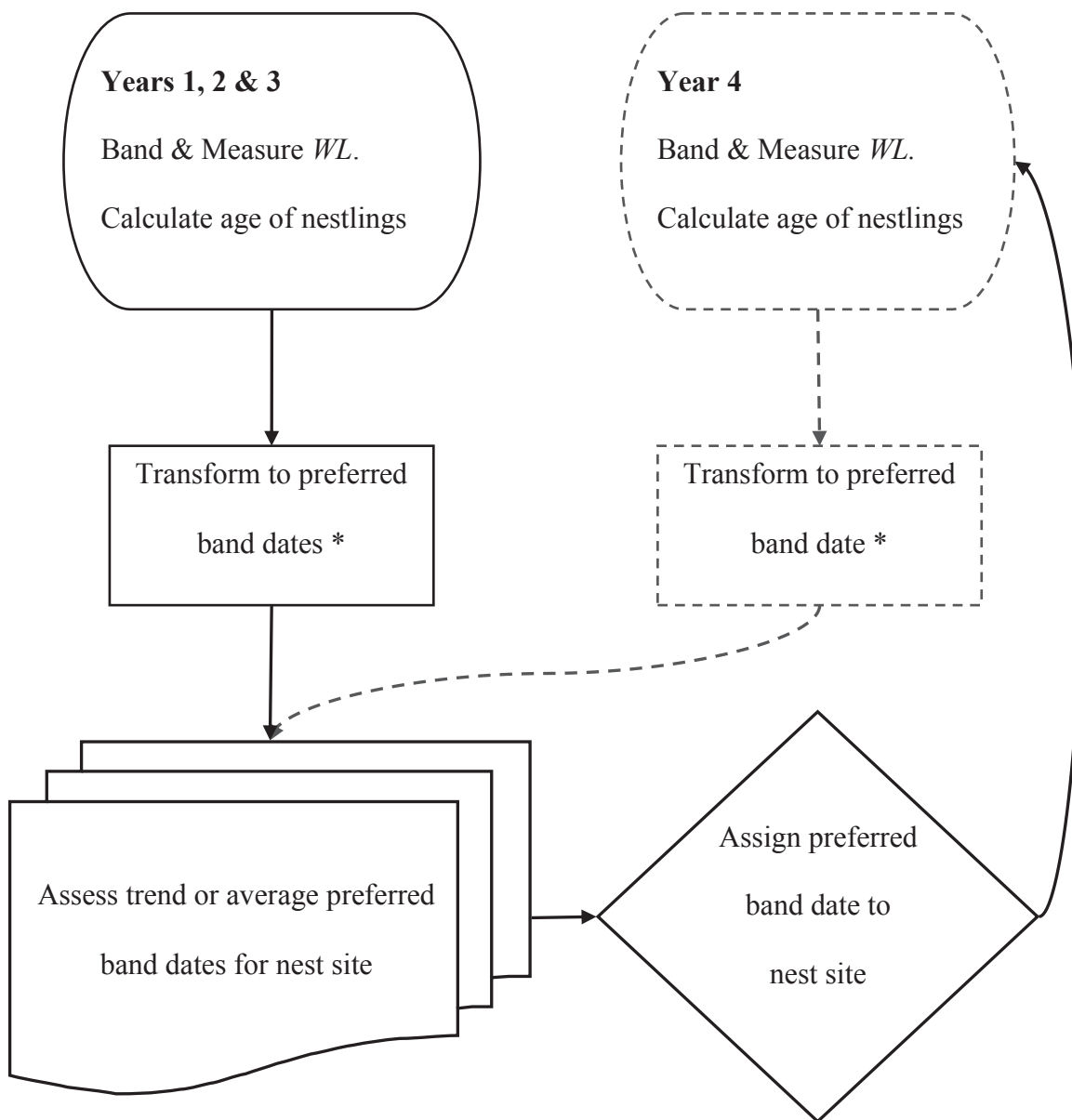


Figure 3.4 Schematic of predicting preferred banding dates at Peregrine Falcon nests.

WL = wing-chord length of the nestling. *Preferred band date for the nestling, at 25 days post-hatching.

3.3.6. 'Re-sight' data collection efficiency

Published quantitative data on the efficiency of collecting re-sighting data (i.e. time per successful re-trap or re-sight) are very limited, with some notable exceptions (Wiersma *et al.*, 2001; Bierregaard Jr. & Harrold, 2008). Therefore, the third aim of the present study was to quantify the time required to collect re-sighting data from VID bands as a benchmark for comparison with other CMR techniques. The total time taken to survey both adults at an active eyrie was recorded. The start time for each site survey was taken as the time the observer was in position and immediately before setting up the spotting scope. The completion of the survey was the time at which the observer had identified and recorded the details of both adults.

All re-sightings of breeding adult Peregrine Falcons at active eyries were made using a tripod mounted Leica Televid 77 spotting scope Vertrieb, Solms, Germany with a 1000-mm apochromatic lens and fitted with a $\times 20$ –60 zoom eye piece. Telescopes used had the eyepiece factory set at 45° to the plain of the objective lens. The adult birds were first viewed with a telescope or binoculars for the presence of bands. When bands were detected on either adult, the observations continued until all band colours on both legs and VID characters were identified.

3.3.7. Statistical analyses

All data were log (natural base) transformed to satisfy assumptions of normality and homogeneity of variances before analyses. Analyses were carried out using IBM SPSS Statistics 21 (IBM Corp. Released 2012. IBM SPSS Statistics for Windows, Version 21.0. Armonk, NY: IBM Corp). All data presented are untransformed for ease of interpretation.

3.4. Results

3.4.1. CMR – selection criteria

Assessing the six CMR techniques against the 10 selection criteria provided a robust and transparent method for selecting the most appropriate marking technique, which, in this case, was VID metal bands (Table 3.1). When assessing how the two different bands (VID and cohort) performed in terms of longevity, they ranked extremely well, with no band loss over the 20 year study period ($n = 570$ re-encounters of 277 individuals, ♂ 140, ♀ 137). More importantly, the bands appeared to cause no discernible injuries to any bird. The oldest bird re-encountered was 13 years and 9 months post-banding. This bird was recovered alive with a mild concussion and released the following day at the same coastal site at which it was encountered. The powder-coated dark green (mistletoe by Dulux© (www.Dulux.com.au)) on the cohort band was clearly identifiable. However, the VID-band colours (green over purple) had faded to such an extent that there was no evidence of either colour when inspecting the bands in the hand. The saline moist coastal air is very corrosive to aluminium and the thin anodised colour dye also breaks down under UV light. In contrast to this, four individuals (2 ♂, 2 ♀) were re-sighted at 11 years old (at non-coastal sites) as breeding adults and the colour on their VID bands, although faded, was still identifiable via telescope from a distance of ~100 m. Two adult females (8 years old and 12 years old) re-encountered had VID bands showing considerable fading, although still discernible. The most faded colours appeared to be purple, orange and green, whereas red, dark blue and black appeared to retain colour for longer. In summary, powder coating appeared to be more durable ≥ 14 years, whereas the durability of the anodising appeared to be less reliable, approaching 10 years in the field in Australian conditions.

The use of metal VID bands for a long-term CMR study was highly appropriate for Peregrine Falcons because of the relative ease of re-sighting and reading bands on their unfeathered tarsi. However, an alternative CMR technique may be required for other species where tarsus bands are not so visible, such as for eagles (i.e. *Aquila* spp., many owl species (i.e. *Bubo* spp. and *Ninox* spp.) and vultures (i.e. who defecate over their legs for thermo-regulation and so readily obscure bands). The accumulation of faeces between the band and tarsus has been shown to interfere with the health of the bird, making any tarsus bands an unacceptable marking method (Varland *et al.*, 2007). Species that periodically move to a new nest site will require additional early season survey time to be factored into each field season just to confirm the nest location each year.

3.4.2. Broad-scale marking

At 188 Peregrine Falcon eyries, a total of 1,444 potential breeding events was monitored during the 20-year study period (Table 3.2), which equated to an average of 72 eyries monitored per year. In total, 2,325 nestlings were banded from 1991 to 2010, averaging 116.5 nestlings per year. Banding of nestlings was successfully completed at an average of 48 breeding events per year. The targeted nestling age for banding was 25 days post-hatching and the median age of nestlings banded was 26.0 days (s.d. $\pm$ 6.6 days). Also of 2,325 nestlings banded over 968 breeding events, a total of 44 (1.9%) nestlings were found dead in the nest after banding and before fledging in 32 (3.3%) of breeding events. Although not critical to the present study, the causes of death before fledging were known in 63.4% of cases. In descending order they were infection from *Trichomoniasis* (38.5%), being illegally shot (26.9%), predation (predator unknown; 7.7%) and unintentional poisoning (3.8%). With such a low mortality rate between banding and fledging, the number banded was generally taken as the number fledged for the LRS study, except in cases where nestling mortality was detected in subsequent visits.

3.4.3. *Predicting banding dates*

Using the traditional method (Method A), 67.4% of complete broods were successfully banded during previous Victorian studies (Emison & Bren, 1981). Of the two methods developed in the present study to predict preferred banding dates, Method B, using *a priori* knowledge, resulted in 97.4% (75 of 77) complete broods being banded (Table 3.2). However, this method had a built-in disadvantage in that it required two eyrie visits for each breeding season (one to measure eggs and one to band nestlings). The second method (Method C), based on *a posteriori* knowledge, required only one site visit (to band) after collecting 3 years of breeding data and proved to be very successful, with complete broods being banded in 94.3% (893 of 947) of breeding events (Table 3.2). The combined result using both Methods B and C was a 94.5% success rate in banding complete broods. The application of these methods became critical to the successful broad-scale banding of an average of 116 Peregrine Falcon nestlings per year at an average of 51 eyries per year over 20 years by a single banding team.

3.4.4. *Cost-benefit comparison*

An average cost for a single nest site visit (AU\$130) was determined by taking the annual project budget for a single year (2009) and subtracting one-off costs such as spotting scopes, long-lasting climbing equipment and bands. Retained in the budget figure were vehicle costs, annual replacement of essential climbing gear, field accommodation and meals. Because volunteers conducted all field work there were no salary components to the project. On average, banding was completed at 2.43 sites per day (median 2.0, s.e. ± 0.23 , range 1–6). The multiplier effect of extra site visits over a field season is easily determined (Table 3.2).

Table 3.2 Summary of the outcomes of monitoring potential breeding events at Peregrine Falcon eyries in Victoria. These events are sub-grouped by the method employed to determine the date of banding for each breeding event. Method A = traditional ad hoc visitation, Method B = same season eggs aged to predict the preferred banding date, and Method C = breeding history based on preferred banding dates in previous years. Method A was used between 1975 and 1984, Method B from 1991 to 2010 and Method C from 1995 to 2010. The numbers are counts and the numbers in parentheses are percentages of complete broods banded from successful breeding events where banding was attempted.

Monitoring outcome	Method A	Method B	Method C	Sub-totals (method B + C)
Potential breeding events monitored	253	112	1332	1444
Site not occupied	32	0	96	96
Eggs only	5	0	0	0
Breeding not successful	53	30	202	232
Breeding successful	163	82	1034	1116
Banding not attempted	28	5	87	92
Breeding successful & banding attempted	135	77	947	1024
Percentage of successful breeding events where banding was attempted	(82.8%)	(93.9%)	(91.6%)	(91.8%)
Banding mis-timed ^A	44	2	54	56
Complete brood banded	91	75	893	968
Percentage of complete broods banded	(67.4%)	(97.4%)	(94.3%)	(94.5%)
Monitoring visits required	2.47	2	1.05	n.a.
Range of monitoring visits	1 - 7	2	1 - 2	n.a.
Cost benefit comparison				
Cost per field visit ^B	\$130	\$130	\$130	n.a.
Average cost per site to complete banding	\$321.10	\$260.00	\$136.50	n.a.
Range of costs per site per season	\$130 - \$910	\$260	\$130 - \$260	n.a.

^A One or more nestlings already flying or too young to band ^BNote: these figures do not include salaries.

3.4.5. *Re-encounter rates*

In total, 277 individual Peregrine Falcons (140♂, 137♀) wearing bands were re-encountered, totalling 570 re-encounters comprising the following re-encounter categories: breeding 335, dead 156, sick or injured 66, and alive not breeding 13. In all cases, no loss of bands was detected and no injuries as a result of the bands could be detected (Table 3.3).

Table 3.3 The number of Peregrine Falcon nestlings banded between 1991 and 2010 is presented by sex, re-encounter status and totals. Listed is the number banded, status (or type) of re-encounter, the number of individuals identified of each sex and status, the percentage of these and the number of re-encounters.

Sex	Number banded	Re-encounter Status	Individuals - identified	Percent	Number of re-encounters
Male	1,049 ^A	Breeding	59	5.6%	191
Female	990 ^A	Breeding	47	4.8%	144
Totals	2,039 ^A		106	5.2%	335
Male	1,186	Other	81	6.8%	109
Female	1,139	Other	90	7.9%	126
Totals	2,325		171	7.4%	235

^A = number of nestlings banded minus those banded up to and including 2008. Young banded after 2008 were not sexually mature by the end of this study in 2010.

3.4.6. *Re-sight data collection*

Early in the CMR study, the maximum distance published for reading VID bands by using the same telescope make and model was 245 m in ideal conditions in the United States (Tordoff & Redig, 1997). More recently in Sweden, VID bands have been reported to be read at distances of ~200 m with the same equipment as used in the present study, and at greater distances if a digi-scope video recorder was attached (Lindberg,

2009). During the present study, in ideal weather conditions (i.e. cloudy day with little or no wind), the maximum effective range for reading VID bands was 280 m.

The time to observe and identify both adult Peregrine Falcons at an active eyrie was recorded for 240 breeding events at 107 active eyries. These surveys were timed at active eyries on cliffs, buildings and in tree nests (both stick nests and tree hollows) and during the site visit to band nestlings (before banding was attempted) (Table 3.4). The average time to complete these surveys was 30.3 min (± 1.69 s.e., range 2–120), regardless of whether either adult was wearing bands or not (Table 3.4). In the majority (72.4%) of surveys, the female was identified before the male of a breeding pair.

Variation in diurnal activity of some species during breeding has been found to influence survey results (Bibby *et al.*, 2000; Hoodless *et al.*, 2006; Calladine *et al.*, 2010). To test for this, an independent-samples *t*-test was conducted after grouping times into morning and afternoon samples and natural log-transforming the time to survey, to satisfy assumptions of normality and homogeneity of variances. Adult band survey times did not differ between morning and afternoon site visits ($t = -0.863$, d.f. = 238, $P = 0.389$).

Further to this, we assessed whether eyrie type (i.e. building, cliff, tree hollow or stick nest) had an influence on the time required to survey both adults. Survey time did not differ on the basis of eyrie type ($F = 1.649$, d.f. = 3, 236, $P = 0.179$), ultimately suggesting that time of visit and eyrie type do not influence the efficiency of site visits.

Table 3.4 Descriptive statistics of the total time (decimal minutes) to survey both adults of a breeding pair at an active Peregrine Falcon eyrie under different scenarios of band status referred to as survey results. Listed are the following statistics: *n* = number of timed surveys, mean, standard error of the mean, standard deviations, Min. = minimum, Max. = maximum.

Survey results	<i>n</i>	Mean	Std. error	Min.	Max.	Median	Std. deviation	Variance
Both adults banded	22	29.55	6.19	4	100	21.0	28.93	836.93
Neither adult banded	122	30.61	2.43	2	120	20.0	26.89	722.88
Male only banded	50	29.82	3.82	4	111	21.0	27.01	729.50
Female only banded	46	30.15	3.37	2	93	30.0	22.84	521.69
<i>All surveys combined</i>	<i>240</i>	<i>30.26</i>	<i>1.69</i>	<i>2</i>	<i>120</i>	<i>21.5</i>	<i>26.22</i>	<i>687.46</i>

3.5. Discussion

The present study is in support of longitudinal CMR studies by addressing the increasing demand for better-designed monitoring studies (Nichols & Williams, 2006; Lindenmayer *et al.*, 2012). This was achieved by investigating and testing improvements in three key aspects of the planning and conduct of a longitudinal study of a raptor by using CMR techniques. These were (1) development of robust selection criteria with project-specific parameters and an assessment of the efficacy of the CMR technique selected, (2) testing of two methods for increasing the number of whole broods banded and (3) quantifying the cost (in time) per re-sight datum collected. The efficiencies gained and quantified here with suitable species-specific modifications have application to any long-term, large-scale CMR bird study collecting LRS data.

Some of the CMR selection criteria presented have been listed in other studies (Newton, 2001; Thomas *et al.*, 2011) and wildlife manuals (Varland *et al.*, 2007; Silvy *et al.*, 2012). However, the present study is the first to present a comprehensive list explicitly applied to a range of commonly used CMR techniques. For the successful application of these criteria when designing a CMR study, it is critical to prepare project-specific parameters for each selection criterion. These parameters inform the whole selection process so that it addresses the requirements of the study and the species under investigation in an unambiguous and transparent manner. The CMR technique selected (metal VID bands) fulfilled all of the selection criteria during the 20 years of the present study. The use of metal VID bands for a long-term CMR study was highly appropriate for Peregrine Falcons because of the relative ease of re-sighting and reading bands on their unfeathered tarsi. However, an alternative CMR technique is required for species with fully feathered tarsi (i.e. members of the eight genera of ‘booted’ eagles, notably the *Aquila* spp. and *Hieraaetus* spp. in Australia and many owl species globally (i.e. *Bubo* spp. and *Ninox* spp.). Also, individuals of the cathartid (New World) vultures must not be banded because they excrete faeces on their legs, which can become affected between band and tarsus, potentially leading blocked circulation to the feet and necrosis (del Hoyo, Elliot *et al.* 1994; Varland, Smallwood *et al.* 2007). These few examples illustrate how vital it is that the anatomy and biology of each species is taken into account when writing the parameters for each selection criterion. The selection criteria (with well written parameters) tested in the present study have application for the planning phase of any avian study using CMR techniques.

Overcoming annual and regional variances in the phenology (Moussus *et al.*, 2009) of clutch-initiation dates (by accurately predicting banding dates) was one of the significant

outcomes of the present study. The Peregrine Falcon was an ideal model species because of its long-term nest-site fidelity, reliable seasonal breeding patterns and relatively stable breeding phenology. It is important to note that not all species will be as consistent in these attributes. Species that breed in less predictable environments or relocate nests more regularly will require greater pre- or early season survey effort to predict breeding phenology. It is expected that long-term phenology data will not necessarily be able to account for the effects of significant weather events (i.e. severe storms, floods or wildfires) or recent turn-over of adults will tend to delay or prevent egg laying or the loss of a first clutch because of predation or egg collecting. The replacement of adults and significant weather events such as the drought of 2000–2009, the Black Saturday bushfires (February 2009) and the 2010 La Niña rainfall event certainly did occur in Victoria during the present study (1991–2010) and may have affected the phenology of nearly all sites. However, the overall 20-year average of complete brood-banding rate of 94.5% in the present study suggests that the quantitative approach to predicting phenology is quite robust, despite fluctuations in phenology at least for this species. In those regions and years where extreme weather events occur, there is merit in undertaking some early season sampling (Method B) at a subset of sites to calibrate the timing of seasons against recent phenological trends. One of the strengths of using a quantitative approach (Methods B or C) to track phenology is that it is sensitive to gradual temporal changes (such as shifts as a result of climate change) and so can inform the scheduling of field work over time, without multiple site visits per year just for the banding component of the study.

Breeding phenology can also be affected by the loss and replacement (turn-over) of adults; however, again, this would tend to have a delaying effect, so that, generally,

nestlings would be too young for banding on the basis of previous-season phenologies, requiring a second site visit to band. This has, in part, been overcome by the accuracy of sex determination for banding of nestlings as young as 15 days post-hatching, developed earlier in the broader study (Hurley *et al.*, 2007). In cases in which a new adult (or pair) is breeding, the delayed breeding phenology of their first year together may be reversed so that breeding will be significantly earlier in their second breeding season. Where turnover rates of adults is high at a nest, we recommend early season surveys and adopting Method B, to determine the most appropriate banding date each year.

Considerable time and effort can be expended if sites need to be visited multiple times to successfully band animals. Methods that optimise the number of visits have the potential to significantly reduce cost and fatigue. The *a priori* approach (i.e. ageing eggs) to predict the optimal date for banding the nestling proved to be highly accurate. However, we caution that the method of egg measurements should be used sparingly because it can involve significant disturbance (Fyfe & Olendorff, 1976; Rosenfield *et al.*, 2007) at the nest during a delicate stage of the breeding cycle (Steenhof & Kochert, 1982; Buehler, 2000) and increases the risk of predation on eggs (Emison & Bren, 1981). Care should always be taken to reduce the impacts of researcher disturbance wherever possible (Olsen & Olsen, 1978; Götmark, 1992). Peregrine Falcons are, however, considered more robust to nest-site disturbances than are other raptor species, most notably white-bellied sea-eagles, *Haliaeetus leucogaster* (Wiersma *et al.*, 2001), Swainson's hawk, *Buteo swainsoni* (England *et al.*, 1997), and ferruginous hawks, *Buteo regalis* (White & Thurow, 1985). The egg-measurement method is particularly useful when new sites are found during the incubation period and breeding phenology is unknown. Phenological data can also be accumulated using the *a priori* approach (Method B). Despite the

compulsory two visits of this method, one clear advantage lies in this method providing clutch size, and so giving hatch rates as a natural consequence from the two site visits.

The *a posteriori* approach based on creating a history of breeding phenology from ageing nestlings (in previous years) also requires detailed growth curves of the study species (Bortolotti, 1984b; Olsen & Olsen, 1987b; Arroyo *et al.*, 2000; McDonald, 2003; Penteriani *et al.*, 2005). Once nestlings can be accurately aged, 2–3 years of breeding data can be used to accurately predict the next year's preferred banding date for the site. Limitations of this method are that it does not automatically provide clutch size, it will not necessarily give fledging rates and it is not sensitive to large, rapid changes in phenology. Although backing this method up with Method B at a representative sample of sites in years of extreme weather events will maintain banding rates. To collect a full set of reproduction data, additional site visits are required to determine clutch size (via egg counts) and a later visit to determine fledging rates. A history of breeding phenology will also assist in the timing of these site visits each year.

The present study has represented a novel and practical application of a range of techniques to greatly improve the efficiency of planning and conducting a long-term CMR study at a large spatial scale. We demonstrated how significant efficiencies can be gained by using quantitative methods for predictions of breeding phenology, to band large numbers of nestlings across widely dispersed nest sites. The time it takes to collect re-sighting data was measured as a benchmark that demonstrated the efficiency of using VID bands as a CMR technique for this species. It is hoped that other researchers will publish the efficiencies and costs involved in other projects, so that future researchers can

make evidence-based comparisons of the various CMR techniques available. Having techniques for accurate age and sex determination of nestlings in the field provided a larger window of opportunity for banding at each eyrie. Any long-term CMR study will benefit from the publication of such species-specific methods.

4.

Peregrinations: Less dispersive Peregrine Falcons (*Falco peregrinus macropus*) are more likely to adopt atypical nests.



Stick nesting ♀ Peregrine Falcon fledged from a cliff, west of Geelong, 2004.

Revered by falconers, detested by pigeon fanciers, and an icon to conservation biologists.

Few species evoke such curiously strong responses to something,
that after all, is just a bird.

Helen MacDonald

4.1. Abstract

Nest site selection is a critical decision for birds, especially those with strong fidelity to a single nest territory for life. Overcoming nest type imprinting allows more adaptive behaviours in nest site selection, leading to potentially improved breeding performance through higher quality nest selection. Peregrine Falcons are considered to be cliff nesting specialists, however, in Victoria, Australia they also use stick nests of other birds (13.9%), tree cavities (15.2%) and buildings (10.5%). This study used capture-mark-re-sight techniques to determine both nest site origin and eventual nest site adoption. In addition to nest selection choices, the effect of search effort (dispersal distance) and search time (age at first breeding) on lifespan and lifetime reproductive output were examined. Females dispersed further than males ($t = -4.983$, $df = 100$, $P < 0.001$; ♀ $61.2 \text{ km} \pm 6.4 \text{ km}$; ♂ $24.4 \text{ km} \pm 5.8 \text{ km}$; mean $\pm$ s.e.). No bias in dispersal direction was recorded. Novel dispersals (i.e. natal dispersals from one nest type to another) accounted for 30.4% of dispersals with no sex bias. Novel dispersers were less dispersive with no sex bias ($F_{(1,98)} = 26.0$, $P < 0.001$). Breeding success measured through clutch success rates was lowest on building ledges and greatest in tree stick nests or cavities.

The level of novel dispersals recorded strongly suggests that once traditional nest sites (i.e. cliffs) are saturated, Peregrine Falcons will spontaneously adopt atypical (non-cliff) nest sites. This occurs among individuals that disperse significantly shorter distances.

4.2. Introduction

Natal dispersal and nest site selection strategies bring differing costs and benefits (Bonte *et al.*, 2012) to both the philopatric and the dispersive individuals of a species (Baker & Rao, 2004; Serrano & Tella, 2012). Sex biased natal dispersal has been well described amongst vertebrate species (Greenwood, 1980; Pusey, 1987) and is generally explained by either the resource defense or mate defense patterns of dispersal across taxa (Sutherland *et al.*, 2000) with few variations on these themes (Clarke *et al.*, 1997; Perrin & Mazalov, 2000). Natal dispersal, in part, serves to reduce incidents of inbreeding (Hardouin *et al.*, 2012) and contributes to a specie's ability to maintain and expand their range (Lowe, 2010; Serrano & Tella, 2012).

Natal dispersal involves leaving the territory within which they were raised and moving into a new area, searching for and selecting nests from available sites (Martin *et al.*, 2004). Nest site choice is a critical decision for an individual, particularly in species where they maintain long-term nest site fidelity (Mooney & Brothers, 1993). Choice of a poor quality nest can impact significantly on breeding success (Olsen & Olsen, 1989b; Quader, 2006) and survival of young (Kolbe & Janzen, 2002). Nest predation is considered the major cause of nest failure (up to 80%) in most bird species (both passerine and non-passerine; Martin *et al.* (2004); Remeš *et al.* (2012)). As such, nest quality tends to be assessed in the context of, and is considered inversely proportional to, the risk of predation (Martin, 1993; Badyaev, 1995). To avoid predation, nest selection has led to cases of trade-offs in the thermal quality of nests (Amat & Masero, 2004) or increased risks of flooding to nest sites (Espie *et al.*, 1996).

It is worth noting here that even raptors are susceptible to predation in the nest. Various predators in different ecosystems have been recorded to take eggs, young and adults. Breeding adults and young have been recorded killed by Eurasian Eagle Owls (*Bubo bubo*) in France (Juillard & Rebetez, 1991), the Alps in Switzerland and Italy (Brambilla *et al.*, 2006), Pieniny Mountains, Poland (Bonczar & Kozik, 2009) and or Northern Goshawks (*Accipiter gentilis*) in Sweden (Lindberg, 2009). The Golden Eagle (*Aquila chrysaetos*) can act as a nestling and adult predator of Peregrine Falcons in Europe (Sergio *et al.*, 2004). Great Horned Owls (*Bubo virginianus*) have similarly been recorded predating upon adult Peregrine Falcons and nestlings for several locations in North America (Redig & Tordoff, 1988; Cade *et al.*, 1989). A Gyrfalcon (*Falco rusticolus*) has been recorded killing a Peregrine Falcon nestling in Yamal Peninsula, Russia (Pokrovsky *et al.*, 2010). Eggs of Peregrine Falcons have been recorded being taken by Pine Martens (*Martes martes*) in France (Monneret, 1983) and Poland (Bonczar & Kozik, 2009). Young have been killed in the nest by a Black Mamba snake (*Dendroaspis polylepis*) in South Africa (Jenkins, 1994). Peregrine Falcon remains have been found in regurgitated pellets from Wedge-tailed Eagles (*Aquila audax*) Canberra, Australia (Olsen *et al.*, 2010). Peregrine Falcon eggs have been recorded taken by the Tasmanian Devil (*Sarcophilus harrisii*) and Spot-tailed Quoll (*Dasyurus maculatus maculatus*) and young from cliff nests taken by the Forest Raven (*Corvus tasmanicus*) and the Tasmanian Devil and free flying young taken by White-bellied Sea Eagle (*Haliaeetus leucogaster*) in Tasmania, Australia (Olsen & Olsen, 1988b; Mooney, 2013). Eggs and young have been recorded in four separate breeding attempts taken by rodents (*Rattus sp.*) at a cliff nest in north east Victoria, Australia (unpublished data from this study). Although it is unclear if the maggots or the rodents would be the ultimate cause of death amongst the nestlings. At the time the nestlings were discovered they had been

partially eaten by both and were still alive (Figure 4.1). The Red Fox (*Vulpes vulpes*) and the feral Domestic Cat (*Felis catus*) have also been recorded taking young (unpublished data from this study). The introduced Hedgehog (*Erinaceus europaeus*) have been recorded taking eggs of the ground nesting New Zealand Falcon (*Falco novaeseelandiae*) (Kross *et al.*, 2013). The introduced Stoat (*Mustela erminea*) has been recorded taking eggs and young of the New Zealand Falcon and a feral Domestic Cat has also been video recorded taking well developed nestlings (Kross *et al.*, 2013).



Figure 4.1 Nestling Peregrine Falcon dying with flow blown open chest cavity wound and partially eaten right wing. Primary injuries caused by rodents (*Rattus sp.*), 2008.

However, among species more capable of defending their nest, nest site selection is still considered a trade-off between nest defense and foraging commitments (Martindale,

1982). Sexual dimorphism among monogamous species may in part be due to specialisation for these two roles (Martindale, 1982). Among raptor species, where reversed sexual dimorphism is highly developed and these roles are well defined (i.e. *Accipiter* and *Falco* species), nest quality may be assessed by predation risk (Warkentin & James, 1988), levels of human disturbance (Strasser & Heath, 2013 *in press*) and by other criteria such as susceptibility to inundation from rainfall in nests on cliff ledges (Olsen & Olsen, 1989b; Emison *et al.*, 1993). For cliff nesting or secondary nest occupier raptor species, that exhibit high nest territory fidelity over their lifetime, the choice of nest can significantly impact on their lifetime reproductive success (Mearns & Newton, 1988).

The search effort (time spent and area covered) invested during nest site selection has been demonstrated to be positively correlated with breeding success of the ground nesting Wild Turkey (*Meleagris gallopavo*) in Arkansas, USA (Badyaev *et al.*, 1996). In the absence of tracking studies, search effort is difficult to quantify. The factors effecting nest site selection are particularly challenging to measure in species that are slow to reach sexual maturity and disperse long distances to settle at a nest site that will be used over their life time. In such species, age at first breeding may be seen as an indication of time spent selecting a nest site, and dispersal distance an indication of the area searched or search effort, correlations between each of these two factors, and subsequent nest quality can be assessed. These two assumptions equating; a) age at first breeding to search time, and b) dispersal distance to search area are derived from two studies in particular. First in southern Scotland, on the Sparrowhawk (*Accipiter nisus*) that undertook breeding dispersals to a higher quality territory were rewarded with improved breeding (Newton, 1991, 1993) and second, where costs and benefits of dispersal were correlated as a

function of dispersal time spent searching and distance moved by the Desert Isopod (*Hemilepistus reaumuri*) (Baker & Rao, 2004).

Highly adaptable species that adopt a variety of nest types are presented with many choices in quality within and between different nests. The Peregrine Falcon (*Falco peregrinus*) is one such species, preferring to nest on rocky or gravel cliff ledges (Cade, 1982), but is also known to nest on the ground in Finnish bogs (Ollila, 2009), on buildings (Frank, 1994; Bird *et al.*, 1996) and in trees (Emison *et al.*, 1997; Kleinstäuber & Kirmse, 2009) where large tree hollows (cavities) or the stick nests of other birds maybe used (Marchant & Higgins, 1993). Tree cavity use by Peregrine Falcons is currently unique to Australia (Emison *et al.*, 1997) and the adoption of stick nests still occurs in Australia despite population declines during the DDT era (1946-1987) (White *et al.*, 1981). The use of stick nests and tree cavities in north America, whilst never common, was widely distributed across the Mississippi drainage system and beyond in Louisiana (Lowery, 1974), Indiana and Illinois (Ridgway, 1895), Iowa (Bailey, 1918), Tennessee (Spofford, 1947) and Kansas (Goss, 1878) but has not been reported since 1974 (Lowery, 1974). In Europe, from the Netherlands to western Siberia the lowland breeding Peregrine Falcon bred in stick nests in trees (Mizera & Sielicki, 1995). Before 1946 the tree nesting population was estimated at 1,300 pairs in Germany and Poland alone (Kirmse, 2004). The breeding population in Poland was considered to be functionally extinct by the 1960s (Mizera & Sielicki, 2009) and also went extinct in east Germany by 1973 (Kirmse, 2004). Regular breeding in these countries/regions did not re-occur until the 1990s (Kleinstäuber & Kirmse, 2009; Mizera & Sielicki, 2009). It is worth noting that a single breeding event was recorded in 1980 in the Tatra Mountains, Poland where there is an abundance of vacant traditional cliff breeding sites (Kirmse

(1991) in German cited in Mizera and Sielicki (2009)). Considerable effort is being expended to re-establish this nesting trait by transferring nestlings from urban buildings to artificial stick nests in distant forest locations and providing food to the nestlings until they fledge (Kleinstäuber & Kirmse, 2009). This process is referred to as a hack release or hacking (Sherrod *et al.*, 1982).

It has been assumed that natal experience influences the type of nest site selected by Peregrine Falcons (Kirmse, 1994, 2004; Mizera & Sielicki, 2009). The only other study on Peregrine Falcon natal dispersal choices, in the mid-west USA, investigated dispersals between cliffs and three types of built structures (i.e. buildings, smokestacks at power plants and bridges Tordoff *et al.* (1998)). Within the mid-west population 7.3% of Peregrine Falcons undertook natal dispersals from cliffs to built structures. This indicates that natal experience leading to a form of nest type imprinting may not be as significant a driver of nest selection, for the Peregrine Falcon, as has been claimed (Kirmse, 2004; Kleinstäuber & Kirmse, 2009).

The Victorian Peregrine Falcon (*Falco peregrinus macropus*) population in south-eastern Australia has been the subject of long-term nest surveys (White *et al.*, 1981; Emison & Hurley, 1995; Emison *et al.*, 1997) and banding studies (Emison & Bren, 1981; Emison *et al.*, 1998; Hurley *et al.*, 2013). These studies, coupled with the diversity of nesting habits displayed by this population, provide a unique opportunity to test hypotheses concerning the levels of flexibility in, and the consequences of, nest site selection. Data to test this from a healthy, non-migratory population, without a history of captive bred and released birds (Olsen & Olsen, 1988b), has not been previously available.

This study investigates a number of aspects associated with dispersal and nest site selection by the Peregrine Falcon in south-eastern Australia. Specifically this study aims to determine whether:

1. Natal experience of a nest type influences nest site selection during dispersal;
2. Nest site search effort (measured as dispersal distance) influences the reproductive output and lifespan of breeding individuals;
3. The time spent searching for a nest (measured as age at first breeding) influences the reproductive output and lifespan of breeding individuals;
4. Natal nest experience (based on natal nest experience of nest type) influences dispersal distance, age at first breeding, lifetime reproductive output or lifespan of breeding adults.

4.3. Methods

4.3.1. Study Area

This study was undertaken in Victoria, south-eastern Australia and covered an area of approximately 227,000 km². The geographic range of the study area included a latitudinal span of four degrees (34° 30' to 38° 45' S) north to south and seven degrees (141° to 148° E) of longitude west to east. The type of nest was determined for 237 sites across Victoria with maximum distances between monitored nests being 589 km (west to east) and 521 km north to south (Figure 4.2). The location of sites and altitude (meters above sea level (asl)) were recorded using a hand held Garmin Mark II *plus* GPS and this data was mapped in Arc GIS 10 Esri©. The nests were classified into four main groups, cliff (combining natural and quarry), building, tree cavity and stick nest (built by other bird species).

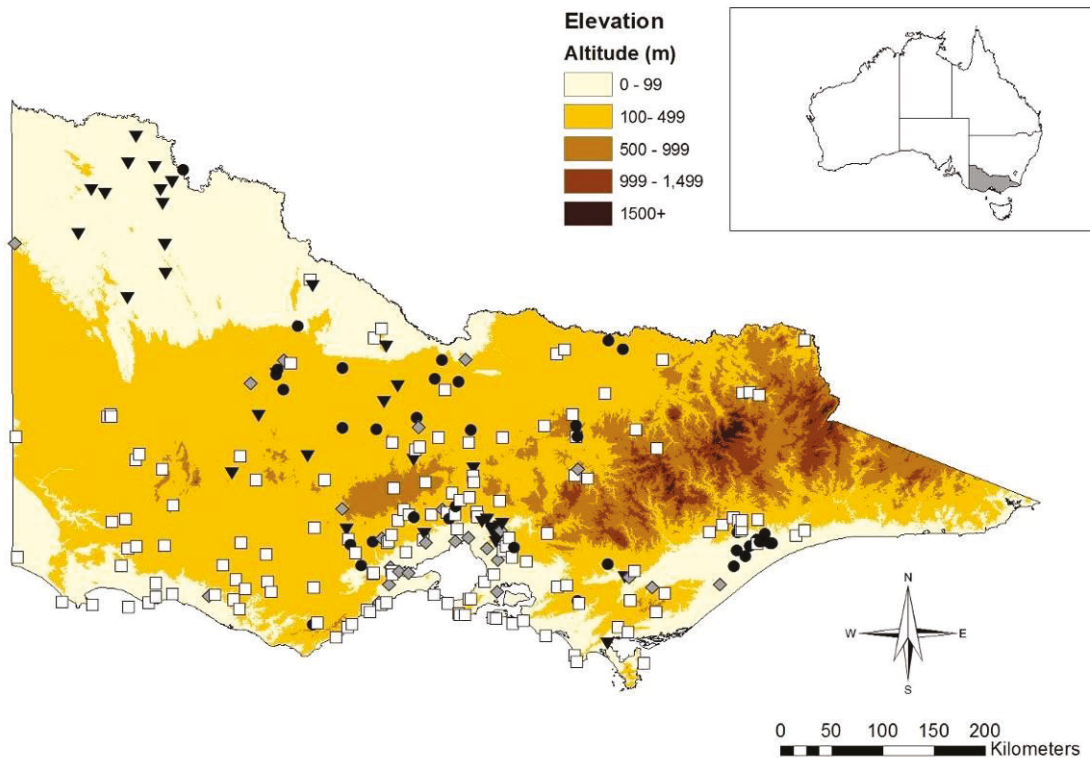


Figure 4.2 Location of Peregrine Falcon nests presented on a digital elevation map of Victoria ($n = 237$). $\square$ = cliff, $\blacklozenge$ = building, $\blacktriangledown$ = stick nest, $\bullet$ = tree hollow.

4.3.2. Terminology

For the purpose of this study the following definitions have been adopted. Natal dispersal is the movement from hatch site to breeding site which is referred to from now on as dispersal (James *et al.*, 1989; Morrison & Wood, 2009). Dispersals were further categorised based on movements to a nest type similar to or different from their natal nest site: 1) traditional dispersal is where a bird dispersed and adopted the same nest type for breeding as that from which it fledged and 2) novel dispersal is where an individual fledged from one nest type and dispersed and settled at a different nest type (e.g. dispersing from a cliff to a stick nest). The term ‘breeding event’ is used to refer to one year’s breeding in a single territory.

4.3.3. Field procedures

Each nest was classified according to the level of protection from extremes in weather and was assessed in terms of angles of exposure. Exposures were measured by placing a compass in the centre of the nest scrape and taking bearings to obstacles on either side, the difference in degrees between the bearings being the horizontal exposure. Using a digital long arm protractor (Winkelfix, Festool Art. No.: 450121-267), vertical exposure was measured from the centre of the nest scrape as the difference in degrees between the horizontal floor and the first obstacle above the nest (Pruett-Jones *et al.*, 1981b). Due to variations in techniques for measuring the levels of nest site exposure the data was arranged in to three broad classes. The three exposure categories used in this study were: low = open site with no over-head protection (includes all stick nests), medium = vertical exposure $> 80^\circ$ and horizontal $> 160^\circ$, high = vertical exposure $< 81^\circ$ and horizontal exposure $< 161^\circ$.

Nests were visited and fledglings banded on an annual basis from 1991 to 2010. Where successful breeding occurred nestlings were banded with metal visual identification (VID) coloured bands with a two digit alpha-numeric code that could be read with a spotting scope (Hurley *et al.*, 2013). Monitoring of adults at nests for the presence of bands was undertaken during the spring breeding season each year. The natal dispersal distance was recorded as the straight-line distance between their fledge nest and their first recorded breeding site using measuring tools in ArcGIS 10 Esri©. The type of dispersal was assigned to each individual depending on whether it was a traditional or novel dispersal.

The number of years between banding (as a nestling) and the year it was first identified breeding was calculated to give the age at first breeding. Age at first breeding was only assigned to individuals where monitoring data confirmed a different adult (of the same sex) had been identified breeding at the same site the year before. Similarly, the age at last breeding was only assigned to an individual once monitoring confirmed it had been replaced as the resident at a nest site. The difference between these two ages then provided the total number of years breeding for an individual, and the age at last breeding indicates life span.

Further to this, breeding data was collected where practicable at each site during the breeding season. The total number of eggs laid (clutch size) was used as a measure of reproductive effort. Clutch success rate was determined by the number of clutches which hatched one or more eggs. The number of nestlings surviving to banding (~26 days post hatching) was used to indicate reproductive output. This was used as a surrogate for reproductive success which is normally measured by the number of nestling surviving to first flight (fledging). Where the cause of egg failure or nestling deaths (prior to banding) could be determined this was also recorded.

The type of nest was classified for 237 nests by; cliff, building, stick nest or tree hollow. Banding and monitoring was conducted at 188 (study sites). An independent samples t-test was used to determine whether there was an effect of sex on dispersal distance and longer dispersing females and their lifetime reproductive output to the less dispersive individuals. Chi square tests were used to determine whether the study sites ($n = 188$) were representative of the broader state-wide population ($n = 237$) and whether there was

an effect of sex on type of dispersal (traditional versus novel) and nest type and breeding success.

4.3.4. *Statistical analyses*

The type of nest was classified for 237 nests into cliff, building, stick nest or tree hollow. Banding and monitoring was conducted at 188 study sites. An independent samples t-test was used to determine whether there was an effect of sex on dispersal distance and longer dispersing females and their lifetime reproductive output to the less dispersive individuals. Chi square tests were used to determine whether the study sites ($n = 188$) were representative of the broader state-wide population ($n = 237$) and whether there was an effect of sex on type of dispersal (traditional versus novel) and nest type and breeding success.

Two-way ANOVAs were used to test the following interactions: sex, dispersal type and dispersal direction; sex, dispersal type and distance; sex, dispersal distance and nest quality used; sex, age at first breeding and quality of nest used; sex, dispersal type and lifespan; sex, dispersal type and lifetime reproductive output (LRO); sex, dispersal distance and LRO.

All data was log (natural base) transformed to satisfy assumptions of normality and homogeneity of variances before analyses. Analyses were carried out using IBM SPSS Statistics 21. All data is presented untransformed for ease of interpretation except in graphs where axes have been labelled accordingly.

4.4. Results

4.4.1. Survey locations

The location and site details of 237 active Peregrine Falcon nests were recorded across Victoria between 1991 and the austral spring of 2010. Within Victoria cliff nests accounted for 143 (60.3%) sites and the remaining 39.7% comprised buildings (10.5%), stick nests of other bird species (13.9%) and tree cavities (15.2%) (Table 4.1). In the present study, a subset of 188 sites were surveyed for a minimum of five years (maximum 20 years) for the presence of banded adults and breeding data collected from 1991 to 2010. Non-cliff sites accounted for 73 (38.8%) of this subset of sites. The ratio of nest types (i.e. cliff, building, stick nest and tree cavity), surveyed in this study is representative of the broader statewide population in Victoria ($X^2 = 2.269$, $df = 3$, $P = 0.158$) (Table 4.1).

Table 4.1 Nest sites used by Peregrine Falcons listed by nest type, number of Victorian sites and number of study sites surveyed between 1991 and 2010. Numbers in parentheses are percentages of each nest type derived from the (totals) of each group of nests.

Nest Type	Victorian	Study sites
Cliff	143 (60.4)	115 (61.2)
Building	25 (10.5)	24 (12.8)
Stick nest	33 (13.9)	29 (15.4)
Tree hollow	36 (15.2)	20 (10.6)
Totals	237	188

4.4.2. Dispersal distances

In this population there was a strong sex bias in natal dispersal distances (Figure 4.3), with females dispersing further than males ($t = -4.983$, $df = 100$, $P < 0.001$; ♀ 61.2 km $\pm$

6.4 km; ♂ $24.4 \text{ km} \pm 5.8 \text{ km}$; mean $\pm$ s.e.). All males dispersed less than 100 km and 81.8% of females dispersed less than 100 km.

Dispersal direction was grouped into four equal 90 degree compass bearing groups centered on North, South, East, or West. There was no relationship between dispersal distance and dispersal direction ($F_{(3, 94)} = 0.576$, $P = 0.633$). There was a significant relationship between sex and dispersal distance ($F_{(1, 101)} = 28.751$, $P < 0.001$). The interaction effect between sex and dispersal direction was not significant, ($F_{(1, 3)} = 0.488$, $P = 0.692$).

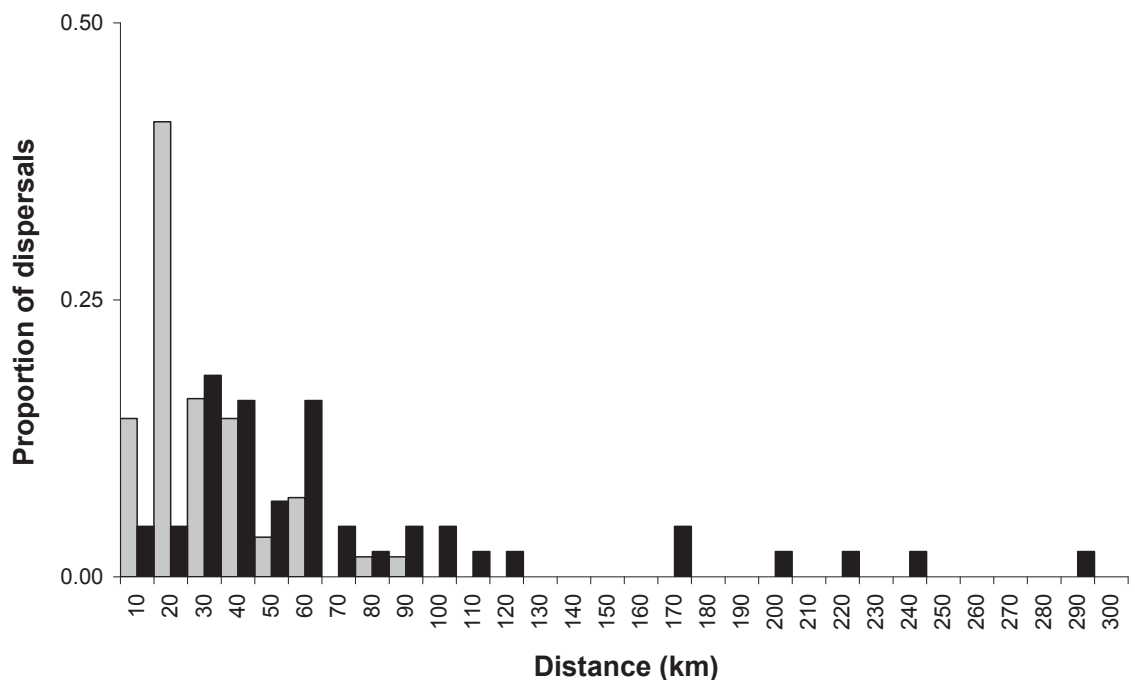


Figure 4.3 Frequency distribution of natal dispersal distances (km) of Peregrine Falcon, males (grey; $n = 58$) and females (black; $n = 44$) in Victoria, 1991-2010.

4.4.3. Dispersal type

Of the 102 dispersal events that were recorded in this study 31 (30.4%) were novel dispersals (Figure 4.4). While some novel dispersals were not observed (i.e. building to stick nest) there is no logical reason for these not to occur. At a population level similar

proportions of each sex undertook novel dispersals (♂ 31%, ♀ 34%), therefore, sex does not appear to play a role in determining whether birds will make novel dispersals.

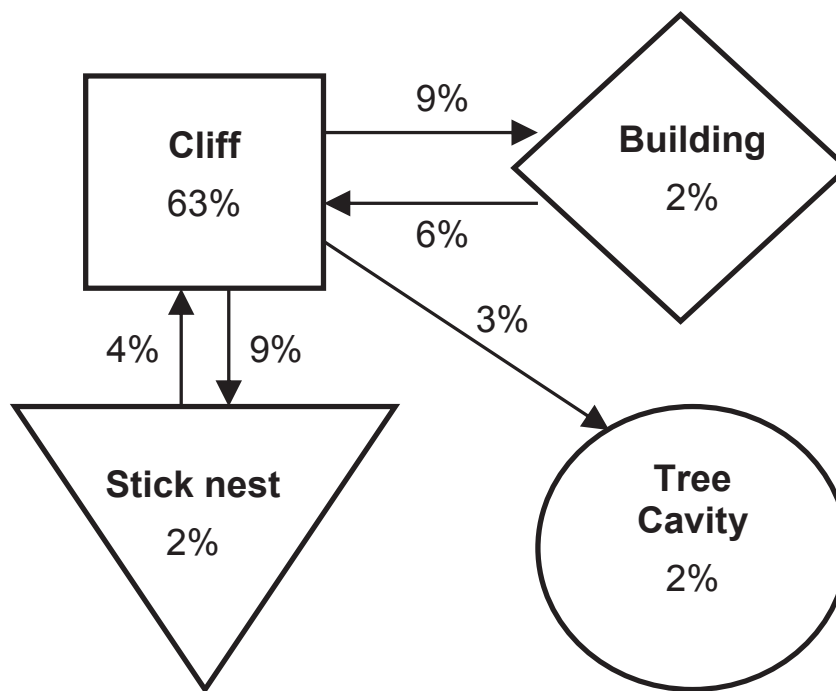


Figure 4.4 Different nest types used and observed patterns of dispersal by Peregrine Falcons in Victoria, Australia between 1991 and 2010. Nest types are represented by shapes and are labeled: $\square$ = cliff, $\diamond$ = building, ∇ = stick nest and $\circ$ = tree cavity. Numbers represent percentages of 102 natal dispersals. Numbers within each shape are traditional dispersals to this nest type. Arrows represent direction of novel dispersals with associated numbers.

4.4.4. Dispersal distance and type

The type of dispersal undertaken (i.e. novel versus traditional) had an influence on the dispersal distance, with individuals undertaking traditional dispersals averaging greater dispersal distances than those undertaking novel dispersals ($F_{(1,98)}=13.818$, $P < 0.001$; Traditional $69.0 \text{ km} \pm 4.9 \text{ km}$; Novel $26.6 \text{ km} \pm 7.1 \text{ km}$; mean $\pm$ s.e.). There was also a significant relationship between sex and dispersal distance ($F_{(1,98)} = 25.991$, $P < 0.001$; ♀ $61.2 \text{ km} \pm 6.4 \text{ km}$; ♂ $24.4 \text{ km} \pm 5.8 \text{ km}$; mean $\pm$ s.e.). There was no interaction between dispersal type and sex ($F_{(1,1)}=1.920$, $P = 0.169$) (Figure 4.5).

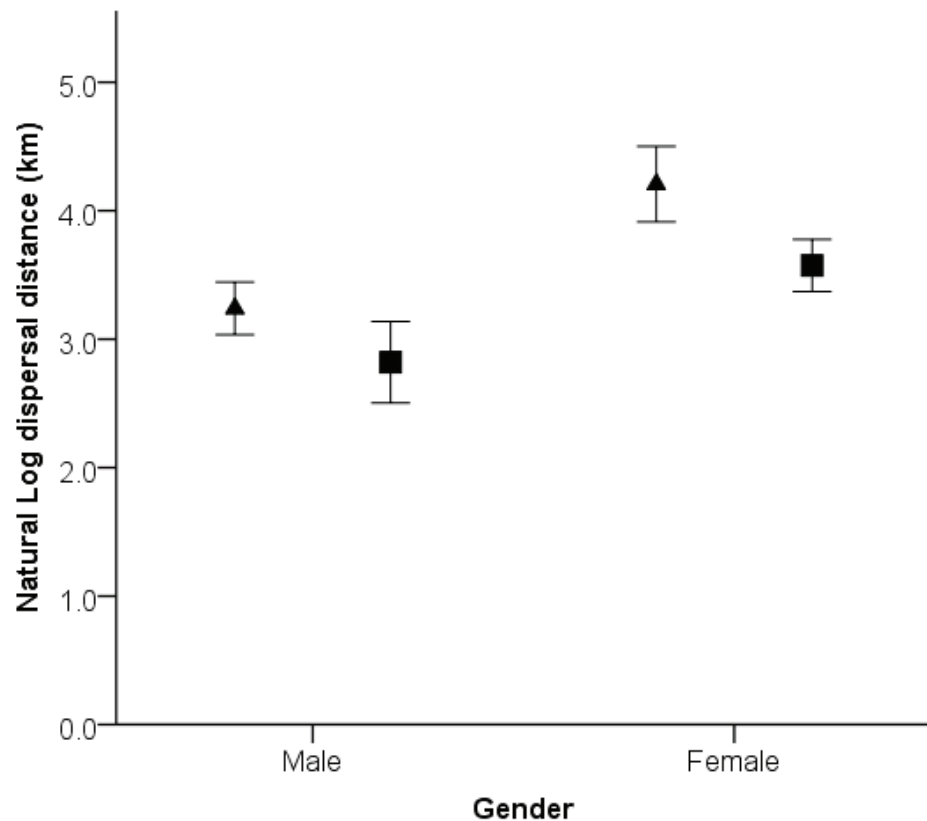


Figure 4.5 The dispersal distances (mean $\pm$ 1 s.e.) of individuals of different sexes using the two differing dispersal strategies. $\blacktriangle$ = Traditional dispersal events, $\blacksquare$ = Novel dispersal events.

4.4.5. Nest type Vs clutch success

Atypical (i.e. non-cliff) nest sites accounted for 38.8% of surveyed sites. This raised the question as to whether there were costs or benefits in making dispersal to a nest type other than a cliff. Clutch success for 1,113 breeding events in which the clutch outcomes were known was investigated between nest types. Each breeding event was classified as either a success or failure based on whether at least one egg hatched. These breeding events comprised of 844 on cliffs, 74 on buildings, 90 in stick nests and 105 in tree cavities. The proportion of successful clutches at each nest type were; cliff = 0.82, building = 0.54, stick nest = 0.92, and tree cavity = 0.90. The proportion of successful clutches by Peregrine Falcons is associated with the type of nest site ($X^2=47.712$, $df = 3$,

$P < 0.001$). Egg hatch rates were lower on building ledges than cliff ledges (adjusted residual = -6.4), and to a lesser extent, higher for stick nests and tree cavities (adjusted residual = -2.4 and -2.2 respectively) (Figure 4.6).

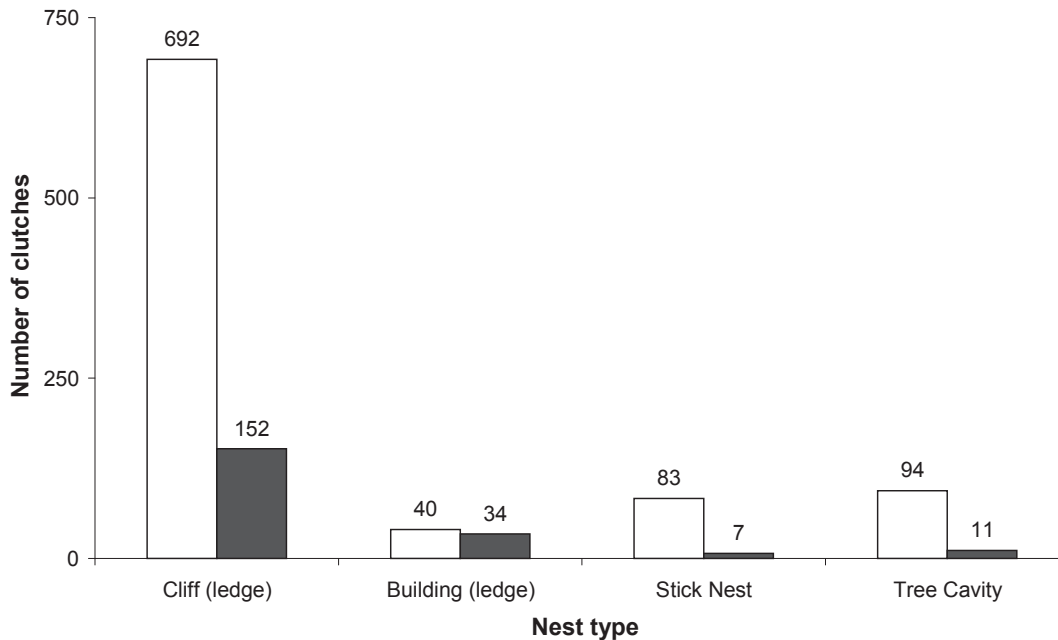


Figure 4.6 Numbers of successful and failed clutches at four different Peregrine Falcon nest types used across Victoria from 1991 to 2010 ($n = 1,113$ breeding events). Numbers above bars = sample sizes (number of clutches). White bars = successful clutches with ≥ 1 eggs hatching, black bars = failed clutches with no eggs hatched.

4.4.6. Dispersal distance and quality of nest obtained

To determine whether the search effort (in the form of net dispersal distance) was rewarded by the quality (i.e. level of protection from rainfall) of the nest adopted by the individual, the impact of sex and dispersal distance on protection was investigated. Sex does have an effect on distance dispersed but there is no relationship between dispersal distance and the level of protection afforded by nest sites that were selected (Sex $F_{(1,96)} = 21.361$, $P = 0.001$; Protection $F_{(2,96)} = 1.440$, $P = 0.242$; and Interaction $F_{(2,96)} = 0.814$, $P = 0.446$). This suggests that search effort does not influence the level of protection of the nest site chosen.

4.4.7. *Dispersal type and age at first breeding*

The age at first breeding can be used as an indication of the search effort (in years) to find and occupy a nest. The age at first breeding was recorded for 88 breeding adults (54 ♂ 3.11 ± 1.298 , 34 ♀, 2.74 ± 0.898 ; mean $\pm$ s.d.). The role of sex and dispersal type on the time taken to find a nest site (i.e. age at first breeding) was examined and neither sex or dispersal type had an influence on the age at the first breeding event of an individual (Sex $F_{(1,84)} = 1.579$, $P = 0.212$; Dispersal type $F_{(1,84)} = 0.136$, $P = 0.713$). There was also no interaction between sex and dispersal type ($F_{(1,1)} = 0.037$, $P = 0.849$). This suggests that the type of dispersal event conducted by an individual does not have an influence on the age at first breeding.

4.4.8. *Dispersal type and lifespan of breeding adults*

The role of sex and dispersal type (i.e. traditional vs novel) on lifespan of individuals surviving to breed was examined. There was no influence of sex or dispersal type on the lifespan of breeding adults ($F_{(\text{sex})} = 0.068$, $df = 1, 73$, $P = 0.795$); ($F_{(\text{disp. type})} = 0.698$, $df = 1, 73$, $P = 0.406$); and ($F_{(\text{interaction})} = 0.212$, $df = 1, 73$, $P = 0.647$).

4.4.9. *Dispersal type and reproductive output*

To determine whether the type of dispersal an individual makes confers an advantage or disadvantage to the individual we examined the impact of dispersal type and sex on reproductive output. To conduct this analysis a sub-set of the 102 breeding adults data set was used, where only individuals who had been monitored their whole breeding life and the total number of nestlings produced (LRO) was known were included. This data sub-set ($n = 70$ individuals) included 42 ♂s and 28 ♀s, and 46 traditional dispersal events (28 ♂, 18 ♀) and 24 novel dispersal events (14 ♂, 10 ♀).

The sex of the individual and the type of dispersal undertaken had no influence on LRO of individuals (Sex $F_{(1,69)} = 0.073$, $P = 0.788$; Dispersal type $F_{(1,69)} = 1.329$, $P = 0.253$). There was also no interaction between sex and dispersal type ($F_{(1,1)} = 0.005$, $P = 0.945$). This suggests that, from a LRO perspective, the type of dispersal event undertaken by an individual does not confer an advantage or disadvantage to the individual.

4.4.10. Dispersal distance versus lifetime reproductive output

Dispersal distance was used as an indicator of the area searched or ‘search effort’ for a nest site (Badyaev *et al.*, 1996). Firstly we tested whether there was a difference between lifetime reproductive outputs (LRO) for each sex. There was no significant difference in LRO based on sex ($\sigma^7 7.3 \pm 0.88$ nestlings, $n = 42$; $\phi^7 7.0 \pm 0.83$ nestlings, $n = 28$; mean $\pm$ s.e.; $t_{(1,68)} = 0.234$, $P = 0.816$, CI95% -2.244 to 2.839).

No males dispersed > 100 km and 81.3% of females dispersed < 100 km. Females were partitioned into two groups based on dispersals of $\leq$ or > 100 km and we tested whether these longer dispersed individuals incurred any lifetime costs or benefits (Plissner & Gowaty, 1996; Baker & Rao, 2004). The effect of these dispersal classes was tested against lifetime reproductive output (the total number of nestlings produced to banding age ~ 26 days post hatching) for a relationship between longer distance dispersers > 100 km ($n = 5$) and those females dispersing ≤ 100 km ($n = 23$). Whilst not statistically significant there is a trend in the cost to lifetime reproductive output for the longer dispersing females suggesting that those few females who make long distance dispersals may not produce as many offspring in their lifetime ($t = 1.732$, $df = 26$, $P = 0.095$, 95% CI -0.674 to 7.891, $\text{Mean}_{\text{LRO} > 100\text{km}} = 4.00$, $\text{Mean}_{\text{LRO} < 100\text{km}} = 7.89$; Tukey (1991)).

4.5. Discussion

Consistent with most bird species (Greenwood, 1980; Pusey, 1987) and other Peregrine Falcon populations studied (Restani & Mattox, 2000; Craig *et al.*, 2004; Lindberg, 2009; Zuberogoitia *et al.*, 2009), natal dispersal of Peregrine Falcons in Victoria was female biased. This dispersal bias is due to Peregrine Falcons having a resource-defense breeding system whereby males obtain territories to attract females who compete for the rare resource of a high quality male with a high quality nest close to a reliable food resource (Olsen & Olsen, 1987a; Wightman & Fuller, 2006). Theory suggests this mating system should exert a cost on females who disperse farthest (Greenwood, 1980). Females that dispersed further than males (i.e. >100 km) adopted high quality nests (i.e. well protected from the effects of weather) but they may also incur a slight reduction in LRO. This finding is not unique as results from other studies of increased dispersal distance have been equivocal, recording an increase (Spear *et al.*, 1998), a decrease (Pärt, 1990) and no effect (Plissner & Gowaty, 1996) on female lifetime reproductive output in other bird species. Negative relationships between dispersal distance and productivity and survivorship have been attributed to benefits gained from familiarity with the natal region (Pärt, 1995; Brown *et al.*, 2008).

Apart from the distance travelled, dispersal also involves the choice of a nest site. The near global breeding distribution of the Peregrine Falcon attests to the adaptability of this species (Santana *et al.*, 2006). The high level of novel dispersals (30.4%) and plasticity in nest site selection has not been reported previously for this species (Tordoff *et al.*, 1998; Kleinstäuber & Kirmse, 2009; Wegner *et al.*, 2009). This is despite the numerous investigations, long-term mark-recapture studies and targeted surveys of this species across many countries for more than 50 years (Hickey, 1969; Porter *et al.*, 1987; Cade *et*

al., 1988; Sielicki & Mizera, 2009). Although cliff sites remained the preferred nest type for this study, the behavioural plasticity in nest site selection displayed in this study challenges the concept of behavioural imprinting from natal habitat preference induction would suggest (Davis, 2008; Kleinstäuber & Kirmse, 2009; Mizera & Sielicki, 2009).

The adoption of atypical (i.e. non-cliff) nest sites can be partly explained by the low lying topography of Victoria, with extensive areas devoid of cliffs, leaving Peregrine Falcons with little choice but to breed in trees or on buildings (Emison *et al.*, 1997). However, the adoption of atypical nests (such as tree cavities or stick nests) within areas of cliff nesting territories, as exhibited by the shorter distances of novel dispersals, challenges the imprinting concept that atypical (i.e. non-cliff) nests will only be adopted in areas lacking cliffs (Stamps & Swaisgood, 2007; Brown & Collopy, 2013). The significantly shorter dispersal distances of novel dispersals among regions with cliff nests explain the process by which these atypical nest sites were first adopted. That is, novel dispersals and the use of atypical nest sites may be a consequence of saturation of cliff sites by this territorial species. However, a single recorded Peregrine Falcon breeding event in Poland in 1980 was in a stick nest in a Spruce (*Picea abies*) (reported in Mizera and Sielicki (1995) from Chichocki (1986) in Polish). This was a very rare breeding event for the time and is additionally unusual in that it occurred in the Tatra Mountains where there was an abundance of vacant cliff breeding sites available (Kirmse, 1991). Optimal foraging theory would suggest the nest territory was selected because of its proximity to an available prey resource (Arditi & Dacorogna, 1988).

The population in Victoria appears to have increased naturally in the number of atypical nests being used following the banning of the use of DDT and Deildrin and may have

saturated the available cliff sites (Ford, 1987). This suggests that in the Victorian population of Peregrine Falcons the use of atypical nest sites may not be as novel as we think. I hypothesize that in other parts of the world where Peregrine Falcon populations are still recovering we could also see the spontaneous use of atypical nest sites as cliff and building locations become saturated. This is supported by several records of the natural adoption of stick nests in trees by Peregrine Falcons bred from cliffs or buildings (Turner, 2005; Olsen *et al.*, 2006; Whitman & Caikoski, 2008; Wegner *et al.*, 2009).

The adoption of stick nests by Peregrine Falcons in the forests of eastern Germany and Poland may well be enhanced more naturally by first allowing the building and cliff nesting habitats to reach saturation levels. Then where stick nests are lacking establish suitable artificial stick nests in forests within the average male dispersal distance (~26 km) of active cliff or building territories (Kleinstäuber & Kirmse, 2009). As the cliff/building populations grow they will naturally expand into these habitats and adopt novel nests in the process. A key reason why this may not have occurred naturally to date in eastern Germany and Poland is that the cliff and building populations have not reached saturation levels and the published practice of removing nestlings from building nest sites wherever possible is actually slowing down the rate at which they will reach saturation levels (Kirmse, 2001).

While novel dispersals tended to be undertaken by the less dispersive individuals of each sex, there was not a consequent reduction in dispersal times to adopt breeding territories and nest sites in Victoria. The average age at first breeding (♂ 3.1 yrs, ♀ 2.7 yrs) for the highly mobile Peregrine Falcon provides ample opportunity to make these selections without the time constraints of short lived species (Mänd *et al.*, 2005).

The strategy of adopting atypical nest types by the less dispersive males and females is both adaptive and maladaptive depending on the nest type selected. This is due to higher rates of clutch success in trees (both stick nests and cavities) than on cliffs and lower on building ledges than on cliffs. The recorded use of trees for nesting (29.1%) is a highly adaptive behaviour with 91% of clutches hatching at least one egg. While adopting buildings as nest sites comprises only 10.5% of the population this proportion of the population is rapidly on the increase. Because of the low clutch success rate (54%) on buildings this is a relatively a maladaptive behaviour. A short caveat must be applied here in that although there is a significant price to be paid for nesting on buildings even poor hatch rates and nestling survival is better than not breeding at all. Having said that these mixed results both support and diverge from the more general rule that longer search effort should be rewarded with higher quality habitats than dispersers with shorter search effort in both vertebrates and invertebrates (Badyaev *et al.*, 1996; Stamps *et al.*, 2005). A rapid rise in the number and proportion of nest sites on buildings would warrant further investigation as how best to improve egg hatch rates and clutch success at these sites.

5.

Longevity legacy: lifetime reproductive output by the Peregrine Falcon (*Falco peregrinus macropus*) is enhanced by lifespan and nest choice rather than landscape level influences.



A mixed brood (2♂, 1♀) of Peregrine Falcons in a decaying River Red Gum tree, Owens River, 2006.

“Look deep in nature, and then you will understand everything better.”

Albert Einstein

5.1. Abstract

Context. Landscape features and nest quality influences on lifetime parameters of breeding Peregrine Falcons.

Aims. 1) document lifetime reproductive output (LRO) and lifespan of breeding and non-breeding Peregrine Falcons, 2) investigate the factors influencing LRO measured as the total number of nestlings produced over the lifetime of an adult.

Methods. Capture-mark-re-sight techniques of breeding adults using metal visual identification bands placed on them as nestlings allowed recording of age at first breeding, lifespan and years spent breeding of 66 Peregrine Falcons. The total number of nestlings produced in a lifetime was recorded by annual breeding season nest surveys. The location and altitude were recorded at nest sites and landscape features recorded in 5 km buffers around each nest using geospatial techniques.

Key results. There is no difference in lifespan between the sexes of breeding Peregrine Falcons ($t=-0.768$, $df=64$, $P = 0.446$). Years spent breeding and lifetime production of nestlings were all positively correlated. Landscape features did not influence LRO, however, the level of protection of a nest site did.

Conclusions. Peregrine Falcons mate for life and display strong nest site fidelity. Moving to a higher quality and occupied territory involves mortal combat with the resident pair. A safer strategy to overcome poor site quality (highly exposed to the weather) is adopt a more protected nest and longevity to increase LRO.

Implications. For healthy recovering populations of the Peregrine Falcon the most important conservation action is the management of nest quality to facilitate successful breeding.

5.2. Introduction

Lifetime reproductive output (LRO) is accepted as a measureable estimate of evolutionary fitness in studies of natural populations (Brommer *et al.*, 2004). There are two main drivers of LRO, these being the breeding lifespan of the individual and the number of young raised per breeding event (Herényi *et al.*, 2012). The role of breeding longevity as one of the most important factors determining LRO is supported in studies of both birds (Newton, 1985; Gustafsson, 1989; Merilä & Sheldon, 2000) and mammals (Clutton-Brock, 1988; Bérubé *et al.*, 1999; Robbins *et al.*, 2011). Longevity, however, does not guarantee enhanced LRO. Factors such as habitat and nest quality, anthropogenic disturbance and seasonal and regional weather conditions can influence both annual and or lifetime productivity (Newton, 1989; Blums & Clark, 2004; Smart *et al.*, 2010; Amar *et al.*, 2012).

Investigating factors affecting LRO may inform us as to the strategies species adopt to deal with these impacts (Stearns, 1976; Brommer *et al.*, 2004). The maintenance of a territory and occupancy of a nest-site by a territorial animal is a critical life-history tactic used to enhance LRO (Martínez *et al.*, 2006). Territorial behaviour amongst predatory species implies a trade-off between the potentially risky strategy of searching and fighting for a higher quality territory and the potential costs and benefits of maintaining a territory (Newton, 1992; Gordon, 1997; Adams, 2001; Ferrer & Bisson, 2003). Among some bird of prey (raptor) species, however, trading up to a higher quality territory can be a successful strategy to enhance reproduction (i.e. the Northern Goshawk (*Accipiter gentilis*) (Newton, 1993; Ferrer & Bisson, 2003; Squires & Kennedy, 2006)). Some raptors such as the Peregrine Falcon however, maintain extremely high territory and nest

site fidelity throughout their life (Mooney & Brothers, 1993; Hurley *et al.*, 2013).

Consequently, territory and nest selection may have life-long implications.

Factors influencing the annual reproductive outputs of individuals have been studied in a wide variety of diurnal and nocturnal raptor species (Krüger, 2004; Macias-Duarte *et al.*, 2004; Solonen & Ursin, 2008; Dykstra *et al.*, 2009). Fewer studies have investigated the influence of site and landscape scale factors on the lifetime reproductive output of individuals (Newton, 1985; Brommer *et al.*, 1998; Krüger & Lindström, 2001; Krüger, 2002; Linkhart & Reynolds, 2006). Modeling the relative impact of nest level and landscape scale habitat features on lifetime reproductive parameters, however, has not been well studied for healthy populations of most raptor species. Although the value of lifetime reproductive studies is clearly recognised (Clutton-Brock, 1988; Newton, 1989; Brommer *et al.*, 2004), logistical and financial constraints have limited such studies in long-lived groups such as raptors (Clarke, 1997; Bednarz, 2007). For species that occupy a diverse range of landscapes, but exhibit a strong lifetime fidelity to a single breeding territory and often the same nest site, understanding the differing effects of key habitat features on lifetime parameters can assist in identifying those features that are most favourable to the conservation of the species. Results from such studies can provide useful benchmarks of lifetime and reproductive attributes of a species for use in recovery planning (Hoekstra *et al.*, 2002; Wakamiya & Roy, 2009).

This study uses the Peregrine Falcon (*Falco peregrinus macropus*) as a model species to investigate the role of landscape scale and nest site level influences on LRO. The Peregrine Falcon is a long-lived species (maximum age 15 years 4 months in Australia (ABBBS, 2013)) which has extremely high breeding territory fidelity throughout their life, and as such territory and nest site selection are critical decisions for the individual

(Olsen & Olsen, 1989b; Mooney & Brothers, 1993). This species also inhabits an extremely high diversity of differing landscapes from coastal plains, to semi-arid Mallee, to tall forests up to the snowline through to cities (Emison *et al.*, 1997).

Previous research has demonstrated that seasons with heavy rainfall have a negative impact the breeding success of some raptors including the Peregrine Falcon (Mearns & Newton, 1988; Olsen & Olsen, 1989b; Emison *et al.*, 1993) and has been shown to impact the survival of breeding adult Brown Falcons (*Falco berigora*) (McDonald *et al.*, 2004). Heavy snowfalls have been linked with poor egg hatch rates leading to breeding failure at exposed nest sites in arctic Rankin Inlet, Canada (Bradley *et al.*, 1997). The impact on breeding performance of excessive rain/snowfall on Peregrine Falcons is not the result of reduced hunting performance but rather a reduction in the hatch rate of eggs due to the inundation of exposed nests (Olsen & Olsen, 1992; Bradley *et al.*, 1997; Jenkins, 2000a). Whilst significant rainfall events influence annual reproductive performance, it is unknown what effects these annual events have on the reproductive output of Peregrine Falcons over their lifetime.

Urbanisation and other anthropogenic disturbances can affect the breeding performance and ultimately LRO of raptors (Boal & Mannan, 1999; Newsome *et al.*, 2010; Strasser & Heath, 2013 *in press*). Urban breeding Peregrine Falcons in California have recorded Polybrominated diphenyl ether (PBDE) toxins at significantly higher concentration levels than in non-urban birds and higher than any other vertebrate species sampled anywhere on earth (Cone, 2008; Newsome *et al.*, 2010). Peregrine Falcons have been recorded adopting anthropogenic structures in urban habitats across much of their range including

Italy (Taranto, 2009), Germany and Poland (Kleinstäuber & Kirmse, 2009; Wegner *et al.*, 2009), Canada and the US (Cade & Bird, 1990; Cade *et al.*, 1996), the UK (Drewitt & Dixon, 2008) and Australia (Emison *et al.*, 1997). With this increasing growth in urban populations it is important to determine the effect of landscape features on the LRO of Peregrine Falcons.

The data in this chapter is based on an extensive 22 year (1991-2012) capture-mark-re-sight (CMR) study across Victoria, Australia. During this time the reproductive output of known age animals (banded as nestlings and re-sighted as breeding adults) has been followed. In many cases we have been able to establish the lifetime reproductive output of individuals, and as such can investigate drivers of LRO. Broadly, this study aims to determine breeding lifespan and LRO parameters and what influences the LRO of Peregrine Falcons. Specifically, the study will investigate the relative role of nest site factors and landscape level factors on the LRO of Peregrine Falcons.

5.3. Methods

5.3.1. Study area

This study was undertaken in Victoria, south-eastern Australia across an area of approximately 227,000 km². The geographic range of the study area included a latitudinal span of four degrees (34° 30' to 38° 45' S) from north to south and seven degrees of longitude (141° to 148° E) from west to east. In total, 194 nests were monitored across Victoria (Figure 5.1) with the maximum distance between monitored nests being 589 km (west to east) and 521 km (north to south).

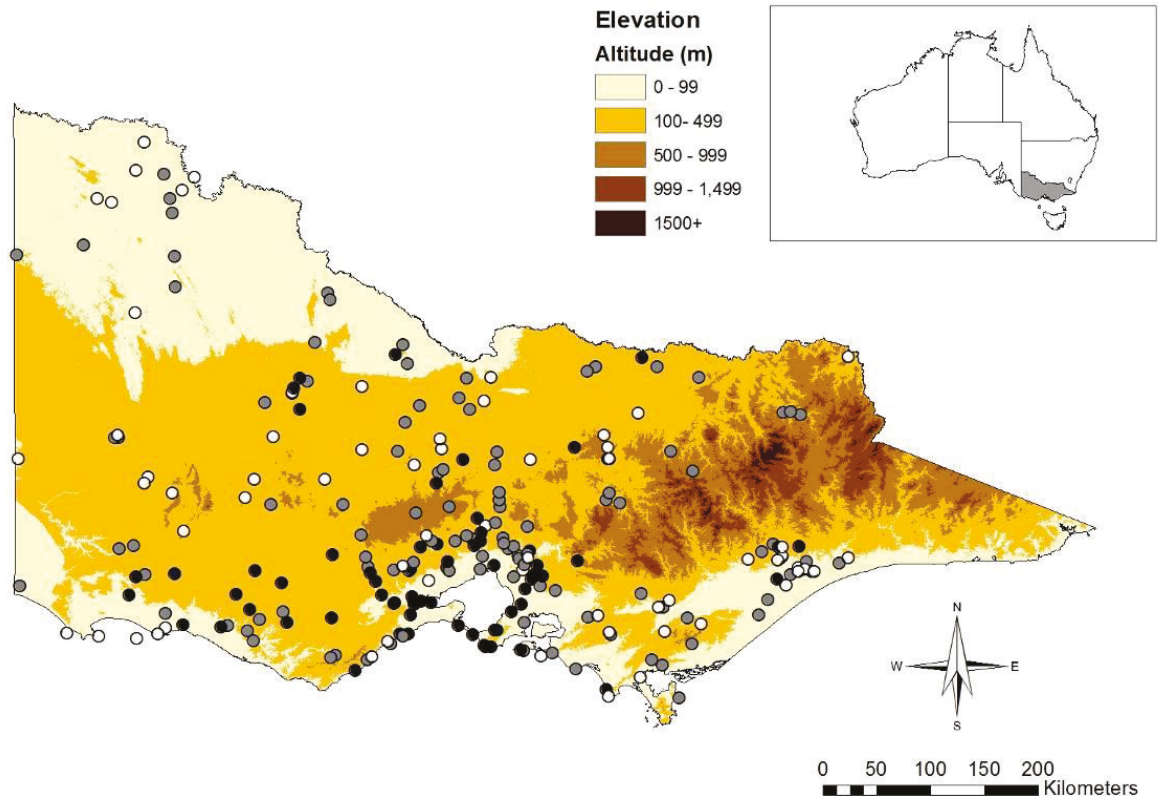


Figure 5.1 Location of Peregrine Falcon nests presented on a digital elevation map of Victoria ($n = 250$ known breeding sites). ● = sites where the complete breeding history (LRO) of an adult has been established ($n = 66$), ● = Sites where breeding has been monitored but the LRO of adults is unknown ($n = 128$), and ○ = Known sites that were not monitored for breeding ($n = 56$).

5.3.2. Terminology

A few terms are used throughout this paper for brevity and are explained here for ease of reading. Lifetime reproductive output (LRO) is the total number of nestlings an individual produces in their lifetime. We distinguish this parameter from lifetime reproductive success (LRS) which was originally coined to describe the total number of nestlings produced over a lifetime that survive to become breeders (Clutton-Brock, 1988). The same term (LRS) has also been used to describe the total number of fledglings produced over a lifetime (Newton, 1989). A ‘breeding event’ refers to a single

nest site's breeding activity and related data for one year's (Austral spring) breeding season. 'Available land' is the terrestrial or dry land that does not include the surface of lakes, reservoirs or oceans below the high tide line. 'Ecotone' in this study refers specifically to the environmental boundary between aquatic and terrestrial environments and includes the length of rivers and the shoreline of lakes, reservoirs and marine environments.

5.3.3. *Data collection methods*

Monitoring visits were made to as many nests as possible during each breeding season to collect data on the identity of adults (by observing metal Visual Identification (VID) tarsus bands), record clutch size and/or brood size, and band nestlings. Breeding adult Peregrine Falcons were individually identified by VID bands which had been applied to them as nestlings (Hurley *et al.*, 2007; Hurley *et al.*, 2013).

This study is based on a 22 year dataset (1991-2012) from monitoring breeding at 194 nest sites across Victoria. An average of 7.8 (± 0.4 s.e.) breeding events per nest site have been monitored (range 1-22) and a total of 1,504 breeding events are documented (68.3 ± 5.8 breeding events per year (mean $\pm$ s.e.), range 10-111). A total of 2,445 nestlings were colour banded (111.1 ± 9.5 per year (mean $\pm$ s.e.), range 14-179). A total of 122 of these banded nestlings have been recorded as breeding adults. Complete lifetime datasets including the age at first breeding, the number of years breeding and the total number of nestlings produced have been established for 66 of these individuals.

5.3.4. *Lifespan and lifetime reproductive output*

Long-term monitoring of adults at nest sites provided the age at first breeding (i.e. the year a banded bird replaced the previous adult), the number of years where breeding was attempted and the life-span (i.e. year and age of last confirmed breeding event) of banded individuals. Breeding adults were considered dead once they were found replaced at a nest site. Given the very high nest site fidelity in Peregrine Falcons (Mooney & Brothers, 1993; Zuberogoitia *et al.*, 2009) variation in lifespan most likely reflects variation in mortality rather than any dispersal effects. Over the lifetime of each of the breeding adults, all of the nestlings they produced were recorded to provide the lifetime reproductive output of individual adults. Where practicable all of these nestlings were also banded with VID bands.

5.3.5. *Landscape level features of breeding territories*

The location and altitude (recorded in meters above sea level (asl)) of active Peregrine Falcon nest sites was recorded using a hand held GPS unit (Garmin[®] II *Plus*). A set of landscape habitat features were measured using GIS layers from the Victorian government's corporate geo-spatial data library, accessed on 14 February 2013.

Landscape features were assessed within a radius of 5 km from each nest using GIS buffer and clip tools in ArcGIS 10.1 (ESRI[®]). This distance is considered to be reflective of the average distance of hunting trips from the nest, based on a radio tracking study of breeding Peregrine Falcons, undertaken in California (Enderson & Kirven, 1983). A further radio tracking study of breeding adults recorded an average hunting distance of 6.5 km from the nest on the Cape Peninsula in South Africa (Jenkins & Benn, 1998). Central place foraging also suggests, when not actively hunting, adults will spend

significantly more time in close proximity to the nest involved in activities such as mate and nest defense (Jenkins & Benn, 1998; Brambilla & Ficetola, 2012). The average distance between nest sites in Victoria was 11.3 ± 0.6 km; mean $\pm$ s.e.; ($n = 194$ nests), which is further indicative of a defended core breeding territory being approximately 5km in radius from the nest site.

A series of habitat features were selected to represent measures of land use, the potential productivity and the potential availability of food within each breeding territory. The length of riparian zones, lake and ocean shores were measured (km) within 5 km of the nest to create a cumulative figure of total water ecotone length (km). These ecotones are considered potentially important foraging areas where prey diversity and abundance tends to be greater than in the surrounding landscape (Kark *et al.*, 2007; Ambasht & Ambasht, 2008). This is due to these areas supporting a group of specialist species of the ecotone in addition to the species from either the terrestrial or aquatic environments, (Hofgaard *et al.*, 2012).

The number of land titles (i.e. addresses) within a 5 km radius from each nest was used to provide an index of the degree of urbanisation occurring within the breeding territory.

An index of urbanisation was included for two broad reasons; first, areas with elevated degrees of urbanisation have been reported as having an elevated and more stable avian prey base (Chace & Walsh, 2006), and second, urban areas present increased threats such as the risk of collisions with overhead wires and windows, electrocutions, direct human persecution (Hager, 2009) and an elevated risk of infection from diseased prey (Boal & Mannan, 1999) or ingestion of and bioaccumulation of anthropogenic poisons or

pollutants (DeMent *et al.*, 1986; Chandler *et al.*, 2004; Hofer *et al.*, 2010; Park *et al.*, 2011).

A further measure of urbanisation was also developed associated with the number of addresses within a 1 km radius of each nest. This second measure was included because in Australia, Peregrine Falcons disperse at approximately 5 months of age (Sherrod, 1983) and 74.6% of recoveries of dead or seriously injured birds < 6 months of age are found within 1 km of the nest (unpublished data). Adults are likely to contend with the same anthropogenic hazards in urban environments as dispersing young (Hager, 2009) with the figures suggesting that many of these anthropogenic induced mortalities will occur within 1 km of the nest.

The validity of applying the 1 km urban buffer to the lifespan of breeding adults will be tested by applying Spearman Rank Order Correlation to the proportion of individuals effected by each major cause of injury or death in each age class. Individuals that had successfully fledged but were found dead or injured ≤ 6 months old were classified as juveniles and those ≥ 2 years old classified as adults.

The extent and density of over story tree cover can provide an indication of how modified an environment has become. Native tree cover also provides an indication of the resources available to support hollow dependent prey species such as parrots (especially the Galah (*Eolophus roseicapillus*) which have been found to be a significant component of the Peregrine Falcon diet in Victoria (Pruett-Jones *et al.*, 1981b; Olsen *et al.*, 1993; Cogley, 1995; MacKinnon, 2011). However, the Peregrine Falcon is predominantly an open country hunting specialist and requires large areas with no or low

density tree cover to access prey (Ratcliffe, 1993; Jenkins, 2000b; Jenkins & Hockey, 2001). Metrics were therefore required which could provide an indication of both tree cover and no-tree cover in the landscape within the core area of the nesting territory.

A tree density layer was used in this study to generate metrics associated with differing tree densities. The tree density layer was created from satellite imagery with a pixel resolution of 10 metres and the tree density is based on projected canopy cover (for product description see DSE (2013)). The tree density layer maps three different densities of tree cover, these being dense, medium and scattered, with the unmapped component representing no tree cover. Dense tree cover includes areas with >80% canopy cover and a minimum block size of 5 ha. Canopy gaps within treed blocks less than 0.1ha were not mapped. Medium tree cover includes areas with 50-80% canopy cover and a minimum block size of 1 ha. Canopy gaps of less than 0.25 ha were not mapped. Scattered tree cover represents areas with 10-50% canopy cover and a minimum block size of 1 ha. Canopy gaps of less than 1ha were not mapped. Areas with <10% canopy cover, with a minimum block size if 1 ha, were not mapped, and represent no tree cover.

Within a 5 km buffer radius out from each nest the amount of tree cover was estimated, based on the three cover classes (high, medium and scattered). Tree cover was expressed as the percentage of the available land within the buffer zone; that is, excluding areas of ocean, lakes and rivers. There is a high degree of co-linearity between the different tree density classes, and as such two measures are used in the modeling conducted as part of this study. Dense tree cover and no tree cover are highly correlated, and as such we chose to use the no tree cover estimates as Peregrine Falcons require open areas in which

to hunt successfully (Emison *et al.*, 1997; Jenkins & Hockey, 2001). As a further measure, we used medium tree cover as it was not correlated with either tree cover metric.

5.3.6. Nest site level metrics

Nest site physical features such as nest size and the level of protection from weather and predators are known to significantly influence clutch size, hatch rates, and nestling mortality (Korpimäki, 1987; Olsen & Olsen, 1988a, 1989a, b; Emison *et al.*, 1993). Each nest was classified according to the level of protection from extremes in weather and was assessed in terms of angles of exposure. Exposures were measured by placing a compass in the center of the nest scrape and taking bearings to obstacles on either side, the difference in degrees between the bearings being the horizontal exposure (Pruett-Jones *et al.*, 1981b). Using a digital long arm protractor (Winkelfix, Festool Art. No.: 450121-267), vertical exposure was measured from the centre of the nest scrape as the difference in degrees between the horizontal floor and the first obstacle above the nest. Due to variability in the accuracy of some of these measurements three nest protection categories were used in this study: low = open site with no overhead protection (includes all stick nests), medium = vertical exposure $> 80^\circ$ and horizontal $> 160^\circ$, high = vertical exposure $< 81^\circ$ and horizontal exposure $< 161^\circ$.

Peregrine Falcons in Victoria use a number of different types of nest site. In this study data was recorded on lifespan and LRO from individuals ($n = 66$) breeding on cliffs ($n = 50$), building ledges ($n = 11$) and in tree hollows ($n = 5$).

5.3.7. *Statistical analysis*

5.3.7.1. *Life history attributes of the Peregrine Falcon*

The relationship between lifespan, the total number of years spent breeding and lifetime reproductive success was investigated using the Pearson product moment correlation coefficient. An independent samples t-test was used to compare between the sexes; the mean lifespan of breeding adults. As a result data for both sexes was pooled. These analyses were conducted in IBM SPSS Statistics 21.0.

5.3.7.2. *Factors affecting lifetime reproductive output*

To determine what factors influence the life time reproductive output (LRO) of Peregrine Falcons in Victoria, an information-theoretic approach was taken, as described by Burnham and Anderson (2002). As this study had a small sample size and the data were not over-dispersed, the second order Akaike information criterion corrected for small sample sizes (AICc) was utilised. Preliminary analyses were performed to ensure no violation of the assumptions of normality, linearity and homoscedasticity. Linear models were used to investigate the relationship between the LRO (Log 10 transformed) of Peregrine Falcons and a series of pre-determined models which we considered may explain the LRO of Peregrine Falcons. These models were developed to investigate the relative influence of nest site level and landscape level factors on the LRO of Peregrine Falcons. It should be noted here all breeding adults in this study remained within the one nest territory. However, where more than one nest ledge was used in a territory during the study, the level of protection of the most commonly used nest was assigned to the territory and used for these analyses.

The variables used in the models included the number of years which a falcon attempted to breed, the degree of protection afforded to the nest site, the type of nest site (i.e. cliff, building or tree cavity), the degree of urbanisation (the number of properties) at two different scales (i.e. within 1 km of the nest, and within 5 km of the nest (both Log 10 transformed)), the length (km) of water ecotone habitats (log 10 transformed), and the two tree cover parameters (i.e. the proportion of the landscape with no tree cover, and the proportion with medium tree cover (both arc sine transformed)). We chose to test five different models that could potentially explain trends in LRO at both the local scale (i.e. nest site), and the broader landscape scale (Table 5.1). As LRO is known to be correlated with the number of years over which an animal attempts to breed, we included the number of years breeding in all models. This was done to determine if there are any local level and landscape scale factors that contribute to LRO over and above the number of years of breeding. Table 5.1 provides details of each competing model and the justification for why each model was selected. A null model was also used within the modeling approach.

Models were developed using the R statistical package (Ihaka & Gentleman, 1996) version 2.15. All modeling was conducted using the MuMIN package, version 1.9.0 (Barton, 2013). Akaike differences (Δ_i) were used to determine the level of support for each model in the candidate set. Burnham and Anderson (2002) suggest that candidate models with Akaike differences less than 2.0 have substantial support. Akaike weights were produced to establish if one model had substantial support as the best model. Anderson *et al.* (2001) suggest an individual model needs an Akaike weight of greater than 0.9, before it can be considered the clearly best model. Multiple R^2 values were generated to establish how well the individual models were able to account for variation in the data.

Table 5.1 Models proposed to explain potential trends in the lifetime reproductive output (LRO) of Peregrine Falcons in Victoria (n = 66). The response variable for all models is LRO (the total number of nestlings produced over a Peregrine Falcon's lifetime (Log10 transformed)).

Model	Variables included	Justification for model
Breeding years model	Years of breeding	A clear trend exists between the number of years over which an animal breeds and its potential life time reproductive output ^{a,b,c,d} . This model is included to establish the base point, from which the other models are ultimately compared to establish if local and landscape factors further influence LRO.
Nest protection and nest type model	Years of breeding Nest protection Nest type	Previous studies have demonstrated that the type and quality of a nest site can have a significant influence on reproductive success ^{e,f,g,h} . Across the breeding life of an individual it would be expected that more protected nests sites may produce more offspring.
Landscape level resource model	Years of breeding Amount of water ecotone (Log10) Amount of land with moderate tree cover (ArcSin) Amount of cleared land (ArcSin) Altitude	Habitat features have been found to influence reproductive success ⁱ with individuals able to improve their reproduction by moving to higher quality habitats ^j . Water ecotones and tree covered areas provide productive habitat for Peregrine Falcon avian prey species. However, Peregrine Falcons are an open country hunter ^{k,l} and some level of open country is essential for them to access prey ^m . Altitude will provide access to different prey species ⁿ and at the higher levels remoteness from urban centres ^o . Combined these landscape features present a diverse range in quality of breeding territories that may produce differences in productivity.
Impact of urbanisation model	Years of breeding Urbanisation within 1km (Log ₁₀) Urbanisation within 5km (Log ₁₀)	Urbanisation levels have been shown to influence raptor reproduction both positively ^{p,q,r} and negatively ^{s,t} . Two urbanisation metrics were used to investigate local and landscape scale influences of urbanisation. It was unclear if urbanisation would have a positive or negative influence on LRO.
Global model	All variables included	This model is included to determine if the combined effect of all the different factors has an overall impact on LRO.
Null model	N/A	A null model was selected to rank all other models.

a=Robbins *et al.* (2011); b=Herényi *et al.* (2012); c=Linkhart and Reynolds (2006); d=Blums and Clark (2004); e=Olsen and Olsen (1989b); f=Emison *et al.* (1993); g=Mearns and Newton (1988); h=Hurley *et al.* (2013); i=Zhu *et al.* (2012); j=Newton (1991); k=Ratcliffe (1993); l=Jenkins (2000b); m=Jenkins and Hockey (2001); n=Barrett *et al.* (2003); o=Emison *et al.* (1997); p=Wegner *et al.* (2009); q=Kauffman *et al.* (2003); r=Charter *et al.* (2007)
s=Newsome *et al.* (2010); t=Boal and Mannan (1999)

5.4. Results

5.4.1. *Lifespan*

The total number of years spent breeding was recorded for 66 individuals (37 ♂, 29 ♀) (3.7 ± 0.3 ; mean $\pm$ s.e., range 1-9). Data for the number of years spent breeding was pooled for this study as there was no difference between the sexes (♂ 3.5 ± 0.4 ; mean $\pm$ s.e., range 1-9; ♀ 4.0 ± 0.5 ; mean $\pm$ s.e., range 1-9; $t = -0.768$, $df = 64$, $P = 0.446$).

5.4.2. *Causes of injury Vs age class*

Based on banding recoveries of dead or injured Peregrine Falcons, individuals were aged and injuries classified into one of ten distinguishable injury causes. Ten distinguishable causes of injury were identified from a total of 92 individuals banded as nestlings found dead or seriously injured. These were in increasing frequency order: trapped in man made structure, taken by introduced mammal, electrocuted, drowned, poisoned, attacked by other raptor species, shot, hit window, hit overhead wires or fence, and hit by car. Each individual was classified as either successfully fledged and < 6 month old = juvenile ($n = 66$) or ≥ 2 years old = adult ($n = 26$). The relationship between injury class and age class was investigated using Spearman Rank Correlation. Preliminary analyses were performed to ensure no violation of the assumptions of normality, linearity and homoscedasticity. There was a strong, positive correlation between the two variables (Spearman $\rho = 0.70$, $n = 10$, $P < 0.05$, $CI95\%$). That is the likelihood of being impacted by any injury cause is just as likely independent of age class.

5.4.3. *Lifetime Reproductive Output*

The complete lifetime reproductive output (LRO), which is the total number of nestlings surviving to banding, was recorded for the same 66 individuals (7.3 ± 0.7 ; mean $\pm$ s.e., range 0-20). LRO data was pooled for this study due to there being no difference in LRO between the sexes ($\sigma^7.1 \pm 0.9$; mean $\pm$ s.e., range 0-20, $n = 37$; $\phi^7.6 \pm 0.9$; mean $\pm$ s.e., range 0-20, $n = 29$, ($t = -0.377$, $df = 64$, $P = 0.707$).

5.4.4. *Drivers of lifetime reproductive output in Peregrine Falcons*

The six different proposed models to explain the lifetime reproductive output of Peregrine Falcons in Victoria (Table 5.1) were tested in a series of linear models. Two of these models had support as being able to explain trends in LRO, these being the breeding years model and the nest protection and nest type model (i.e. $\Delta AIC < 2$ Table 5.2). Neither model had support as the best model (i.e. AIC weight > 0.9), but the AIC weight of 0.678 for the nest protection and nest type model suggests it is a better model than the breeding years only model (AIC weight = 0.253, Table 5.2). Further, the delta AIC score of 1.97 for the breeding years only model is relatively low, and as such we considered that the nest protection and nest type model best explains trends in LRO. The high R^2 values for this model (i.e 0.7) suggest the model describes a considerable amount of the variation in LRO. From the nest protection and nest type model, LRO was clearly influenced by two of the variables included, these being years of breeding ($t = 0.092$, $P < 0.001$) and nest protection ($t = 2.729$, $P = 0.008$). LRO was positively associated with both years of breeding (0.109 ± 0.009 ; coefficient $\pm$ s.e.) and the protection afforded by the nest site (0.130 ± 0.048 ; coefficient $\pm$ s.e., Figure 5.2).

The modeling suggests that whilst LRO is heavily influenced by the number of years in which an individual attempts to breed, there is also a nest site level influence associated with the protection afforded by the nest location. More importantly, there was no support for models which incorporated landscape scale influences on LRO. Ultimately, this suggests that Peregrine Falcons may be largely unaffected by the surrounding landscape when it comes to their lifetime reproductive output.

Table 5.2 AICc model selection results for the six competing models used to explain the life time reproductive output (LRO) of Peregrine Falcons in Victoria. Listed are; the model description, the number of parameters (K), the log likelihood of the model (logLik), Akaike's Information Criterion for small samples (AICc), the differences in Akaike values (ΔAIC), and the goodness of fit of the model (Multiple R^2).

Model	K	logLik	AICc	ΔAIC	AIC weight	Multiple R^2
Nest protection and nest type model	5	17.578	-21.7	0	0.678	0.696
Breeding years model	2	13.073	-19.8	1.97	0.253	0.652
Impact of urbanisation model	4	13.731	-16.5	5.27	0.049	0.659
Landscape level resource model	6	15.073	-14.2	7.52	0.016	0.672
Global model	11	20.838	-11.8	9.94	0.005	0.725
Null model	1	-21.722	47.6	69.37	0	0

The question then arises, “are the number of years of breeding influenced by the site and landscape level variables used in the models?”. We conducted correlations between the number of years breeding and all the site and landscape scale variables used in the models and found no trends ($P > 0.05$). This further adds support to the concept that Peregrine Falcons are largely resilient to the different landscapes in which they inhabit, and if they are able to survive and breed over a number of years they will have reasonable LRO.

However, LRO, is further enhanced if the individuals nest site choice was good with a high degree of protection of the nest.

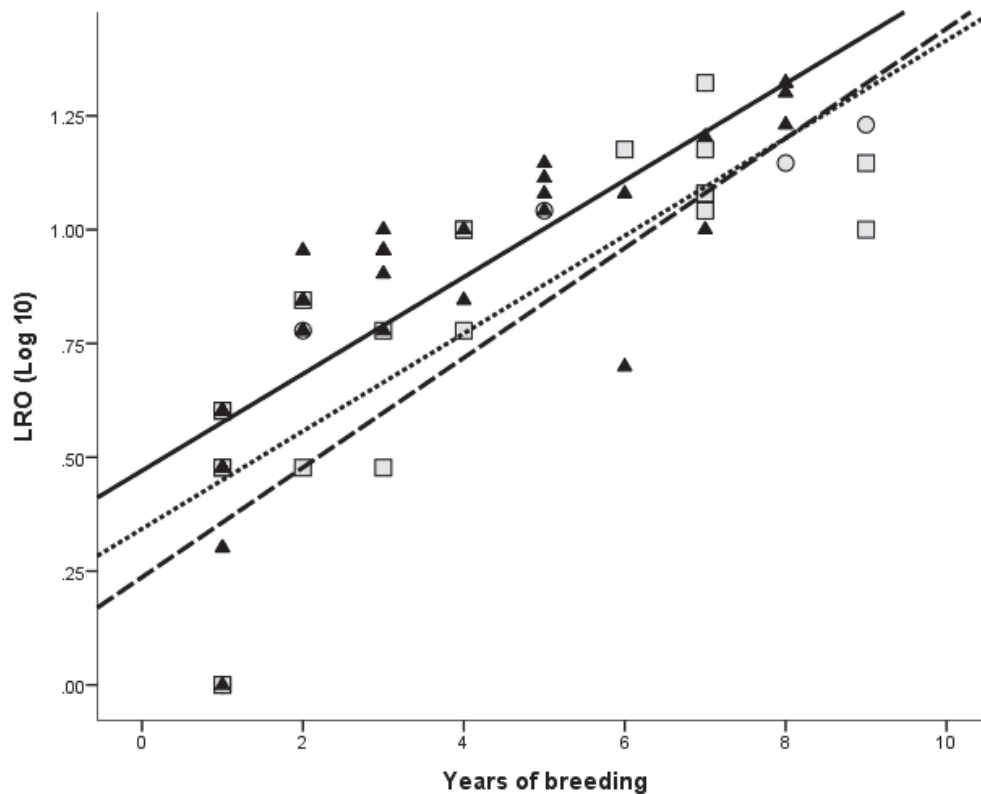


Figure 5.2 The relationship between the number of years of breeding and the lifetime reproductive output (LRO) of Peregrine Falcons in Victoria. The solid line and ▲ = nest sites with high protection, the dotted line and ◻ = nest sites with moderate protection, and the dashed line and ○ = nest sites with low protection.

5.5. Discussion

In this study we found that the LRO of Peregrine Falcons is mainly associated with the number of years over which an individual attempts to breed. LRO was further enhanced for individuals breeding at nest sites with higher degrees of protection from the elements. This suggests that, whilst successful breeding can occur at nest sites with lower protection, the initial decision of choosing a highly protected nest site potentially confers

increased fitness on the individual. The landscape features we considered (amount of urbanisation, proportion of cleared land, moderate tree cover, and land to water ecotones) were not shown to enhance LRO when compared to the breeding years and nest protection model or the breeding years only model.

Land use and habitat quality has been linked to breeding success in Lesser Kestrels (*Falco naumanni*) in Portugal (Catry *et al.*, 2013), Northern Goshawk (*Accipiter gentilis*) in Finland (Byholm *et al.*, 2007), Tengmalm's Owl (*Aegolius funereus*) in Finland (Korpimäki, 1988) and Sparrowhawks (*Accipiter nisus*) in Scotland (Newton, 1991). So why are landscape variables not good at predicting lifetime reproductive output for Peregrine Falcons in Victoria? At least in terms of this study, there appears to be two key drivers of LRO, nest quality and breeding lifespan. Nest quality (in the form of exposure to the elements) has already been demonstrated to influence annual breeding success in this species (Mearns & Newton, 1988; Olsen & Olsen, 1989b; Emison *et al.*, 1993). So what is the advantage to individuals to remain at a lower quality nest site? Two key factors are most apparent; firstly, Peregrine Falcons have the weapons (talons and avian killing experience) coupled with aggressive territorial willingness to kill interlopers (Zuberogoitia *et al.*, 2002), meaning breeding dispersal to a new territory is a high risk strategy for this species. Secondly, complete clutch failure at poorly protected sites tends to occur only in years of exceptional rain (Olsen & Olsen, 1989b) or snowfall (Mearns & Newton, 1988; Bradley *et al.*, 1997). Increased lifespan leads to increased LRO, even at poorly protected sites. One feature of this phenomenon is high mate and breeding territory fidelity (Mooney & Brothers, 1993).

Nest defense may therefore be an important factor in nest site fidelity even if the nest is of lower quality. Also of the 66 adults monitored in this study none were recorded moving to another territory. This level of nest fidelity and territorial defense is consistent with the resource or mate defense breeding strategy used by the Peregrine Falcon (Wightman & Fuller, 2006). Expanding on the nest defense theory of site fidelity, we have four records of an adult Peregrine Falcon being killed at a nest site during the breeding season. In each case it was a female that died. In one case the resident was killed and in the other cases the intruder was killed. Whilst seldom recorded (Ratcliffe, 1993; Zuberogitia *et al.*, 2002) the cases in this study attest to the risks involved in co-opting an occupied territory by this species.

Peregrine Falcons are extremely flexible in the environments they will occupy, and have been shown to be quite flexible in their diet. Such adaptability in these two aspects of the ecology of a highly mobile species would have assisted in the dispersal of the Peregrine Falcon across the globe (Santana *et al.*, 2006; White *et al.*, 2013). Flexibility in hunting strategies; switching from day to night hunting in urban New York (DeCandido & Allen, 2006); changing the composition of the diet at a nest site over time to improve hunting efficiency and to exploit a new prey species (Dekker & Taylor, 2005); switching from birds to mammals in years of high microtine rodent abundances in arctic Canada (Bradley & Oliphant, 1991); young preying upon micro bats (Silver-haired (*Lasionycteris noctivagans*), Big Brown (*Eptesicus fuscus*), and Red (*L. borealis*)) Lake Michigan, USA; raising young on fish, Alaska (Hetzler, 2013); opportunistically hawking for insects in urban Melbourne at night (unpublished data from this study); taking locusts during tropical grassland fires in Fiji and avoiding starvation by feeding on migrating dragonflies (Lesser Emperor (*Anax parthenope*) and Globe Skimmer (*Pantala*

flavescens)) on an Hongdo island off South Korea (Byre, 1990; White & Brimm, 1990; Cogley, 1995; Choi & Nam, 2012) all attest to a high degree of dietary flexibility.

Selecting a nest site and attempting to breed is likely to be a second order decision compared to the establishment and maintenance of a territory. An individual will only reside in and establish a territory in an area that provides the base resources required for survival. Once a territory has been established, it is likely that the individual will then look towards attempting to breed. This may involve choosing a highly protected nest site and as such maximizing their chance of high LRO, or accepting a lower quality nest site and suffering a reduction in LRO due to failures in those years of high rain/snowfall.

How can these findings be applied to maximize the reproductive output of this and other recovering populations? This is a critical question as Peregrine Falcons have suffered dramatic global declines due to the effects of DDT (Cade *et al.*, 1988; Ratcliffe, 1993). The banning of this class of chemical across much of the Peregrine Falcons' range has removed the major threatening process causing these declines. Considerable global efforts have been invested in recovering populations of Peregrine Falcons (Cade *et al.*, 1988; Cade *et al.*, 2009; Sielicki & Mizera, 2009). This current research has established that reduced protection of the nest site will have a dampening influence on the LRO of individuals. If the level of protection afforded by a nest site can be corrected through intervention approaches such as the use of nest boxes or improving the drainage of a nest ledge, it should be possible to allow individuals to maximise their LRO. If all poorly protected nest sites can be enhanced to correct for this, I propose that the growth rate of recovering Peregrine Falcon populations should increase.

6.

Interventions for improving the breeding success of the Peregrine Falcon (*Falco peregrinus macropus*) at anthropogenic nest sites: plugging an attractive sink.



The author on the 33rd level of 367 Collins St Melbourne

I have run,
I have crawled.
I have climbed highest mountains.
I have scaled these city walls,
these city walls.
Only to be with you.
Now I know,
I have found,
what I was looking for.

With apologies to Bono and U2

6.1. Abstract

Peregrine Falcons in Victoria, south eastern Australia have been recorded nesting on a wide variety of anthropogenic structures, from cliffs in stone quarries to city buildings and even adopting the stick nests of other bird species on high voltage transmission towers. The use of anthropogenic sites for nesting by Peregrine Falcons has grown naturally in Victoria from 7.5% in 1987 to 36.4% by 2012. During this study breeding performance was monitored at 127 nests, for at least five years each, from 1991 to 2012 and anthropogenic sites tended to have lower breeding success than natural sites (72.4% and 88.0% respectively). We tested if this lower breeding success was the result of unsuitable physical features of the nests, exposing the eggs to the effects of temperature or rainfall. Nest boxes were installed at 18 poorly performing anthropogenic sites (8 quarry cliffs, 10 buildings) where egg hatch rates averaged 25.6% (± 5.63 s.e.) compared to 63.25% (± 3.65 s.e.) for 18 reference cliff sites. At the 18 treatment sites, where nest boxes were installed, egg hatch rates increased significantly (Tukey, $P < 0.001$) to 76.64% (± 2.74 s.e.).

Urban growth projections globally suggest that nesting opportunities for Peregrine Falcons on anthropogenic structures are likely to continue to increase. To inform both site managers and biologists, a decision matrix was developed outlining the strategies available for the management of Peregrine Falcons attempting to breed at anthropogenic sites.

6.2. Introduction

Anthropogenic change to natural environments presents significant challenges to species globally (Chace & Walsh, 2006). Conservation biology is increasingly focused on the role of anthropogenic disturbance from both the species perspective, and also the ecosystems we are seeking to protect (Miller & Hobbs, 2002; Thompson *et al.*, 2003). Urbanisation is widely considered one of the most damaging anthropogenic disturbances that can be applied to natural and semi-natural ecosystems (Vitousek *et al.*, 1997). With current projections that over 50% of the world's population will reside in cities within the next 30 years (United Nations, 2012), the challenge of managing the impacts of anthropogenic disturbance processes will become critical to the field of conservation biology. With the impact of anthropogenic change in the landscape extending well beyond the urban footprint of cities (Suárez *et al.*, 2009; Sonne, 2010; Glennon & Kretser, 2013), many species will be presented with limited or no potential for population expansion (Robertson & Hutto, 2006) and numerous species will decline in response to anthropogenic disturbances (Wilcove *et al.*, 1998; Czech *et al.*, 2000; Gowdy *et al.*, 2010).

Native bird species are affected by anthropogenic change in vastly different ways (Chace & Walsh, 2006; Strasser & Heath, 2013 *in press*), however, raptors are a group particularly vulnerable to subtle aspects of these changes (Boal & Mannan, 1999; Ratcliffe, 2003). With a requirement for comparatively large home ranges (Newton, 1979a; Burnham & Newton, 2011), due to elevated food requirements, and often displaying sensitivity to human disturbance near nests (Olsen & Olsen, 1980; Richardson & Miller, 1997; Watson, 2004; Dennis *et al.*, 2011) raptors would be expected to suffer extensively from urbanisation. Furthermore, as with all predators, bioaccumulation of

persistent organic pollutants remains an ongoing threat (de Wit *et al.*, 2006). Despite this sensitivity to human disturbance, a wide range of raptor species are known to nest in urban and other highly modified environments, taking advantage of a variety of anthropogenic structures including high voltage transmission towers (Steenhof *et al.*, 1993; Bunnell *et al.*, 1997; Ledger & Hobbs, 1999; Dell'Omo *et al.*, 2009), hydroelectric dam walls (White *et al.*, 1988), power station structures and chimneys (Tordoff *et al.*, 1998), road and rail bridges (Bell *et al.*, 1996; Septon *et al.*, 1996), large coal mining machines (Wegner *et al.*, 2009) and high rise city buildings (Bird *et al.*, 1996; Cade *et al.*, 1996; Wegner *et al.*, 2009). Raptors breeding on anthropogenic structures have often been attracted to sites by the prior installation of artificial nesting substrates in the form of platforms, nest boxes and artificial burrows (Ewins, 1996; Gottschalk *et al.*, 2011; Libois *et al.*, 2012).

The creation of some anthropogenic structures, particularly buildings and quarry cliffs, has artificially enhanced the primary nesting cue (i.e. topographic relief) for some cliff-nesting raptor species (Bird *et al.*, 1996). In effect, these structures act as supernormal releasers for nesting (Robertson & Hutto, 2006). Cliff-nesting raptors have adopted buildings as nest sites in many different ways, including the use of ceiling spaces and holes in walls in farm houses by the Lesser Kestrel (*Falco naumanni*) in Spain (Franco *et al.*, 2005; Calabuig *et al.*, 2008); the use of window sills by the Eurasian Kestrel (*Falco tinnunculus*) in Israel (Charter *et al.*, 2007); and increasingly, the adoption of city building roof tops or ledges by the Peregrine Falcon (*Falco peregrinus*) across Europe (collated in Sielicki & Mizera, 2009), North America (Frank, 1994; Bird *et al.*, 1996; Burnham & Cade, 2003; Banks *et al.*, 2010) and Australia (Emison *et al.*, 1997). Such

sites are considered to offer secure nest locations protected from ground predators and are potentially exposed to lower levels of human disturbance.

Unlike most raptor species that construct their own stick nests, cliff nesting *Falco* species require nest sites with protection from rainfall, water run-off and ground water seepage (Emison *et al.*, 1993). The level of protection from adverse weather is thought to determine the quality of the nest at the micro level (Olsen & Olsen, 1989b). The local context of the nest location (e.g. a nest on a petrochemical plant compared to one on a small quarry cliff in a rural landscape) may be expected to present further nest site-specific risks to fledglings as they learn to fly. Given the importance of successful breeding to a population, and the apparent global trend towards increased nesting on anthropogenic derived structures (Bird *et al.*, 1996), it is critical that research assesses whether breeding on such structures presents an advantage or disadvantage to the breeding individuals.

An increase in the number of breeding Peregrine Falcons using anthropogenic structures in Europe (Wegner *et al.*, 2009) and North America (Bird *et al.*, 1996; Tordoff & Redig, 1997) has often been initiated and enhanced through the release of captive-bred birds from nest boxes installed on buildings (Marks, 1994; Cade *et al.*, 1996). This has been further supported by the installation of nest boxes on many other industrial constructions to encourage nesting (Tordoff *et al.*, 1998; Carlton, 2003). It is not known how productive these sites would have been for Peregrine Falcons without such interventions (Delibes *et al.*, 2001a). The breeding performance of raptors at anthropogenic sites pre and post nest site intervention has not been well documented. Given the popularity of installing nest boxes (especially for birds) it is important to investigate the efficacy of

this approach for each target species, particularly given that the provision of artificial nest sites to attract species to breed can be counterproductive to the conservation of species (e.g. Mänd *et al.* (2005); Klein *et al.* (2007); Björklund *et al.* (2013)).

In Australia, the Peregrine Falcon has adopted anthropogenic structures for nest sites without the aid of release programmes (Olsen & Olsen, 1988b) or the installation of nest boxes to attract them to nest on anthropogenic structures (White *et al.*, 1988; Emison *et al.*, 1997). This population therefore, presents an ideal opportunity to investigate how these newly adopted anthropogenic nest sites perform relative to natural sites and whether they require particular management interventions to promote successful breeding.

Nest site quality is critical to the breeding success of the Peregrine Falcon (Olsen & Olsen, 1989b; Emison *et al.*, 1993; Wightman & Fuller, 2006). This is especially pertinent within the current context of increasing levels of occupation of anthropogenic structures reported in other studies (Bird *et al.*, 1996; Taranto *et al.*, 2008; Wegner *et al.*, 2009). This research, therefore, aims to investigate the impact of anthropogenic derived nest sites on the breeding performance of the Peregrine Falcon in Australia. More specifically this research aims to:

1. determine whether the number of anthropogenic sites adopted by Peregrine Falcons for breeding (in Victoria) has increased since earlier studies ending in 1984 (White *et al.*, 1988);
2. compare the breeding performance of Peregrine Falcons at anthropogenic sites to natural sites;

3. determine the causes and timing of nest failure at both anthropogenic and natural nests;
4. determine whether nest site interventions could be an effective strategy for aiding reproductive output of Peregrine Falcons, and;
5. consider strategies that can be incorporated in the decision-making process to manage Peregrine Falcon nest sites at anthropogenic sites.

6.3. Materials and methods

6.3.1. Study area

This study was undertaken in Victoria, south-eastern Australia, and covered an area of approximately 227,000 km². The geographic range of the study area included a latitudinal span of four degrees (34° 30' to 38° 45' S) north to south and seven degrees (141° to 148° E) of longitude west to east. Peregrine Falcon nests were actively searched for between 1991 and 2012, to provide information for this research. Active nests were located during this study through a range of methods including detailed area searches, on-ground confirmation of historical nests and data collected in earlier surveys from 1975 to 1984 (White *et al.*, 1981; Emison & White, 1988), the use of government wildlife atlas records, responding to reports from the general public and land managers, and by opportunistic observation. In total 250 nest sites were located across Victoria where Peregrine Falcons had attempted to breed. For each of these nests, the type of nest (cliff, building, tree cavity or stick nest) and its origin (natural or anthropogenic) was determined. Of these sites, 192 were monitored for breeding success. A minimum of five years of breeding data was collected, from 1991 to 2012, for 127 of these nest sites

(Figure 6.1). The maximum distance between monitored nests was 589 km (west to east) and 521 km (north to south).

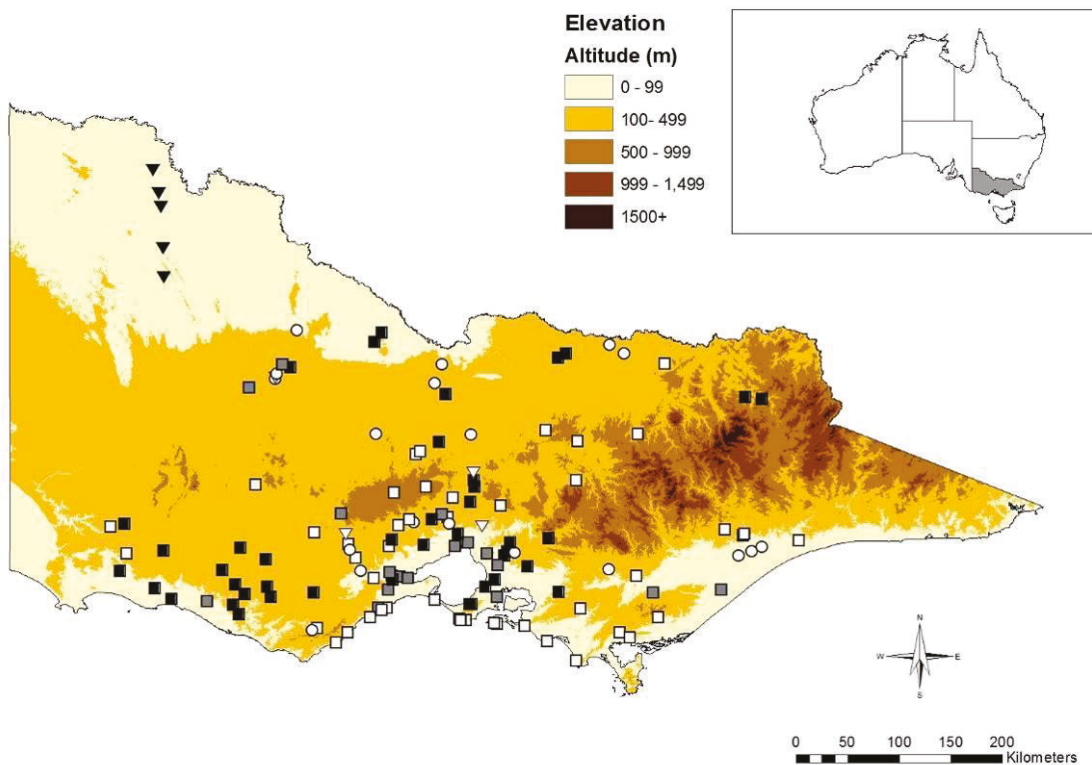


Figure 6.1 Locations of Peregrine Falcon nests monitored for at least five years between 1991 and 2012 displayed on a modeled elevation map of Victoria ($n = 127$). Natural sites are represented by: $\square$ = cliff, $\circ$ = tree hollow, ∇ = stick nest in tree, and anthropogenic sites: $\blacklozenge$ = building, $\blacksquare$ = quarry cliff, and $\blacktriangledown$ = stick nest on tower.

6.3.2. Terminology

Several key terms are used throughout this study and a definition of each is provided as follows (adapted from Steenhof and Newton (2007)). Origin refers to whether the nest is on a structure (cliff or building) that is of anthropogenic origin or a naturally occurring feature (cliff or tree). A breeding event combines the site and the year as a single unit and is defined as when a nest territory is occupied and the resident pair of Peregrine Falcons attempt to lay eggs in a single breeding season (or year). A successful breeding

event is one when one or more eggs hatch. Clutch size is the total number of eggs laid for a single annual breeding event. Brood size is the total number of nestlings hatched as recorded at the time of banding. This method has been adopted because observing actual hatching of all clutches was not possible. Hatch rate is taken as the number of nestlings either known to have hatched (determined during surveys early in the nestling period) as a proportion of the eggs laid or where actual hatch rate is not known the number of nestlings alive at banding is recorded as the hatch rate of the eggs laid.

6.3.3. *Materials and data collection*

Breeding observations were made in two ways. (1) remote observations were made by using a tripod-mounted Leica Televid 77 spotting scope with Apo chromatic lens to count the number of eggs laid (clutch size). (2) at sites where the nest contents could not be observed from a distance, the site was climbed to determine clutch size. Second, nests were visited later in the breeding season to band nestlings and a count of all nestlings that survived or died prior to banding age (26 days post hatching). Surviving nestlings were banded with metal Visual Identification (VID) tarsus bands (Hurley *et al.*, 2007; Hurley *et al.*, 2013). Monitoring visits to determine fledging rates were conducted on an *ad hoc* basis. A further monitoring technique included using the spotting scope to observe the resident adults at each nest site for the presence of VID leg bands. These surveys were undertaken during either the clutch monitoring visit or the visit to band nestlings.

Where practicable, at sites where breeding by Peregrine Falcons had failed, the cause of failure was assessed at each site (Steenhof & Newton, 2007). At anthropogenic sites, information on breeding events including clutch size, brood size and causes of egg or nestling mortality were collected from on-site workers and managers in addition to our

own assessments. At natural sites causes of mortalities were based on visual assessment of the nest contents and the immediate environment. These assessments were either direct (e.g. observation of predator at the nest or lead shot pellets located via x-ray of nestling carcasses) or indirect (e.g. the presence of a full clutch of un-hatched eggs in an undisturbed cliff nest and, in one case, evidence of recent removal of stands of invasive Monterey pine (*Pinus radiata*) above the nest). Removal of the pines (back-dated with the land manager) had occurred during the mid-incubation period for the site causing the adults to cease incubation for eight hours in cold weather.

At anthropogenic sites where breeding had failed for one or more years and nest quality appeared to be the cause of failure (i.e. unsuitable nest substrate or inundation from water) a nest box was installed at the site. On the same day of installation, the old nest ledge was destroyed or removed to prevent future breeding attempts there. Nest boxes were constructed of marine grade plywood (19 mm thick and painted with at least four coats of outdoor grade acrylic paint). Boxes were made to two sizes (the smaller one for buildings and the larger one for cliffs). Small boxes had dimensions; 600 mm wide x 600 mm high x 600 mm deep, and the large boxes were 1,000 mm wide x 600 mm high x 600 mm deep. All boxes comprised of a roof, three walls and a base which had a 60-100 mm layer of coarse gravel and fly-screen mesh covering four drain holes of 25 mm in diameter each. The boxes were open on the long edge with a wall 100 mm high to retain a 90 mm thick layer of gravel which acts as a substrate that the female can form into a nest scrape.

Sites where nest boxes were installed are referred to as treatment sites. Breeding events at these sites are referred to as either pre-nest box or nest box used, which was

determined in relation to when the nest box (the treatment) was installed and used. A second set of sites (all cliffs) each located within 20 km of a treatment site were selected to provide a comparative dataset to the treatment sites and are referred to here as reference sites. The reference sites were selected based on their proximity to the treatment site as they were considered to be subject to similar weather conditions and had access to similar prey resources.

6.4. Results

The earliest surveys of Peregrine Falcon nests in Victoria were undertaken between 1974-79 and identified the nest type for 136 sites (White *et al.*, 1981) with no sites of anthropogenic origin recorded. By 1987, 11 nest sites were recorded of anthropogenic origin (White *et al.*, 1988), comprising 7.5% of the described sites for the State. A subsequent census of the origin of Peregrine Falcon nest sites early in the current study identified 199 sites of which 11.6% (23 of 199) were anthropogenic in origin (Emison *et al.*, 1997). By 2012 in the current study, 250 Peregrine Falcon nests were identified and classified based on their origin (i.e. natural ($n = 159$) or anthropogenic ($n = 91$)). At the state-wide level the prevalence of anthropogenic derived nest locations was 36.4%. This is a substantial increase from recent surveys, suggesting that anthropogenic derived nests have come to form a significant and rapidly growing proportion of the nest sites utilised in this population.

In the current study (1991-2012) each site was further categorised into one of four nest types: cliff, building (i.e. grain or cement silos and commercial buildings), stick nest and tree hollow. Stick nests at sites of anthropogenic origin were built by either Australian magpies (*Cracticus tibicen*) or raven species (*Corvus* sp.) on electricity transmission

towers ($n = 10$), a water storage tower ($n = 1$), or telecommunication towers ($n = 2$). The number of stick nests on anthropogenic structures is considered to be less representative than any of the other nesting categories because of the transient nature of these nests, the lack of targeted surveys of these structures and the difficulty in accessing them. Most anthropogenic cliff sites 68.8% were in actively worked quarries and were subject to limited direct human disturbance. The altitude of the nest was recorded for 219 sites. The mean altitude (meters above sea level (m asl)) of nests was compared between natural and anthropogenic sites, (natural = 201.5 ± 17.8 m, ($n = 130$), anthropogenic = 155.5 ± 13.1 m, ($n = 89$), (mean $\pm$ s.e.)) and was significantly different ($t=2.08$, $df=214.6$, $P=0.038$). This altitudinal distribution of Peregrine Falcon nest sites is reflective of more extensive anthropogenic developments at lower altitudes.

Of the 250 Peregrine Falcon nest sites identified throughout Victoria, a minimum of five years breeding data was collected from 127 sites (9.4 years ± 0.486 years (mean ± 1 s.e.)) from 1991 to 2012 (Table 6.1). These 127 sites provide the base breeding data used to investigate the role of nest origin and type on reproductive output. The ratio of anthropogenic to natural sites differed between the state wide population of known nests and those with more than five years of breeding data ($X^2_{(1)}=4.884$, $P < 0.001$) had been collected. Nest sites of anthropogenic origin were more prevalent than expected in the data where more than five years of breeding data were collected (adjusted residual = 2.3).

The dominant type of anthropogenic nest type is cliffs (21.2%) which are largely found in quarries, however, buildings also now constitute 10% of the overall nests in Victoria (Table 6.1). The composition of nest types in the data where more than five years of data were collected differs to that of the state wide population ($X^2_{(5)}=12.479$, $P = 0.029$). The

subset of nests where long-term breeding data is available contains more anthropogenic cliffs than expected (adjusted residual=2.7) and less natural stick nests (adjusted residual = -2.2).

Table 6.1 Number and percentages (in parentheses) of the four major nest types (cliff, building, hollow and stick nest) categorised by their origin for 250 Peregrine Falcon nests identified across Victoria from 1991 to 2012. The values in italics represent the 127 sites where more than five years of breeding data was collected.

Origin	Nest Type				Totals
	Cliff	Building	Hollow	Stick nest	
Natural	95 (38.0)	-	41 (16.4)	23 (9.2)	159 (63.6)
	<i>44 (67.7)</i>	-	<i>17 (26.2)</i>	<i>4 (6.2)</i>	<i>65 (51.2)</i>
Anthropogenic	53 (21.2)	25 (10.0)	-	13 (5.2)	91 (36.4)
	<i>43 (69.4)</i>	<i>16 (25.8)</i>	-	<i>3 (4.8)</i>	<i>62 (48.8)</i>
Subtotals	148 (52.9)	25 (10.0)	41 (16.4)	36 (14.4)	250
	<i>87 (68.5)</i>	<i>16 (12.6)</i>	<i>17 (13.4)</i>	<i>7 (5.5)</i>	<i>127</i>

6.4.1. *Breeding outcomes associated with nest origin*

Breeding data was collected for a total of 1,168 breeding events across the 127 sites where more than five years of breeding data was achieved. There was a difference in the proportion of successful breeding attempts between natural (88%, $n = 635$) and anthropogenic nest sites (72%, $n = 533$; $X^2_{(1)}=44.71$, $P < 0.001$).

Clutch size (count of eggs laid) was recorded for 462 breeding events at 136 sites (59 natural, 77 anthropogenic). Overall, there was no significant difference in clutch size between natural sites (2.77 ± 0.052 ; mean $\pm$ 1 s.e.) and anthropogenic sites (2.86 ± 0.043 ;

mean $\pm$ s.e.; $t = -1.332$, $df = 460$, $P = 0.183$). This suggests that nest origin does not have a significant influence on the egg producing capacity of Peregrine Falcons.

For breeding events where brood size was known, a total of 2,420 nestlings hatched successfully. On average across all sites, there were 1.87 nestlings per breeding event and 2.45 per successful breeding event. There was a significant difference in brood size between natural sites (2.18 ± 0.04 , mean $\pm$ 1 s.e.) and anthropogenic sites (1.85 ± 0.06 ; mean $\pm$ 1 s.e.) when the data for both successful and unsuccessful breeding events were considered together ($t=4.79$, $df=969.12$, $P < 0.001$). The brood size for successful breeding events only, did not differ between natural sites (2.42 ± 0.03 ; mean $\pm$ 1 s.e.) and anthropogenic sites (2.45 ± 0.04 ; mean $\pm$ 1 s.e.; $t=-0.478$, $df=950$, $P = 0.633$). This suggests that whilst the overall success rate of anthropogenic nests is lower than natural nests, if a clutch is successful in an anthropogenic nest it will be of a comparable size to a clutch from a natural nest.

6.4.2. *Causes of nest failure*

The failure of a breeding event can occur at any time between the laying of eggs and the final fledging stage. We have collected data for two different stages of the nesting period, the egg phase (incubation), and the nestling period between hatching and eventual fledging from the nest. In the following section we present the sources of failure at each of these two stages of the breeding cycle.

Egg hatch rates were determined for 488 breeding events. One or more eggs failed to hatch in 267 breeding events. The cause of egg failure was able to be confidently ascertained for 233 (87.3%) of these breeding events. In each individual failed breeding

attempt there was only one identified cause of failure (Table 6.2). Water damage from rainwater run-off or ground water seepage filling nest scrapes was the most common cause of incubation failure across all sites (33% for all failures for all sites, Table 6.2). The ratio in causes of egg failure differed between natural and anthropogenic nest sites ($\chi^2_{(7)}=45.201, P < 0.001$). Nesting on an unsuitable substrate (e.g. bare metal or concrete) did not occur in natural sites, but was a significant contributor to the difference between natural and anthropogenic sites (adjusted residual=4.7), contributing to 24% of the nests that failed at anthropogenic nest sites (Table 6.2). In natural sites, predation occurred more frequently than expected when compared to anthropogenic nest sites (adjusted residual=3.9). This data provides some degree of evidence for the suggestion that anthropogenic nests may be afforded some degree of protection from predators, but this comes at the expense of exposed or unsuitable nest substrates.

Table 6.2 Causes of Peregrine Falcon egg loss categorised by the origin of the nest site (natural or anthropogenic) and combined figures for both. Listed are the numbers of breeding events with egg failures. Numbers in parentheses are the percentages of breeding events for failed eggs from each nest group.

Cause of egg loss	Natural	Anthropogenic	Combined
Predation	14 (18.7)	8 (4.2)	22 (8.2)
Human disturbance	2 (2.7)	17 (8.9)	19 (7.1)
Unknown	14 (18.7)	20 (10.4)	34 (12.7)
Death of adult(s)	18 (24.0)	27 (14.1)	45 (16.9)
Water damage	25 (33.3)	64 (33.3)	89 (33.3)
Cracked egg(s)	1 (1.3)	10 (5.2)	11 (4.1)
Thin shelled egg(s)	1 (1.3)	0	1 (0.4)
Unsuitable substrate	0	46 (24.0)	46 (17.2)
Total	75	192	267

6.4.3. *Causes of nestling mortality*

A total of 54 nestlings were recorded dead between hatching and fledging for a total of 37 breeding events. Combined, the 54 nestling mortalities accounted for 2.23% of hatched nestlings recorded throughout this study. Nestling mortality was generally low across both natural and anthropogenic nest sites which precluded the possibility of meaningful statistical comparison. In general the causes of mortality were similar between both natural and anthropogenic nests. Human disturbance, however, was recorded in anthropogenic nests but not in natural nests. Similar to the causes of egg failure, natural nests appeared to have a slightly higher loss of nestlings due to predation than was experienced at anthropogenic nests (Table 6.3).

Table 6.3 Causes of nestling mortalities categorised by the origin of the nest (natural or anthropogenic) and combined figures for both. The first numbers listed are the number of nestling mortalities. Numbers in parentheses are the percentages of the total for each group of nests. Numbers in italics are the number of breeding events for each category. Data are from Peregrine Falcon nests in Victoria from 1991 to 2012.

Cause of nestling mortality	Natural		Anthropogenic		Combined	
Destruction of nest	3 (10.3)	2	2 (8.0)	2	5 (9.3)	4
Disease	3 (10.3)	3	7 (28.0)	7	10 (18.5)	10
Fell from nest	6 (20.7)	5	5 (20.0)	4	11 (20.4)	9
Human disturbance	0 -	0	3 (12.0)	1	3 (5.6)	1
Poisoning	1 (3.4)	1	2 (8.0)	1	3 (5.6)	2
Predation	16 (55.2)	8	6 (24.0)	3	22 (40.7)	11
Totals	29	19	25	18	54	37

6.4.4. *Treating poor performing anthropogenic nest sites*

Based on the data presented thus far, it was clear that some anthropogenic nest sites performed worse than natural nest sites. While not of major concern in itself, the

significant increase in the use of anthropogenic nest sites in Victoria suggests that the Peregrine Falcon population growth could be enhanced if breeding performance at these nest sites could be improved. All the data suggested that the main difference between natural and anthropogenic nests was associated with egg failure. If anthropogenic nests were able to be augmented in a way that could limit egg failure, the data suggests they could produce similar fledgling rates to those of natural nests.

As the main sources of egg failure in anthropogenic nests were associated with an unsuitable substrate and water seepage (57% combined), a nest box provision strategy appeared appropriate. Nest boxes were installed in 18 poorly performing anthropogenic sites, comprised of stone quarry cliffs ($n = 8$) and buildings ($n = 10$).

In all cases the cause of the poor egg hatch rates had been attributed to the quality of the nest site. After at least one year of monitoring breeding performance, a nest box was installed at each of these 18 sites (i.e. treatment sites). The treatment sites represented 19.8% of all anthropogenic sites and 7.2% of the 250 known breeding sites in Victoria. Treatment sites comprised quarry cliffs in exurban (i.e. rural $n = 5$, or suburban $n = 3$) landscapes and buildings in heavy industrial/urban ($n = 6$), peri-urban ($n = 1$) and rural ($n = 3$) landscapes. Breeding data were also collected over the same period at 18 other cliff nests (reference sites), located within 20 km of each of the treatment sites. The reference sites allowed for a spatial and temporal reference dataset from which to test the relative performance of the management strategy.

Breeding events where clutch size was known were grouped by site treatments and the average clutch compared between pre-nest box (2.54 ± 0.142 ; mean $\pm$ 1 s.e., $n = 67$ breeding events), nest box (2.52 ± 0.10 ; mean $\pm$ 1 s.e., $n = 176$) and reference sites

(2.58 ± 0.10 ; mean $\pm$ 1 s.e., $n = 151$). Consistent with our previous data, there was no difference in clutch size between the three treatments ($F_{(3, 391)} = 0.076$, $P = 0.927$, Figure 6.2).

Breeding events where brood size was known were grouped by site treatments and the average brood sizes were pre-nest box (0.95 ± 0.147 ; mean $\pm$ 1 s.e.), $n = 77$ breeding events), nest box (1.99 ± 0.10 ; mean $\pm$ 1 s.e.), $n = 198$) and reference sites (2.09 ± 0.07 ; mean $\pm$ 1 s.e., $n = 296$). There was a difference in brood size between the different treatment types ($F = 25.163_{(2, 568)}$, $P < 0.001$). There was no difference in brood sizes between the nest-box treated sites and the reference sites (Tukey $P = 0.680$). The brood size for the sites prior to nest box installation was, however, significantly lower than that for the post nest box installed sites and the reference sites (Tukey $P < 0.001$, Figure 6.2).

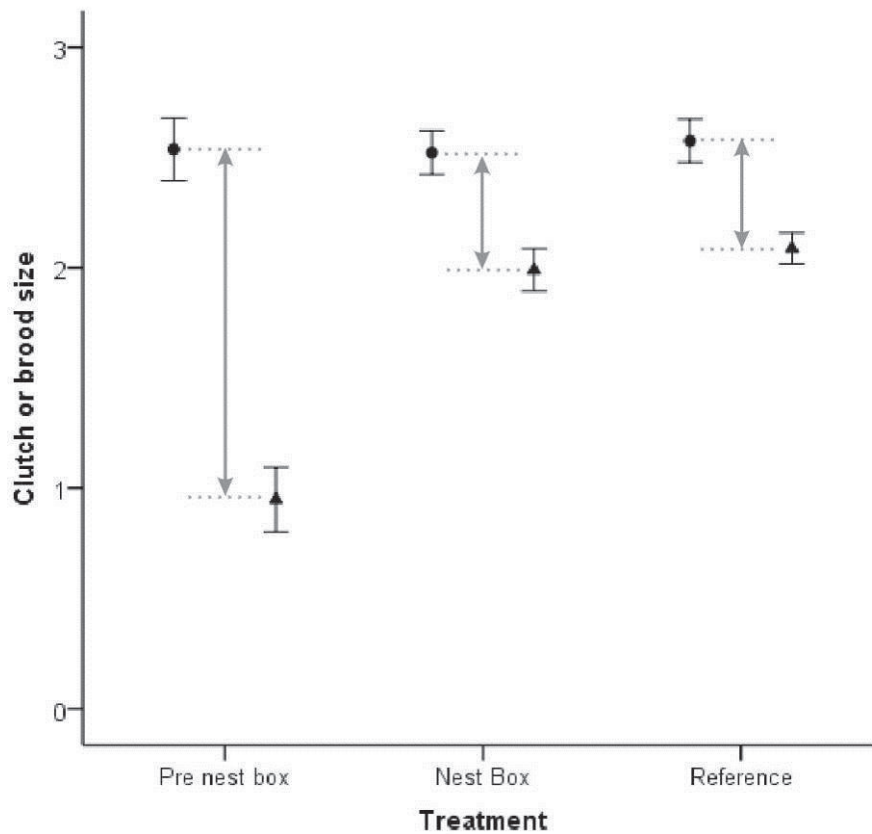


Figure 6.2 Mean number of eggs laid (clutch size) = ● and mean number of nestlings surviving to banding (brood size) = ▲. Whiskers show ± 1 standard error of the mean for three categories of nest site treatment at Peregrine Falcon nests in Victoria. Treatment sites ($n = 18$) are the same group of sites with means displayed for pre-nest box years and years in which a nest box was used. The reference sites are a different group ($n = 18$) of nest sites where nest boxes were not used. Solid gray lines (with arrows) illustrate the relative proportions of egg failure rates.

6.4.5. Egg hatch rates

Breeding events where hatch rate was known were grouped by site treatments and the average percentage hatch rate compared between pre-nest box ($25.64\% \pm 5.63$ (mean ± 1 s.e.), $n = 53$ breeding events), nest box ($76.64\% \pm 2.74$; mean ± 1 s.e., $n = 145$) and reference sites ($63.25\% \pm 3.65$; mean ± 1 s.e., $n = 126$). There was a significant difference in egg hatch rates between the three treatment types ($F_{(2, 321)} = 35.728$, $P < 0.001$). Hatch

rates at the nest-box treated sites were significantly higher than the reference sites (Tukey $P = 0.010$). The hatch rates for the sites prior to nest box installation were, however, significantly lower than that for the post nest box installed sites and the reference sites (Tukey $P < 0.001$).

6.4.6. Nest box cost-benefit assessment

Each nest box was constructed and installed at a cost of ~AU\$2,400 (2013 costings) including a steel frame which is bolted to a cliff face and upon which the nest box is attached. Nest boxes require replacement every ten years due to weather and rock fall damage. At this rate, the deferred cost per installed nest box is ~AU\$240 per year. For all nest boxes an average of 1.99 nestlings year⁻¹ (± 0.10 1 s.e.) were hatched. In terms of costs per nestling produced this equates to AU\$120.60 nestling⁻¹. In years of successful breeding attempts, nest boxes produced an average of 2.61 nestlings year⁻¹ (± 0.07 1 s.e.) which averages AU\$91.95 nestling⁻¹. By comparison the Midwest Peregrine Project in the USA paid US\$2,500 nestling⁻¹ captive raised and hack released (Sherrod *et al.*, 1982; Midwestern Peregrine Society, 2009).

6.5. Discussion

The proportion of anthropogenic sites used for nesting by Peregrine Falcons has increased over the past 30 years. This study presents a compelling case of an attractive sink (Delibes *et al.*, 2001b) that occurs at a significant proportion of anthropogenic nest sites. This sink is due to the physical qualities of the nest leading to significantly reduced egg hatch rates. Nest site interventions (i.e. nest boxes), once used, significantly

improved the egg hatch rate and as such mitigated the proximate negative effects of this sink. Subsequently addressing the primary cause of reduced breeding performance at anthropogenic sites via nest boxes *in situ* for this Victorian population was highly cost effective.

6.5.1. Attractive sink

Much of the recent theory developed around ecological traps has focused on their role in source-sink population dynamics (Remeš, 2000; Gundersen *et al.*, 2001; Battin, 2004).

One of the defining criteria of an ecological trap is that it occurs when rapid environmental change triggers a maladaptive choice for a lower quality habitat over a higher quality habitat (Robertson & Hutto, 2006). In this study, however, a source-sink paradigm is more applicable to individual nests based on their quality and performance as breeding platforms, than it is at the population level for this species (Robertson & Hutto, 2006). We contend that sites acting as attractive sinks, involve the behavioural choices of individuals rather than populations (Battin, 2004). For this species, in this study, sinks are more an individual than a population-level phenomenon (Robertson & Hutto, 2006). More specifically, not all anthropogenic nest sites without nest boxes behave as sinks and not all natural sites act as sources.

For the Peregrine Falcon, the physical quality of each nest is site-specific and independent of, or at least not driven by, broader habitat or landscape attributes (Olsen & Olsen, 1989b). Spatially, there is not an anthropogenic population of Peregrine Falcons because anthropogenic sites are scattered across landscapes and levels of urban development (Pulliam & Danielson, 1991; Emison *et al.*, 1997). Within this context it is

most useful to assess nest quality on a case by case basis instead of considering automatically all anthropogenic sites as attractive sinks for this species.

6.5.2. Ecological trap

The ecological trap operating at some anthropogenic cliffs and nearly all buildings observed in this study can be classified as a severe trap (Robertson & Hutto, 2006). The trap satisfies two criteria simultaneously: **a)** an increase in the attractiveness of these sites for nesting as demonstrated by the large increase in the use of these sites since the 1980s to the present, and the consistency with which they are occupied and the tenacity with which they are fought over, and **b)** a decrease in the quality of the habitat via negative impacts on breeding success. The third criteria for identifying an ecological trap (Robertson & Hutto, 2006) is a preference for the lower quality trap habitat over higher quality habitat. Many of the anthropogenic sites used in this study were in quarries located on flat or low lying areas (<200 m above sea level) that are devoid of natural cliffs. In these breeding territories there are no alternative cliffs to adopt. It is acknowledged that Peregrine Falcons will adopt stick nests of other birds (Emison *et al.*, 1997) and these provide a higher egg hatch rate than do cliff ledges (unpublished data). However, when natal dispersers are presented with cliffs or buildings and stick nests in the same area they prefer to adopt cliffs/buildings until these nest types are saturated (Kleinstäuber & Kirmse, 2009; Wegner *et al.*, 2009). Anthropogenic cliffs and buildings present an increased nesting stimulus to Peregrine Falcons due to the relative height of the visual or actual cliff they present (Bird *et al.*, 1996; Jenkins & Benn, 1998; Wightman & Fuller, 2006).

6.5.3. *Net box cost/benefit*

Cost benefit analyses of nest boxes for threatened species is controversial when working within the small population paradigm of critically endangered species (Caughley, 1994; Spring *et al.*, 2001; Lindenmayer *et al.*, 2002; Harley & Spring, 2003). The use of nest boxes was highly cost effective for this population of Peregrine Falcons (AU\$120.60 nestling⁻¹). This management strategy, however, must be seen more as one of proactive management of a healthy recovering population rather than restorative conservation borne out of necessity (Cade *et al.*, 1988; Sielicki & Mizera, 2009).

6.5.4. *Managing anthropogenic nest sites*

With 36.3% of Peregrine Falcon nests in Victoria currently on anthropogenic structures, and the human population set to increase by 29.3% between 2002 to 2030 (DOI, 2002; ABS, 2011) opportunities for nesting on anthropogenic structures will increase into the future (Bird *et al.*, 1996; Sielicki & Mizera, 2009). The installation of nest boxes overcame the attractive sink due to poor egg hatch rates at 18 anthropogenic sites and addressed the real life application of the scientific method to the conservation management of a species (Laurance *et al.*, 2012). A broader strategic approach is required to manage a range of potential impacts at anthropogenic nest sites. In cases of human disturbances interfering with breeding, well managed exclusion zones, both temporal (during the breeding season) and spatial (visual), can be effective management strategies to support successful breeding (Richardson & Miller, 1997; Rosenfield *et al.*, 2007). Applied correctly these measures can allow successful breeding in highly urbanised and industrial locations.

Following 22 years of working with industry, quarry and building managers, we have identified the most common issues that result in poorly performing Peregrine Falcon nests on anthropogenic structures. In response, we have developed three key intervention strategies. These are distilled into a decision matrix to illustrate the options available to site managers and biologists alike (Figure 6.3). If breeding was successful at a site then the nest is assessed for risks from water in a wet year or potential human disturbances during the normal conduct of business at the location. Management strategies can then be implemented. Where breeding is not successful due to nest quality factors then improvement of the nest through augmentation *in situ* is the first option. If the location of the nest site is not “acceptable” to site management (i.e. a nest on a quarry cliff that needs to be destroyed for stone extraction) then an alternative cliff face with a projected “working life” of ≥ 10 years is selected and a nest box installed. In situations where the cause of nesting failure is some “other factor”, such as human disturbance or an unusual rainfall event, and all other conditions were conducive to successful breeding then a management regime of temporal and spatial exclusion buffers is to be applied. Ultimately, the installation of a nest box at a secure location acceptable to the site manager (and raptor) tends to be the most effective solution. Advising site managers of the biology of the species and its requirements greatly assists in gaining acceptance of these requirements and managing a productive nest.

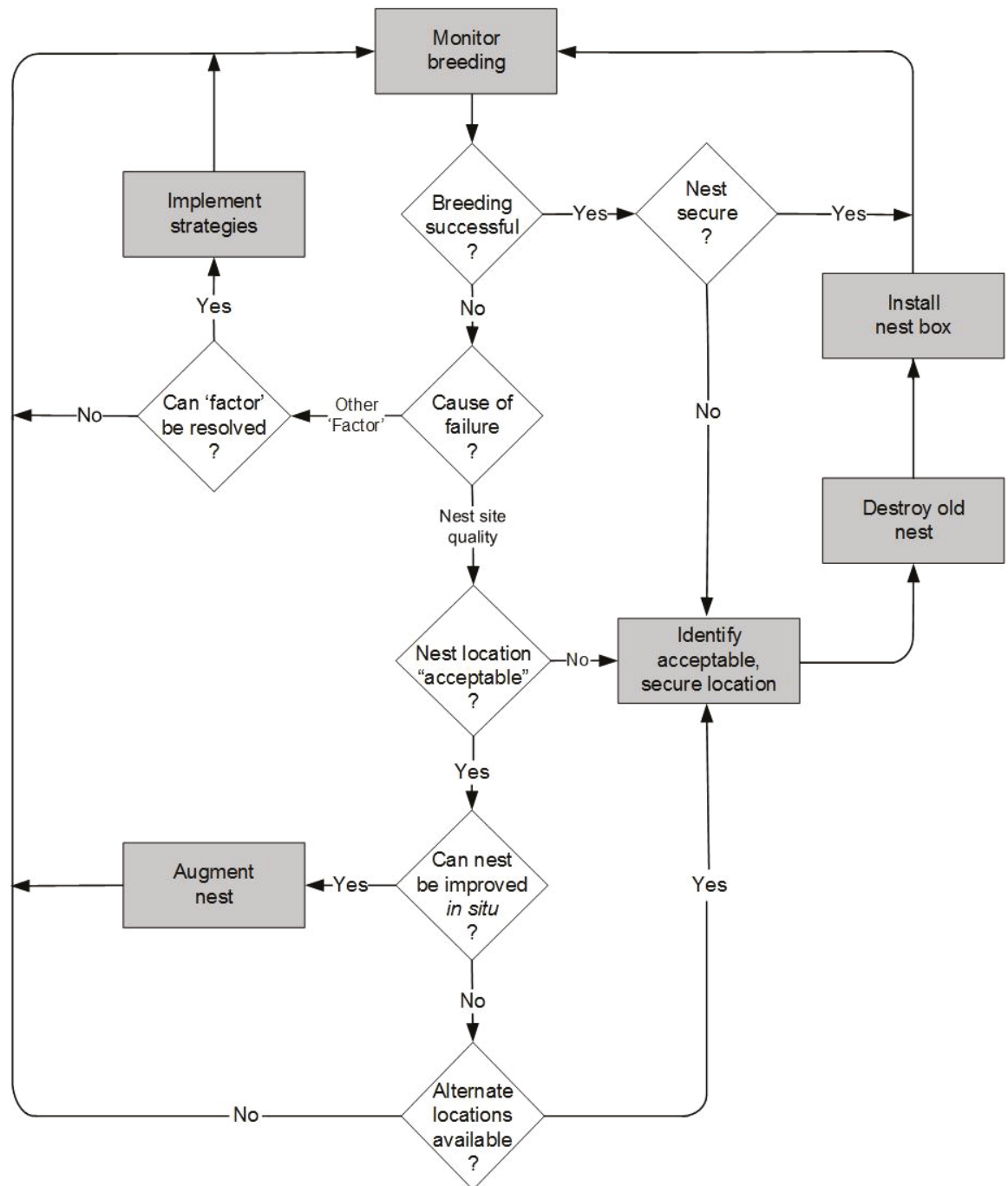


Figure 6.3 Decision matrix for known scenarios in managing Peregrine Falcon nests on anthropogenic structures. Grey boxes are management actions and white diamonds are decision points. All scenarios begin and progress from monitoring breeding, at the top of the decision matrix.

6.6. Conclusion

Peregrine Falcons are a rare example in human history of a native top order predator that has benefitted from some of the anthropogenic changes of the past 200 years in Australia (Emison *et al.*, 1997). Most notably, clearing of low lying areas for pastoral land uses has created ideal hunting habitat (Jenkins, 2000b) and the widespread creation of cliffs in stone quarries and the construction of various built structures has created artificial nesting opportunities where previously these were absent (White *et al.*, 1988; Bird *et al.*, 1996).

This study has shown that the use of anthropogenic sites for nesting by the Peregrine Falcon has become more common in Victoria from 1984 to 2012. These anthropogenic sites do not perform as well as natural sites and can act as attractive sinks, through reduced hatch rates due to exposure to water and temperature impacts. The reduced hatch rate leads to smaller brood sizes to cause a lower reproductive output at anthropogenic nest sites. Installation of nest boxes is a successful conservation management strategy at anthropogenic sites for this species because they improve the protection of the nest from temperature extremes, rainfall and water run-off and in this way allow for more successful incubation. A decision matrix for options to manage nests at anthropogenic sites provides a robust and transparent tool for resolving the interests (at times competing) of conservation biologists, site managers and raptors alike.

7. Synthesis and conclusions



The author, coastal cliff. (Image by K. Taylor, 2010)

“There is no great genius without a mixture of madness.”

Aristotle

7.1. Thesis overview

Longitudinal monitoring of any species provides a broader understanding of its ecology than time-for-space substitution studies (Clutton-Brock & Sheldon, 2010). In particular, long-term monitoring overcomes stochastic events such as drought, floods or wildfires and allows for measuring long-term trends (Magurran *et al.*, 2010; Lindenmayer *et al.*, 2012). Gathering lifetime data on marked individuals in a healthy population at a broad spatial scale also provides ecological benchmarks that are invaluable for species recovery planning should a population become threatened at some later stage (Wakamiya & Roy, 2009; Walsh *et al.*, 2012). Where a species is in a state of recovery following either captive release programmes or removal of the key threatening agent(s), monitoring is still critical (Groom, 2010; Finkelstein *et al.*, 2012). Complacency, even with common species, can lead to their rapid decline going unnoticed (Lindenmayer *et al.*, 2011). Yet it is not feasible to monitor every single species on the planet. Predators tend to be less diverse and less abundant than other bird species, but due to their trophic level are highly sensitive to disturbances in the food web (Smits & Fernie, 2012). Thus, of all the functional groups that can be monitored on a single species basis, monitoring a predatory species can be a strategically efficient decision. Whilst beneficial, the long term study of predators is, however, not without its challenges.

This study investigated a range of ecological attributes of the Peregrine Falcon across Victoria, not only as a top-order predator in recovery from past declines (White *et al.*, 1981; Emison & Hurley, 1995), but also as a species adapting to environmental change in the form of land clearance and urbanisation (Bird *et al.*, 1996). Two distinct themes have shaped the structure of the thesis: (1) development of new field techniques; and (2) investigating breeding success, the factors affecting it and management techniques to enhance it.

Prior to this study there was no direct field-based method available to accurately determine the sex of nestling Peregrine Falcons at the earliest age for banding (~15 days post hatching; Nelson (1988)). Traditional methods relied upon determining weight differences in mixed-sex clutches or delaying banding until nestlings achieved asymptotic weights to determine sex in the latter 22.8% of the nestling period (Nelson, 1988). A field-based method was developed in **Chapter 2** which effectively increased the banding “window of opportunity” three fold at each nest site to the last 65.6% of the nestling period. The morphometric technique developed achieved a level of accuracy of 98.6% to assign the sex of nestlings. This accurate sexing technique increased the window of opportunity for banding so the youngest bandable nestlings could be sexed. Following this the development of predictive methods based on recent phenology assisted scheduling field work so as to reduce the number of repeat site visits for banding was addressed in **Chapter 3**. The number of field visits per nest was reduced and more importantly the proportion of whole broods successfully banded increased from 67.4% to 94.5% compared to non-predictive methods. These innovations combined to significantly enhance the conduct of this study with gains in efficiency of conducting such a large scale CMR study.

The second theme of this thesis investigated breeding success and the factors affecting it in a healthy expanding population (**Chapters 4-6**). With all monitored populations of this species in various stages of recovery globally (Sielicki & Mizera, 2009), healthy naturally growing populations such as those in Victoria can provide insights into Peregrine Falcon ecology not necessarily available to researchers working with threatened, reproductively impaired, or reintroduced populations. **Chapter 4** explores patterns of dispersal and the level of nest site imprinting, attributes that have direct

application to efforts to re-establish the tree-nesting habit by this species across northern Europe (Kleinstäuber & Kirmse, 2009). Having selected a territory and nest site, the landscape context and nest quality factors that potentially affect the number of nestlings produced in a lifetime (lifetime reproductive output LRO) was investigated in **Chapter 5**. LRO appeared unaffected by landscape features but was significantly influenced by the number of years an individual bred and by the level of protection of the nest from the effects of weather.

With the increased use of anthropogenic structures as nest sites by Peregrine Falcons globally (Bird *et al.*, 1996), a detailed investigation as to how well these nests were performing was warranted. **Chapter 6** investigated a situation of testing nest site interventions at poorly performing sites against pre-intervention and control (reference sites). Installation of nest boxes significantly improved breeding performance by increasing the egg hatch rate. A cost-benefit analysis of this management strategy demonstrated it to be very cost effective at improving reproductive outcomes for this species in this population.

As the two themes in this thesis are sequential (i.e. successful research outcomes from the first provided the necessary framework to undertake the second), they will be discussed separately. The aim of this final chapter is to synthesize the study findings in relation to each theme (Table 7.1), and to discuss the associated implications for monitoring and managing breeding success of the Peregrine Falcon into the future.

Table 7.1 Key findings in relation to the objectives of this study and their implications for the conservation and management of the Peregrine Falcon in Victoria.

Theme	Objectives	Key findings & applications
Enhancing field techniques	Develop a field-based method to increase the accuracy in determining the sex of nestlings at the time of banding	- Developed and field tested a morphological method that is 94.5% accurate for sexing nestlings in the field. - This new method increases the banding 'window' for nestlings to a period of 20 days for ♂s and 27 days for ♀s.
	Improve efficiencies of conducting long-term CMR studies at a large spatial scale.	Developed and applied a rigorous process for selecting wildlife marking techniques applicable to any CMR study.
	Increase accuracy of predicting banding schedules	- Developed <i>a priori</i> and <i>a posteriori</i> quantitative methods to predict preferred banding dates. - Applied site histories of phenology to track long-term changes.
	Quantify a time efficiency benchmark for the collection of re-sight data	Measured survey time of VID banded adults as ~30 minutes per active nest site.
	Cost/benefit analysis of quantitative methods for predicting banding dates	Calculated the cost/benefit ratio of quantitative prediction based on phenology.
Patterns of dispersal	Determine natal patterns of dispersal	- Dispersal represents a resource defense model of reproduction – females disperse further. 30% of both sexes undertake novel dispersals – the highest level recorded for this species. This challenges current theories of natal nest site imprinting.
	Determine primary influences of dispersal type	Novel dispersals are less dispersive. This further challenges the concept of 'traditions' being maintained out of necessity (i.e. atypical nests are not only used in regions devoid of cliffs).
	Costs of dispersal type	As a highly adaptive species there are few costs incurred for distance and novel dispersals. (i.e. age at first breeding, lifespan, and reproductive output are not affected).
Influences on lifetime reproductive output	Determine the influence of landscape features surrounding nest sites on LRO	- The lifetime reproductive output (LRO) is most affected by the number of years breeding. - Increased years of breeding increases LRO but LRO is effected by poorer quality nest sites.
Managing anthropogenic sites	Measure the uptake of anthropogenic nest sites over time.	Confirmed a 6 x increase in the use of anthropogenic sites for nesting by Peregrine Falcons since 1987 in Victoria.
	Evaluate the efficacy of nest site interventions.	Nest boxes increased egg hatch rates by 50% at poorly performing anthropogenic sites.
	Cost/benefit analysis of nest site interventions in species recovery.	Calculated nest boxes cost AU\$120.60 per nestling produced as compared to US\$1,500 for captive bred hacked released Peregrine Falcons.

7.2. Enhancing field techniques

The field work to support this thesis, carried out over such a long period and at a large spatial scale, required the development of new techniques for it to be conducted as efficiently as possible. While annual field work targets were set for the number of nests monitored and a high priority was given to the number of nestlings banded, there remained an overall requirement that field work, and banding in particular, was undertaken ethically.

Studies of other dimorphic diurnal raptors presumably rely upon a traditional approach to assign sex before banding. This involves using some form of relative size index of nestlings post-asymptotic weight based on reversed sexual dimorphism (RSD), to assign sex before banding. I say ‘presumably’, because there are few published studies on sexing techniques for nestlings compared with the number of raptor species studied globally. The traditional approach restricts the window of opportunity for banding to the latter stages of nestling growth and places the nestlings and the bander at greater risk (Olsen & Olsen, 1987b; Nelson, 1988; Silvy *et al.*, 2005). The nestlings are at risk of injury or death due to premature fledging, and they have stronger beaks and talons which are more capable of injuring the bander. A new approach was required to accurately sex nestlings and band them as young as possible.

The accurate sexing of nestlings in the field (**Chapter 2**) addressed any ethical concerns with the more traditional approach (i.e. weight differences between brood siblings Nelson (1988)) and increased the efficiency of fieldwork. Publication of methodological studies can be problematic because they are not viewed as ‘discovery science’ (Nisbet, 2007)

and yet the development or refinement of a more efficient method is in a sense a discovery in itself (Freckleton & Iossa, 2010).

The application of molecular techniques to determine the sex of nestling birds is not new (Griffiths *et al.*, 1998; Kahn *et al.*, 1998; Fridolfsson & Ellegren, 1999), nor is the application of a discriminant function based on morphological measurements to determine nestling sex of raptors (Sarasola & Negro, 2004; Bavoux *et al.*, 2006). However, the accuracy of the method developed in **Chapter 2** and the relatively young age of nestlings at which this can reliably be applied is new for this species. This provides a model approach that can be applied to almost any raptor that displays RSD. This method gives certainty in sexing at the youngest age possible. The increased window of opportunity for banding was important due to the number of nests visited per spring breeding season in this study (range = 10-111, 68.4 ± 5.8 ; mean $\pm$ s.e.) and the scheduling of banding across a large area $\sim 227,000 \text{ km}^2$ (Bloom *et al.*, 2007).

In the future, a more accurate field-based sex allocation method may be developed and could involve some form of portable molecular analysis tool. A field-portable microarray platform is already being developed for the identification of arboviruses and species identification of mosquitoes and the species of their bloodmeals (Vora *et al.*, 2004; Grubaugh *et al.*, 2013). It is conceivable that advances in this technology may lead to portable systems for molecular sex determination in bird species and not just the Peregrine Falcon. Even with a more accurate sexing technique there will always remain a size and age limit below which a nestling's leg and foot will not retain bands (Emison & Bren, 1981). This places a practical constraint on how much larger the window of

opportunity for banding nestlings can become for the Peregrine Falcon and other altricial species (Olsen & Olsen, 1987b; Lowe, 1989).

Literature available at the beginning of this study in 1991 gave few clear indications of how to match the study hypotheses with the most appropriate and affordable capture-mark-re-sight (CMR) methods. More recently, there have been some notable exceptions investigating CMR techniques (Varland *et al.*, 2007; Thomas *et al.*, 2011; Silvy *et al.*, 2012). Furthermore, the efficiency of the chosen technique has seldom been measured, and when published focused on the effective range to re-sight and read VID bands (Tordoff & Redig, 1997; Lindberg, 2009). Having the efficiency, or a cost-benefit analysis, published for any marking technique would have helped in the selection of a CMR technique for this study. The evolution of CMR techniques that use tarsus bands has progressed from metal to plastic to VID metal bands, and more recently, to micro-chips or PIT tags on tarsus bands (McCulloch, 1990; Baillie, 2001; Smith & McGrady, 2009; Lutmerding *et al.*, 2012). These electronic tags may be the future in long-term CMR studies, however, this technology is still developing (Eymann *et al.*, 2006) and the reported error rates (i.e. PIT tags failing to be read generating false negatives) and the costs associated with each tag reader remains a concern (Smith & McGrady, 2009). No doubt, in time, unit costs will diminish and the reliability of these systems will improve.

A further approach to enhance field techniques was to determine the most appropriate method for marking and collecting re-sight data because a crucial component of this research was to monitor breeding adults of known age and origin. Several earlier studies have examined lifetime breeding parameters but relied primarily on monitoring breeding birds banded as adults or by taking photographs of breeding birds to identify individuals

through plumage patterns (Ambrose & Riddle, 1988; Enderson & Craig, 1988). The approach used here of marking nestlings, incurs a time lag (mean = 2.7 years age at first breeding) until these nestlings appear as breeding adults at nest sites. The benefit of banding nestlings instead of adults led to a thorough knowledge of age at first breeding, dispersal distances, longevity and age related breeding which are critical to understanding the ecology of this species.

The accurate sexing of nestlings increased the window of opportunity for banding nestlings and removed the reliance on banding Peregrine Falcons later in the nestling period (i.e. $\geq$ age 25 days post-hatching; Olsen and Olsen (1987b)). The date of first egg laying, however, varied by as much as 74 days over this study which presented an added challenge when scheduling fieldwork for banding. Most other intensive studies of this species based on capture-mark-re-sight involved significantly fewer sites and multiple nest site visits (Zuberogoitia *et al.*, 2009), allowing the banding of most nestlings from each breeding event. A less labour-intensive approach, however, was required due to the scale of this study. The use of breeding phenology from past years as a predictive tool was therefore developed in **Chapter 3** as a method to overcome the need for multiple site visits.

Research that aims to mark large numbers of nestlings of this species, or any other widely dispersed breeding species, may be able to further increase the proportion of clutches banded by basing phenological predictions on egg measurements of the year in which banding is intended. Refinement of both the egg aging formula and the volumetric egg measurement methods may improve the predictive power of this approach (Hoyt, 1979; Burnham, 1983).

7.3. Monitoring and managing breeding

The primary threatening agent that had been impacting on the breeding success of this species prior to this study had been addressed in the banning of the importation and use of persistent organochloride pesticides by Australian agriculture in 1987 (Ford, 1987). Monitoring Victoria's Peregrine Falcon population from 1991 was intended to record its breeding response with the reduction in this threatening process. The Peregrine Falcon population in Victoria, had not declined to the point where it was subject to Caughley's 'small population' paradigm (Caughley, 1994) and so the monitoring undertaken in this study was directed at investigating aspects of the species' ecology other than population size.

7.3.1. Dispersal

One of the key motivations for initiating the study (in 1991) was to answer a relatively simple question raised in a report in 1977 (White & Jones, 1977): namely, do individuals raised at tree nest sites 'imprint' on these sites and therefore influence their nest site selection? For a species capable of dispersal distances in the hundreds of kilometers, establishing a study area of sufficient size to examine patterns of dispersal was a challenge (Franzén & Nilsson, 2007). The efficiencies in CMR techniques developed in chapters 2 and 3 catered for an in-depth study of dispersal and its consequences in

Chapter 4.

The reduced distances of novel dispersals are presumably due to maintaining access to available prey resource in a familiar environment (Bilde *et al.*, 2002). This new insight has significance for programmes working on the re-establishment of tree nesting by the Peregrine Falcon in northern Europe (Kleinstäuber & Kirmse, 2009). The tree nesting

population of Peregrine Falcons in Germany and Poland went extinct in 1976 due to organochloride pesticide contamination and human persecution (Kleinstäuber & Kirmse, 2001). In light of the results presented in **Chapter 4**, it is clear that the active discouragement of nesting on buildings to somehow force Peregrine Falcons to adopt stick nests in trees is flawed (Kirmse, 2004). A more enlightened approach would be to install artificial stick nests in forest locations within the mean dispersal distance of the less dispersive sex (i.e. male Peregrine Falcons). Strategically placing these stick nest in relation to known building or cliff nest sites warrants investigation. Then, allow urban populations to increase such that the excess birds will naturally disperse and adopt stick nests in trees. Once some of these nests have been adopted, gradually adding additional stick nests or similar platforms in trees deeper into forests will cater for further expansion of this growing population. The time frame of this approach, however, may not accommodate that of humans wishing to see a more rapid return of a self-sustaining population. This alternative, less intensive approach, may in-fact prove to be quicker and less costly. Such an approach could at least supplement (i.e. not replace the existing approach), and so provide a useful conservation biology experiment.

7.3.2. *Lifetime Reproductive Output*

The temporal and spatial scale of this research project is uncommon amongst raptor studies. The temporal span of this study allowed for lifetime data to be collected from breeding adults that had been banded as nestlings. Several studies of this species have investigated the effects of nest quality on annual breeding success (Mearns & Newton, 1988; Olsen & Olsen, 1989b, 1992; Emison *et al.*, 1993). Other studies have focused on habitat features and quality (Verdejo & López-López, 2008). The spatial scale provided the opportunity to investigate landscape effects on lifetime reproductive outputs of

breeding adults. Lifetime reproductive output was selected because it provides a better indication of evolutionary fitness than annualised reproductive measures (Newton, 1989; McGraw & Caswell, 1996). The highly adaptable nature of this species allows it to live in a diverse range of habitats (Jenkins & Hockey, 2001; White *et al.*, 2013). Analyses in **Chapter 5** found that lifetime reproductive output appears to be limited primarily by the quality of an individual's nest, rather than properties of the surrounding landscape.

Nest quality has been recognized as important for other raptors. The number of eggs laid (clutch size) was highly correlated with the floor area of nest boxes adopted by Tengmalm's Owl (*Aegolius funereus*) in Finland (Korpimäki & Higgins, 1985). A further refinement of the concept of nest quality may be made by measuring the dimensions and area of nest ledges among Peregrine Falcon nests in Victoria. This additional data would contribute to a more robust definition of what constitutes a 'quality nest' for this species.

7.3.3. *Managing anthropogenic nest sites*

Ecosystem change, due to native vegetation removal to access natural resources such as timber and minerals or for farm or urban development, presents challenges to the survival of resident native species. While the use of anthropogenic structures by Peregrine Falcons for nesting in Victoria, however, is partly in response to losses of natural nesting sites it is also primarily a response by an expanding population of birds since the banning of the use of persistent organochloride pesticides. Anthropogenic environments present a stable prey base that attract a variety of raptor species, including the Peregrine Falcon. The challenge to site managers is how best to manage locations where this species chooses to breed.

Nest boxes, used to provide a secure nesting environment, are a popular management tool that has been applied to the conservation of a wide range of birds and mammals (Libois *et al.*, 2012; Catry *et al.*, 2013). As a management action to improve egg hatch rates at anthropogenic nests of the Peregrine Falcon in Victoria, nest boxes proved to be highly efficient and cost effective (**Chapter 6**). The efficacy of nest boxes as a management or conservation action for some species is controversial (Mänd *et al.*, 2005; Klein *et al.*, 2007; Lindenmayer *et al.*, 2009; Björklund *et al.*, 2013). The case of the endangered Leadbeater's Possum (*Gymnobelideus leadbeateri*) in old-growth Mountain Ash (*Eucalyptus regnans*) forests of Victoria is illustrative of the difficult issues involved with using nest boxes where natural tree cavities are in short supply.

The arboreal Leadbeater's Possum occupies cavities formed by microbial and fungal decay in forests of Mountain Ash trees typically 190 and often 300-400 years old (Lindenmayer *et al.*, 2002). The economics of a long-term nest box programme have been proposed (Spring *et al.*, 2001), challenged (Lindenmayer *et al.*, 2002) and further defended (Harley & Spring, 2003) on the grounds that loss of suitable cavity-bearing trees due to wildfires, natural decay and current logging practices will lead to the collapse of this critical resource and then extinction of the species. Apart from the practical and economic feasibility of using nest boxes, there is the philosophical/conservation concern that nest boxes will be seen as a panacea to the conservation threats to the Leadbeater's Possum without actually addressing the primary threatening process (Lindenmayer *et al.*, 2009). More broadly, nest boxes can be seen as addressing the proximal cause of a species' decline but not the ultimate cause (Caughley, 1994). Within the context of the Peregrine Falcon selecting anthropogenic sites to breed in Victoria, nest boxes are supporting the natural recovery of a species by addressing the ultimate cause of current

poor reproductive outputs. That is, the enhancement of nest sites to protect them from the negative effects of weather, to allow increased egg hatch rates.

Tangible benefits may be gained in managing nests on anthropogenic structures by investigating the design of nest boxes. Design modifications of nest boxes for Peregrine Falcons could be informed by more detailed nest measurements, such as nest dimensions and platform area. A co-operative project with material design engineers may lead to longer lasting and less costly nest box construction and installation methods (Root-Bernstein & Ladle, 2010).

7.3.4. Threats to the Peregrine Falcon in anthropogenic environments

The research in this thesis has demonstrated nest boxes to be a practical and cost effective approach to overcoming the poor quality of nests on some anthropogenic structures. However, other threats at anthropogenic sites remain and are not as straightforward to resolve. These additional threats include; direct persecution, disturbance impacting on breeding (both direct and indirect), bioaccumulation of a range of toxic chemicals and heavy metals and increased risk of collisions with anthropogenic structures while flying. Top-order predators such as raptors tend to be at higher risk to these threats than lower order consumers (Hager, 2009).

7.3.4.1. Direct persecution

The direct persecution of raptors is a major contributor to their heightened risk profile associated with anthropogenic threatening processes. This was illustrated in Europe, where band recovery rates for some raptors from shooting were as high or higher than for

many game-bird and waterfowl populations exposed to annual hunting seasons (Newton, 1979b). Furthermore, this illegal persecution currently continues in large areas such as the moorlands managed for the hunting of Red Grouse (*Lagopus l. scoticus*) in northern England (Amar *et al.*, 2012). Illegal killing is also the key cause of slow population growth of a re-introduced population of the Red Kite (*Milvus milvus*) in Northern Scotland (Smart *et al.*, 2010) and the Golden Eagle (*Aquila chrysaetos*) in northern Italy (Pedrini & Sergio, 2001). In contrast, this ‘war on raptors’ appears to have lessened in southern Europe where relatively recent economic development and the subsequent electrocutions and collisions with increasing infrastructure have replaced the shooting of raptors as a more common anthropogenic cause of death (Martínez-Abraín *et al.*, 2009). The overall anthropogenic impact on raptors has not lessened in southern Europe; rather, it is simply less direct now, being caused by the infrastructure associated with a post-industrial way of life.

In Victoria, band recoveries among first year Peregrine Falcons found dead or brought into care between 1991 and 2012, 17.8% ($n = 142$) had been shot or poisoned (unpublished data). In fact the most recent case was detected during the final stages of writing this thesis (Appendix VIII). In Tasmania and internationally engagement with pigeon racing clubs has been encouraged to deter some of this persecution (Mooney, 1985; Dixon *et al.*, 2009; López-López *et al.*, 2009).

7.3.4.2. Nest site disturbance during the breeding season

Peregrine Falcons nesting in quarries and in urban environments have to contend with various human disturbances including the noise and constant movement of heavy machinery not to mention the intermittent blasting of neighbouring cliff faces. As such

they appear to be remarkably tolerant of a range of disturbances. Studies of the effects of rock wall blasting on the breeding of cliff nesting Prairie Falcons (*Falco mexicanus*) in America found large explosions may render nest substrate unstable and can be associated with clutch hatch failure (Holthuijzen *et al.*, 1990). However, that study found incubating and brooding falcons flushed from their nests in 25/112 (22%) instances in response to dynamite blasts. But returned to their nests within an average of 3.4 minutes. The presence of the Peregrine Falcon breeding in highly urbanized environments also suggests a high level of tolerance to noise. However, the one disturbance that consistently causes breeding Peregrine Falcons to flush is human traffic on foot above the nest site. Security guards patrolling on the top of the 36 story building in Melbourne where the city's resident Peregrine Falcon pair breed regularly report being swooped on by screaming adults breeding on the 33 level of the building (direct observations and unpublished data). It appears that provided visual disturbances are not above the nest and are below and beyond the flushing distance the Peregrine Falcon will breed successfully in a diversity of anthropogenic environments (Richardson & Miller, 1997).

7.3.4.3. *Bioaccumulation of toxins*

The negative impact on the reproduction of raptors (including the Peregrine Falcon) from persistent organochloride pesticides has only been overcome in populations where the use of these chemicals has been banned (Grier, 1982). Bioaccumulation of long-range transported anthropogenic contaminants and heavy metals (i.e. DDT, polybrominated diphenyl ether (PBDE), perfluorinated compounds (PFCs), lead and mercury) has been measured among predators in remote Arctic locations and not just in highly urbanised environments. Peregrine Falcons in Greenland and Polar Bears (*Ursus maritimus*) in Alaska have recorded high levels of the chemicals (de Wit *et al.*, 2006; Wegner & Fürst,

2009; Sonne, 2010). These species can act as chemical ‘sentinels’ for the health of the environment(s) in which they live (Smits & Fernie, 2012). It will take a multi-nation approach to effectively diminish the rate of dispersal of these toxic chemicals into the environment (Wegner & Fürst, 2009). Given how the policy development process generally operates the onus of proof will remain with scientists to unequivocally demonstrate the effect of each chemical on humans and not just the natural environment (Juntti *et al.*, 2009; Strydom *et al.*, 2010; Tanner, 2011; Sayre, 2012). However, until these chemicals have a significant impact on human populations it is unlikely that legislation to prevent their continued pollution of the environment will occur. The legislative banning of the use of persistent organochloride pesticides and the resulting recovery of the Bald Eagle and the Peregrine Falcon in North America is an encouraging example of what can be achieved.

7.3.4.4. *Infrastructure impacts*

The characteristic high speed dives for which the Peregrine Falcon is most famous (Macdonald, 2006) make this species to be particularly susceptible to flying accidents associated with anthropogenic structures (Hager, 2009). Heightened risks to the Peregrine Falcon in anthropogenic environments include; collisions with motor vehicles (including airplanes), single overhead wires, building windows, drowning in roof top cooling towers, electrocution from power utilities and a myriad of other unpredictable hazards associated with anthropogenic environments (Lehman, 2001; Tint *et al.*, 2010). Mitigation measures can be applied to each of these, and industry tends to be accepting of addressing these issues when made aware of their impacts and the options for remediation. Currently, in Victoria the process for addressing these issues is generally one of *ad hoc* reactions on a case by case basis to information arising from the injury or

death of a raptor that had been wearing bands. The responses tend to be tailored to the situation and pertaining to the specific location. A broader, industry-targeted education programme may be a more efficient approach to address these threats on an issue by issue or industry by industry basis.

7.4. Conclusions

Despite its global distribution, its adaptability in both diet and nest site selection, and its hunting prowess, the Peregrine Falcon is still vulnerable to anthropogenic chemicals and heavy metals due to its high trophic level (Ratcliffe, 1993; Park *et al.*, 2011).

Consequently, it is considered an ideal indicator for monitoring ecosystem health in areas of environmental concern or in areas subjected to anthropogenic chemical contaminants (Smits & Fernie, 2012). As such, the results of this study go beyond species-specific knowledge but have implications regarding ecosystem health more generally. The relatively straightforward programme of monitoring nest site occupancy and egg hatch rates and reproductive success of Peregrine Falcons over 22 years across Victoria proved to be an efficient method for determining the health of this population. Since this study began in 1991, four years after the banning of persistent organochloride pesticide use (Ford, 1987), results have shown a population no longer demonstrating the effects (i.e. egg-shell thinning) of these chemicals. Although the population has increased and adapted to a range of anthropogenic structures for nesting, the quality of these nest substrates is a key factor potentially limiting the growth and stability of the population. Projections for further urban growth in Melbourne (Victoria's capital city, population 4.0 M in 2011 (ABS, 2011)) are trending above the planned increase of 29.3% from 3.4M in 2002 to 5 M by 2030 (DOI, 2002). This means that opportunities for the Peregrine Falcon to nest on anthropogenic structures are likely to increase. In this context the

management of anthropogenic nest sites for this species will become increasingly important (**Chapter 6**).

The Peregrine Falcon in Victoria is in a healthy state of recovery from long-term population decline. The primary cause of that decline has been removed. A large marked population now exists that is ideally suited to ongoing monitoring to address a range of theoretical and practical issues in conservation biology (Table 7.2).

Table 7.2 Suggested themes for future research on the Peregrine Falcon in Victoria.

Theme	Objectives	Key aspects
Patterns of dispersal	Detailed patterns of dispersal	Electronic tracking of movements between fledging and breeding sites.
Home range	Quantify home range size	Electronic tracking and with comparison between habitat types.
Resource use	Identify key habitat elements and relative usage	Mapping of resources and hunting efficiency compared between habitat types.
Breeding success	Record long-term fitness consequences of nestling condition	The effect of hatch order on the likelihood to breed and breeding success.
Lifetime reproduction	Measure age effects on reproductive success	Profiling reproductive output and production of young to breeding status.
Managing anthropogenic sites	Evaluate the efficacy of alternative nest box construction materials	Engage with material design engineers to improve materials, design and construction to increase longevity of nest boxes.
Likelihood of breeding	Determine the effects of clutch size and hatch order on likelihood to breed.	Profiling clutch status to ultimate breeding success.
Appropriate study size and detection probabilities	Quantify survey effort and rates of identifying breeding adults.	Correlate detectability and survey effort and study area to evaluate biases in identifying breeding adults.

The large-scale monitoring reported in this thesis may no longer be necessary and smaller sub-samples of Victoria's Peregrine Falcon population may be monitored to maintain an index of breeding success. Coupled with this, the 'living with wildlife' message is a critical component of any strategy to conserve this species (Decker & Chase, 1997;

Meijaard *et al.*, 2012). The ‘living with wildlife’ approach is one of adapting human behaviours so as to allow native species to survive and thrive in the modified environments we have affected. In response, the Peregrine Falcon will do its best to persist and live amongst us despite the ongoing effects of the Anthropocene.

References



Female Peregrine Falcon banking turn, 2009. (M. MacKinnon ©)

“Conservation of the Peregrine is inseparable from people’s interest and attitudes about the bird.”

Derek Ratcliffe

- ABBBS (2013) *Maximum movement and time elapsed: Peregrine Falcon in Australia*. Available at: <http://www.environment.gov.au/cgi-bin/biodiversity/abbbs/abbbs-search.pl> [accessed 22 July 2013]
- ABS (2011) *Australian Bureau of Statistics - Census Data*. Available at: http://www.censusdata.abs.gov.au/census_services/getproduct/census/2011/quickstat/2?opendocument&navpos=220 [accessed 6 April 2013].
- Adams, E.S. (2001) Approaches to the study of territory size and shape. *Annual Review of Ecology & Systematics*, **32**(1), 277.
- Amar, A., Court, I.R., Davison, M., Downing, S., Grimshaw, T., Pickford, T. & Raw, D. (2012) Linking nest histories, remotely sensed land use data and wildlife crime records to explore the impact of grouse moor management on peregrine falcon populations. *Biological Conservation*, **145**(1), 86-94.
- Amat, J.A. & Masero, J.A. (2004) Predation risk on incubating adults constrains the choice of thermally favourable nest sites in a plover. *Animal Behaviour*, **67**(2), 293-300.
- Ambasht, R.S. & Ambasht, N.K. (2008) Land-water ecotone ecology. *Proceedings of the National Academy of Sciences India Section B - Biological Sciences*, **78**(special issue), 99-104.
- Ambrose, R.E. & Riddle, K.E. (1988) Population dispersal, turnover, and migration of Alaska Peregrines. In: *Peregrine Falcon populations: Their management and recovery*. Eds. T.J. Cade, J.H. Anderson, C.G. Thelander and C.M. White, pp. 677-684. The Peregrine Fund Inc., Boise Idaho.
- Anderson, A. (1980) The effects of age and band wear on color bands. *Journal of Field Ornithology*, **51**(3), 213-308.
- Anderson, D.R., Link, W.A., Johnson, D.H. & Burnham, K.P. (2001) Suggestions for Presenting the Results of Data Analyses. *The Journal of Wildlife Management* **65**(3), 373-378.
- Arditi, R. & Dacorogna, B. (1988) Optimal Foraging on Arbitrary Food Distributions and the Definition of Habitat Patches. *The American Naturalist*, **131**(6), 837-846.
- Arroyo, B.E., DeCornulier, T. & Bretagnolle, V. (2000) Sex and age determination of Short-eared Owl nestlings. *The Condor*, **102**(1), 216-219.
- Badyaev, A.V. (1995) Nesting habitat and nesting success of Eastern Wild Turkeys in the Arkansas Ozark highlands. *The Condor*, **97**(2), 221-232.
- Badyaev, A.V., Martin, T.E. & Etges, W.J. (1996) Habitat sampling and habitat selection by female Wild Turkeys: ecological correlates and reproductive consequences. *The Auk*, **113**(3), 636-646.
- Bailey, B.H. (1918) The raptorial birds of Iowa. *Iowa Geological Survey Bulletin*, **6**
- Baillie, S.R. (2001) The contribution of ringing to the conservation and management of bird populations: A review. *Ardea*, **89**(1), 167-184.
- Baker-Gabb, D.J. (1984) Morphometric data and dimorphism indices of some Australian raptors. *Corella*, **8**(1), 61-63.
- Baker, M.B. & Rao, S. (2004) Incremental Costs and Benefits Shape Natal Dispersal: Theory and Example with *Hemilepistus reaumuri*. *Ecology*, **85**(4), 1039-1051.
- Balbontín, J., Ferrer, M. & Casado, E. (2001) Sex determination on Booted Eagles (*Heiraaetus pennatus*) using molecular procedures and discriminant function analysis. *Journal of Raptor Research*, **35**(1), 20-23.
- Banks, A.N., Crick, H.Q.P., Coombes, R., Benn, S., Ratcliffe, D.A. & Humphreys, E.M. (2010) The breeding status of Peregrine Falcons *Falco peregrinus* in the UK and Isle of Man in 2002. *Bird Study*, **57**(4), 421-436.

- Barrett, G., Silcocks, A., Barry, S., Cunningham, R. & Poulter, R. (2003) *The new atlas of Australian birds*, 1st Edn. RAOU, Melbourne.
- Barton, K. (2013) *MuMIn: Multi-model inference. R package, Version 1.9.0*. Available at: <http://R-Forge.R-project.org/projects/mumin> [accessed 6 June 2013].
- Battin, J. (2004) When Good Animals Love Bad Habitats: Ecological Traps and the Conservation of Animal Populations. *Conservation Biology*, **18**(6), 1482-1491.
- Bavoux, C., Burneleau, G. & Bretagnolle, V. (2006) Gender determination in the Western Marsh Harrier (*Circus aeruginosus*) using morphometrics and discriminant analysis. *Journal of Raptor Research*, **40**(1), 57-64.
- Bednarz, J.C. (2007) Study design, data management, analysis and presentation Ch. 4. *Raptor research and management techniques*. Ed. by D.M. Bird and K.L. Bildstein, pp. pp 73-88. Hancock House Publishers Ltd, Surrey, BC, Canada.
- Bell, D.A., Gregoire, D.P. & Walton, B.J. (1996) Bridge use by Peregrine Falcons in the San Francisco Bay area. *Raptors in human landscapes: adaptations to built and cultivated environments*. Ed. by D.M. Bird, D. Varland and J.J. Negro, pp. 15-24. Academic Press Inc., London.
- Berggren, Å. & Low, M. (2004) Leg problems and banding-associated leg injuries in a closely monitored population of North Island Robin (*Petroica longipes*). *Wildlife Research*, **31**(5), 535-541.
- Bérubé, C.H., Festa-Bianchet, M. & Jorgenson, J.T. (1999) Individual differences, longevity, and reproductive senescence in Bighorn ewes. *Ecology*, **80**(8), 2555-2565.
- Bibby, C.J., Burgess, N.D., Mustoe, S., Hill, D.A. & Lambton, S. (2000) *Bird census techniques*, 2nd Edn. Published in collaboration with Ecoscope Applied Ecologists, British Trust for Ornithology, RSPB, BirdLife International, London.
- Bierregaard Jr., R.O. & Harrold, E.S. (2008) Behavioural conditioning and techniques for trapping Barred Owls (*Strix varia*). *Journal of Raptor Research*, **42**(3), 210-214.
- Bilde, T., Maklakov, A.A., Taylor, P.W. & Lubin, Y. (2002) State-dependent decisions in nest site selection by a web-building spider. *Animal Behaviour*, **64**(3), 447-452.
- Bird, D.M. & Bildstein, K.L. (2007) *Raptor research and management techniques*, 2nd Edn. Hancock House Publishers Ltd., Surrey, BC, Canada.
- Bird, D.M., Varland, D.E. & Negro, J.J. (1996) *Raptors in human landscapes: adaptations to built and cultivated environments*. Academic Press, Harcourt Brace and Co., Publishers, Charlotte, North Carolina.
- Björklund, H., Valkama, J., Saurola, P. & Laaksonen, T. (2013) Evaluation of artificial nests as a conservation tool for three forest-dwelling raptors. *Animal Conservation*, **16**(2), 1-10.
- Black, S. & Groombridge, J.I.M. (2010) Use of a Business Excellence Model to Improve Conservation Programs. *Conservation Biology*, **24**(6), 1448-1458.
- Bloom, P.H., Clark, W.S. & Kidd, J.W. (2007) Capture techniques Ch 12. *Raptor Research and Management Techniques*. Ed. by D.M. Bird and K.L. Bildstein, pp. pp 193-219. Hancock House, Surrey, BC, Canada.
- Blums, P. & Clark, R. (2004) Correlates of lifetime reproductive success in three species of European ducks. *Oecologia*, **140**(1), 61-67.
- Boal, C.W. & Mannan, R.W. (1999) Comparative breeding ecology of Cooper's Hawks in urban and exurban areas of southeastern Arizona. *The Journal of Wildlife Management*, **63**(1), 77-84.
- Boal, C.W., Wallace, M.C. & Strobel, B. (2010) Perspectives on animal welfare legislation and study considerations for field-orientated studies or raptors in the United States. *Journal of Raptor Research*, **44**(4), 268-276.

- Bonczar, Z. & Kozik, B. (2009) The Peregrine Falcon in the Pieniny Mountains. In: *Peregrine Falcon populations: Status and perspectives in the 21st century*. Eds. J. Sielicki and J. Mizera, pp. 633-640. University of Life Sciences Press, Warsaw, Poznan, Poland.
- Bonte, D., Van Dyck, H., Bullock, J.M., Coulon, A., Delgado, M., Gibbs, M., Lehouck, V., Matthysen, E., Mustin, K., Saastamoinen, M., Schtickzelle, N., Stevens, V.M., Vandewoestijne, S., Baguette, M., Barton, K., Benton, T.G., Chaput-Bardy, A., Clobert, J., Dytham, C., Hovestadt, T., Meier, C.M., Palmer, S.C.F., Turlure, C. & Travis, J.M.J. (2012) Costs of dispersal. *Biological Reviews*, **87**(2), 290-312.
- Bortolotti, G.R. (1984a) Sexual size dimorphism and age-related size variation in Bald Eagles. *The Journal of Wildlife Management*, **48**(1), 72-81.
- Bortolotti, G.R. (1984b) Criteria for determining age and sex of nestling Bald Eagles. *Journal of Field Ornithology*, **55**(4), 467-481.
- Boulet, M., Olsen, P.D., Cockburn, A. & Newgrain, K. (2001) Parental investment in male and female offspring by the Peregrine Falcon, *Falco peregrinus*. *Emu*, **101**(1), 95-103.
- Bradley, M. & Oliphant, L.W. (1991) The Diet of Peregrine Falcons in Rankin Inlet, Northwest Territories: An Unusually High Proportion of Mammalian Prey *The Condor*, **93**(1), 193-197.
- Bradley, M., Johnstone, R., Court, G.S. & Duncan, T. (1997) Influence of weather on breeding success of Peregrine Falcons in the Arctic. *The Auk*, **114**(4), 786-791.
- Brambilla, M. & Ficetola, G.F. (2012) Species distribution models as a tool to estimate reproductive parameters: A case study with a passerine bird species. *Journal of Animal Ecology*, **81**(4), 781-787.
- Brambilla, M., Rubolini, D. & Guidali, F. (2006) Eagle Owl *Bubo bubo* proximity can lower productivity of cliff nesting Peregrines *Falco peregrinus*. *Ornis Fennica*, **80**(1), 20-26.
- Brommer, J.E., Pietiäinen, H. & Kolunen, H. (1998) The effect of age at first breeding on Ural owl lifetime reproductive success and fitness under cyclic food conditions. *Journal of Animal Ecology*, **67**(3), 359-369.
- Brommer, J.E., Merilä, J. & Kokko, H. (2002) Reproductive timing and individual fitness. *Ecology Letters*, **5**(6), 802-810.
- Brommer, J.E., Gustafsson, L., Pietiäinen, H. & Merilä, J. (2004) Single-Generation Estimates of Individual Fitness as Proxies for Long-Term Genetic Contribution. *American Naturalist*, **163**(4), 505-517.
- Brown, C.R., Brown, M.B. & Brazeal, K.R. (2008) Familiarity with breeding habitat improves daily survival in colonial cliff swallows. *Animal Behaviour*, **76**(4), 1201-1210.
- Brown, J.L. & Collopy, M.W. (2013) Immigration stabilizes a population of threatened cavity-nesting raptors despite possibility of nest box imprinting. *Journal of Avian Biology*, **44**(2), 141-148.
- Brown, L. & Amadon, D. (1989) *Eagles, Hawks and Falcons of the world*, 1 Edn. Spring Books, Hong Kong.
- Buehler, D.A. (2000) Bald Eagle (*Haliaeetus leucocephalus*), No. 506. *The Birds of North America*. Ed. by A. Poole and F. Gill, pp. 1-3. The Birds of North America, Inc., Philadelphia, PA, USA.
- Bunnell, S.T., White, C.M., Paul, D. & Bunnell, S.D. (1997) Stick nests on a building and transmission towers used for nesting by large Falcons in Utah. *Great Basin Naturalist*, **57**(3), 263-267.
- Burnham, K.K. & Newton, I. (2011) Seasonal movements of Gyrfalcons *Falco rusticolus* include extensive periods at sea. *Ibis*, **153**(3), 468-484.
- Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*, 2 Edn. Springer-Verlag, New York.

- Burnham, W. (1983) Artificial incubation of Falcon eggs. *The Journal of Wildlife Management*, **47**(1), 158-168.
- Burnham, W. & Cade, T.J. (2003) *Return of the Peregrine*, 1 Edn. The Peregrine Fund Inc., Boise Idaho.
- Burnham, W.A., Heinrich, W., Sandfort, C., Levine, E., O'Brien, D. & Konkel, D. (1988) Recovery effort for the Peregrine Falcon in the Rocky Mountains. *Peregrine Falcon populations: Their Management and Recovery*. Ed. by T.J. Cade, J.H. Enderson, C.G. Thelander and C.M. White, pp. 565-574. The Peregrine Fund, Boise.
- Byholm, P., Nikula, A., Kentta, J. & Taivalmäki, J.P. (2007) Interactions between habitat heterogeneity and food affect reproductive output in a top predator. *Journal of Animal Ecology*, **76**(2), 392-401.
- Byre, V.J. (1990) A group of young Peregrine Falcons prey upon migrating bats. *The Wilson Bulletin*, **102**(4), 728-730.
- Cade, T. & Bird, D.M. (1990) Peregrine Falcons, *Falco peregrinus*, nesting in an urban environment: A review. *The Canadian Field Naturalist*, **104**(2), 209-218.
- Cade, T., Redig, P.T. & Tordoff, H.B. (1989) Peregrine Falcon restoration: Expectation vs. Reality. *The Loon*, **61**(Winter), 160-162.
- Cade, T., Burnham, W. & Burnham, P. (2009) *Return of the Peregrine - A North American Saga of Tenacity and Teamwork*. The Peregrine Fund, Boise, Idaho.
- Cade, T.J. (1982) *The Falcons of the world*, 1 Edn. Cornell Univ. Press, Ithaca, N.Y.
- Cade, T.J., Enderson, J.H., Thelander, C.G. & White, C.M. (1988) *Peregrine Falcon Populations: their management and recovery*, 1st Edn. The Peregrine Fund Inc.
- Cade, T.J., Martell, M.S., Redig, P.T., Septon, G. & Tordoff, H.B. (1996) Peregrine Falcons in urban North America. In: *Raptors in human landscapes: adaptations to built and cultivated environments*. Eds. D.M. Bird, D. Varland and J.J. Negro, pp. 3-13. Academic Press Limited, London.
- Calabuig, G., Ortego, J., Aparicio, J.M. & Cordero, P.J. (2008) Public information in selection of nesting colony by lesser kestrels: which cues are used and when are they obtained? *Animal Behaviour*, **75**(5), 1611-1617.
- Calladine, J., Garner, G., Wernham, C. & Buxton, N. (2010) Variation in the diurnal activity of breeding Short-eared Owls *Asio flammeus*: implications for their survey and monitoring. *Bird Study*, **57**(1), 89-99.
- Campbell-Thompson, E., Vargas, F.H., Watson, R.T., Muela, A. & Cáceres, N.C. (2012) Effect of sex and age at release on the independence of hatched Harpy Eagles. *Journal of Raptor Research*, **46**(2), 158-167.
- Carlton, R. (2003) Attracting and managing the Peregrine Falcon at electricity utilities, EPRI. Dairyland Power Cooperative, LaCrosse, WI and Xcel Energy, Minneapolis, MN, Palo Alto, CA.
- Catry, I., Franco, A.M.A., Rocha, P., Alcazar, R., Reis, S., Cordeiro, A., Ventim, R., Teodósio, J. & Moreira, F. (2013) Foraging Habitat Quality Constrains Effectiveness of Artificial Nest-Site Provisioning in Reversing Population Declines in a Colonial Cavity Nester. *Plos One*, **8**(3), e58320. doi:10.1371/journal.pone.0058320.
- Caughley, G. (1994) Directions in Conservation Biology. *Journal of Animal Ecology*, **63**(2), 215-244.
- Chace, J.F. & Walsh, J.J. (2006) Urban effects on native avifauna: a review. *Landscape and Urban Planning*, **74**(1), 46-69.
- Chandler, R.B., Strong, A.M. & Kaufman, C.C. (2004) Elevated lead levels in Urban house sparrows: A threat to Sharp-shinned Hawks and Merlins? *Journal of Raptor Research*, **38**(1), 62-68.

- Charter, M., Izhaki, I., Bouskila, A., Leshem, Y. & Penteriani, V. (2007) Breeding success of the Eurasian Kestrel (*Falco tinnunculus*) nesting on buildings in Israel. *Journal of Raptor Research*, **41**(2), 139-143.
- Chichocki, W. (1986) Some species of breeding birds in Tatra National Park. *Parki Narod. Rezerw. Przyr.*, 757-62.
- Choi, C.Y. & Nam, H.Y. (2012) Migrating dragonflies: Famine relief for resident Peregrine Falcons *Falco peregrinus* on islands. *Forktail*, **28**(2), 149-151.
- Christidis, L. & Boles, W.E. (2008) *Systematics and Taxonomy of Australian Birds*. 2 Edn. CSIRO Publishing, Melbourne.
- Clarke, A.L., Roskaft, E. & Saether, B.E. (1997) Sex biases in avian dispersal: a reappraisal. *Oikos*, **79**(3), 429-438.
- Clarke, M.F. (1997) A review of studies of the breeding biology of Australian birds from 1986-95: Biases and consequences. *Emu*, **97**(4), 283-289.
- Clutton-Brock, T.H. (1988) *Reproductive Success*. University of Chicago Press, Chicago, IL, USA.
- Clutton-Brock, T.H. & Sheldon, B.C. (2010) Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology and Evolution*, **25**(10), 562-573.
- Cogley, V. (1995) *Prey-selection by urban Victorian Peregrine Falcons (Falco peregrinus macropus)*. Honours, University of Melbourne, Melbourne.
- Cone, M. (2008) Peregrine Falcons in California's urban areas are contaminated with toxic chemicals. Los Angeles Times, 1, Los Angeles
- Cooper, C.B. & Walters, J.R. (2002) Experimental evidence of disrupted dispersal causing decline of an Australian passerine in fragmented habitat. *Conservation Biology*, **16**(2), 471-478.
- Court, G.S., Gates, C.C. & Boag, D.A. (1988) Natural history of the peregrine falcon in the Keewatin District of the Northwest Territories. *Arctic*, **41**(1), 17-30.
- Cowling, S. (1981) The Peregrine Falcon in Victoria. *Emu*, **80**(Supplement), 251-296.
- Craig, G.R., White, G.C. & Enderson, J.H. (2004) Survival, recruitment and rate of population change of the Peregrine Falcon population in Colorado. *The Journal of Wildlife Management*, **68**(4), 1032-1038.
- Crutzen, P.J. (2002) Geology of mankind. *Nature*, **415**(6867), 23-23.
- Czech, B., Krausman, P.R. & Devers, P.K. (2000) Economic Associations among Causes of Species Endangerment in the United States. *BioScience*, **50**(7), 593.
- Davis, J.M. (2008) Patterns of Variation in the Influence of Natal Experience on Habitat Choice. *The Quarterly Review of Biology*, **83**(4), 363-380.
- Dawson, R.D., Mossop, D.H. & Boukall, B. (2011) Prey use and selection in relation to reproduction by Peregrine Falcons breeding along the Yukon River, Canada. *Journal of Raptor Research*, **45**(1), 27-37.
- de Wit, C.A., Alae, M. & Muir, D.C.G. (2006) Levels and trends of brominated flame retardants in the Arctic. *Chemosphere*,
- DeCandido, R. & Allen, D. (2006) Nocturnal hunting by Peregrine Falcons at the empire state building, New York City. *The Wilson Journal of Ornithology*, **118**(1), 53-58.
- Decker, D.J. & Chase, L.C. (1997) Human dimensions of living with wildlife - a management challenge for the 21st century. *Wildlife Society Bulletin*, **25**(4), 788-795.
- Dekker, D. & Taylor, R. (2005) A change in foraging success and cooperative hunting by a breeding pair of Peregrine Falcons and their fledglings. *Journal of Raptor Research*, **39**(4), 394-403.

- Delgado, M.d.m. & Penteriani, V. (2004) Gender determination of Eurasian Eagle-Owls (*Bubo bubo*) by morphology. *Journal of Raptor Research*, **38**(4), 375-377.
- Delibes, M., Ferreras, P. & Gaona, P. (2001a) Attractive sinks, or how individual behavioural decisions determine source-sink dynamics. *Ecology Letters*, **4**(5), 401-403.
- Delibes, M., Gaona, P., Ferreras, P. & Doak, D.F. (2001b) Effects of an attractive sink leading into maladaptive habitat selection. *The American Naturalist*, **158**(3), 277.
- Dell'Omo, G., Costantini, D., Lucini, V., Antonucci, G., Nonno, R. & Polichetti, A. (2009) Magnetic fields produced by power lines do not affect growth, serum melatonin, leukocytes and fledging success in wild kestrels. *Comparative Biochemistry and Physiology Part C: Toxicology and Pharmacology*, **150**(3), 372-376.
- DeMent, S.H., Chisholm Jr, J.J., Barber, J.C. & Strandberg, J.D. (1986) Lead exposure in an "urban" peregrine falcon and its avian prey. *Journal of Wildlife Diseases*, **22**(2), 238-244.
- Dennis, T.E., McIntosh, R.R. & Shaugnessy, P.D. (2011) Effects of human disturbance on productivity of White-bellied Sea-Eagles (*Haliaeetus leucogaster*). *Emu*, **111**(2), 179-185.
- Dixon, A., Haffield, P., Lawrence, M., Lowe, A., Richards, C., Roberts, G. & Thomas, M. (2009) Peregrine population surveys: a case study from Wales. In: *Peregrine Falcon populations: Status and perspectives in the 21st Century*. Eds. J. Sielicki and J. Mizera, pp. 77-86. Poznan University of Life Sciences Press, Poznan, Poland.
- DOI (2002) Melbourne 2030 - Planning for sustainable growth. Department of Infrastructure, Government of Victoria, Melbourne, Australia.
- Drewitt, E.J.A. & Dixon, N. (2008) Diet and prey selection of urban-dwelling Peregrine Falcons in southwest England. *British Birds*, **101**(1), 58-67.
- DSE (2013) http://www.dse.vic.gov.au/data/assets/pdf_file/0019/117073/VegetationProdescV204090_6.pdf Available [accessed 12-June- 2013].
- Duffy, J.E. (2002) Biodiversity and ecosystem function: the consumer connection. *Oikos*, **99**(2), 201-219.
- Dykstra, C.R., Hays, J.L. & Simon, M.M. (2009) Spatial and temporal variation in reproductive rates of the red-shouldered hawk in suburban and rural Ohio. *Condor*, **111**(1), 177-182.
- Ellis, D.H., Ellis, C.H., Sabo, B.A., Rea, A.M., Dawson, J., Fackler, J.K., Larue, C.T., Grubb, T.G., Schmitt, J., Smith, D.G. & Kery, M. (2004) Summer diet of the Peregrine Falcon in faunistically rich and poor zones of Arizona analyzed with capture-recapture modelling. *The Condor*, **106**873-886.
- Emison, W.B. (1979) The Peregrine Falcon in Victoria: a summary of current research. *Victoria's Resources*, **21**(2), 12-14.
- Emison, W.B. & Bren, W.M. (1981) Banding of Peregrine Falcon chicks in Victoria, Australia. *Emu*, **80**(Supplement), 288-291.
- Emison, W.B. & White, C.M. (1988) The Peregrine Falcon in Victoria. *Common Ground.*, **1**(1), 27-29.
- Emison, W.B. & Hurley, V.G. (1995) Occupancy of Peregrine Falcon eyries near Melbourne during 1976-1984 and 1992. *The Victorian Naturalist*, **112**(2), 100-101.
- Emison, W.B., Bren, W.M. & White, C.M. (1993) Influence of weather on the breeding of the Peregrine Falcon *Falco peregrinus* near Melbourne. *Australian Raptor Studies*. Ed by P.D. Olsen, pp. 26-32. Brisbane.
- Emison, W.B., White, C.M., Hurley, V.G. & Brimm, D.J. (1997) Factors Influencing the Breeding Distribution of the Peregrine Falcon in Victoria, Australia. *Wildlife Research*, **24**(4), 433-444.

- Emison, W.B., Hurley, V.G., White, C.M. & Brimm, D.J. (1998) Results from a banding study of Peregrine Falcon chicks in Victoria, 1972-1997. *Corella*, **22**(3), 87-91.
- Enderson, J.H. & Kirven, M.N. (1983) Flights of nesting Peregrine Falcons recorded by telemetry. *Journal of Raptor Research*, **17**(2), 33-37.
- Enderson, J.H. & Craig, G.R. (1988) Population turnover in Colorado Peregrines. In: *Peregrine Falcon populations: Their Management and Recovery*. pp. 685-688. The Peregrine Fund Inc., Sacramento, California.
- England, A.S., Bechard, M.J. & Houston, C.S. (1997) Swainson's Hawk (*Buteo swainsoni*). In: *The Birds of North America*, No. 265. Eds. A. Poole and F. Gill, pp. 4-5. The Birds of North America, Inc., Philadelphia, PA, USA, Philadelphia, PA, USA.
- Environment Australia (2012) *The Australian Bird and Bat Banding Scheme's searchable database. Version update 2011-Apr-10*. Available at: <http://www.environment.gov.au/cgi-bin/biodiversity/abbbs/abbbs-search.pl> [accessed 14 January 2013].
- Espie, R.H.M., Brigham, R.M. & James, P.C. (1996) Habitat selection and clutch fate of Piping Plovers (*Charadrius melodus*) breeding at Lake Diefenbaker, Saskatchewan. *Canadian Journal of Zoology*, **74**, 1069-1075.
- Ewins, P.J. (1996) The use of artificial nest sites by an increasing population of Ospreys in the Canadian Great Lakes Basin. In: *Raptors in human landscapes: adaptations to built and cultivated environments*. Eds. D.M. Bird, D. Varland and J.J. Negro, pp. 109-123. Academic Press Inc., London.
- Eymann, J., Webley, L.S., Cooper, D.W. & Herbert, C.A. (2006) Performance of passive integrated transponders (PIT tags) as a marking system for common brushtail possums *Trichosurus vulpecula* - a cautionary tale. *Journal of Australian Mammalogy*, **28**(2), 209-214.
- Ferguson-Lees, J. & Christie, D.A. (2005) *Raptors of the world*, 2 Edn. Princeton University Press, Princeton and Oxford.
- Ferrer, M. & Bisson, I. (2003) Age and territory quality effects on fecundity in the Spanish Imperial Eagle (*Aquila adalberti*). *Auk*, **120**(1), 180.
- Finkelstein, M.E., Doak, D.F., George, D., Burnett, J., Brandt, J., Church, M., Grantham, J. & Smith, D.R. (2012) Lead poisoning and the deceptive recovery of the critically endangered California condor. *Proceedings of the National Academy of Sciences of the United States of America*, **109**(28), 11449-11454.
- Fleming, T., Buchanan, J.B. & Irwin, L.L. (1991) Footpad dimorphism as a possible means to determine sex of adult and juvenile Northern Spotted Owls (*Strix occidentalis caurina*). *North American Bird Bander*, **16**(3), 66-68.
- Ford, J. (1987) Australia pays to get rid of its beef of DDT and dieldrin. *New Scientist*, **157**, 924.
- Franco, A.M.A., Marques, J.T. & Sutherland, W.J. (2005) Is nest-site availability limiting Lesser Kestrel populations? A multiple scale approach. *Ibis*, **147**(4), 657-666.
- Frank, S. (1994) *City Peregrine*. Hancock House Publishers, Ltd, Surrey, BC.
- Franzén, M. & Nilsson, S.G. (2007) What is the required minimum landscape size for dispersal studies? *Journal of Animal Ecology*, **76**(6), 1224-1230.
- Freckleton, R.P. & Iossa, G. (2010) Methods in Ecology and Evolution. *Methods in Ecology and Evolution*, **1**(1), 1-2.
- Fridolfsson, A.K. & Ellegren, H. (1999) A simple and universal method for molecular sexing of non-ratite birds. *Journal of Avian Biology*, **30**(1), 116-121.
- Fuller, M.R., Seegar, W.S. & Schueck, L.S. (1998) Routes and travel rates of migrating Peregrine Falcons *Falco peregrinus* and Swainson's Hawks *Buteo swainsoni* in the Western Hemisphere. *Journal of Avian Biology*, **29**(4), 433.

- Fyfe, R.W. & Olendorff, R.R. (1976) Minimizing the dangers of nesting studies to raptors and other sensitive species. In: *Canadian Wildlife Services Occasional Paper, no. 23*. pp. 1-17, (Canadian Wildlife Service, Ottawa, Canada).
- Garden, J., McAlpine, C., Peterson, A.N.N., Jones, D. & Possingham, H. (2006) Review of the ecology of Australian urban fauna: A focus on spatially explicit processes. *Austral Ecology*, **31**(2), 126-148.
- Garton, E.O., Horne, J.S., Aycrigg, J.L. & Ratti, J.T. (2012) Research and experimental design Ch 1. *The wildlife techniques manual - research*. Ed. by N.J. Silvy, pp. 1-40. Published in affiliation with The Wildlife Society, The John Hopkins University Press, , Baltimore, USA.
- Glennon, M.J. & Kretser, H.E. (2013) Size of the ecological effect zone associated with exurban development in the Adirondack Park, NY. *Landscape and Urban Planning*, **112**(1), 10-17.
- Gordon, D.M. (1997) The population consequences of territorial behaviour. *Trends in Ecology & Evolution*, **12**(2), 63-66.
- Goss (1878) Breeding of the duck hawk in trees. *Bulletin of the Nuttall Ornithology Club*, **3**(1), 32-34.
- Götmark, F. (1992) The effect of investigator disturbance on nesting birds. *Current Ornithology, Vol. 9*. Ed. by D.M. Power, pp. 63 - 104. Plenum Press, New York, NY, USA.
- Gottschalk, T.K., Ekschmitt, K. & Wolters, V. (2011) Efficient placement of nest boxes for the Little Owl (*Athene noctua*). *Journal of Raptor Research*, **45**(1), 1-14.
- Gowdy, J., Hall, C., Klitgaard, K. & Krall, L. (2010) What Every Conservation Biologist Should Know about Economic Theory. *Conservation Biology*, **24**(6), 1440-1447.
- Greenwood, P.J. (1980) Mating systems, philopatry and dispersal in birds and mammals. *Journal of Animal Behaviour*, **28**(4), 1140-1162.
- Grier, J.W. (1982) Ban of DDT and Subsequent Recovery of Reproduction in Bald Eagles. *Science* **218**(4578), 1232-1235.
- Griffiths, R., Double, M.C., Orr, K. & Dawson, R.J.G. (1998) A DNA test to sex most birds. *Molecular Ecology*, **7**, 1071-1075.
- Groom, C. (2010) Justification for continued conservation efforts following the delisting of a threatened species: A case study of the woylie, *Bettongia penicillata ogilbyi* (Marsupialia: Potoroidae). *Wildlife Research*, **37**(3), 183-193.
- Grubaugh, N.D., Petz, L.N., Melanson, V.R., McMenamy, S.S., Turell, M.J., Long, L.S., Pisarcik, S.E., Kengluocha, A., Jaichapor, B., O'Guinn, M.L. & Lee, J.S. (2013) Evaluation of a Field-Portable DNA Microarray Platform and Nucleic Acid Amplification Strategies for the Detection of Arboviruses, Arthropods, and Bloodmeals. *The American Journal of Tropical Medicine and Hygiene*, **88**(2), 245-253.
- Gundersen, G., Johannesen, E., Andreassen, H.P. & Ims, R.A. (2001) Source-sink dynamics: how sinks affect demography of sources. *Ecology Letters*, **4**(1), 14-21.
- Gustafsson, L. (1989) Collared Flycatcher. *Lifetime reproduction in birds*. Ed. by I. Newton, pp. 75-88. Academic Press Limited, London.
- Hager, S.B. (2009) Human-related threats to urban raptors. *Journal of Raptor Research*, **43**(3), 210-226.
- Hardouin, L.A., Nevoux, M., Robert, A., Gimenez, O., Lacroix, F. & Hingrat, Y. (2012) Determinants and costs of natal dispersal in a lekking species. *Oikos*, **121**(6), 804-812.
- Harley, D.K.P. & Spring, D.A. (2003) Reply to the comment by Lindenmayer *et al* on "Economics of a nest-box program for the conservation of an endangered species: a reappraisal"¹. *Canadian Journal of Forest Research*, **33**(6), 752-753.

- Hartley, R.R. & Mundy, P.J. (2003) Morphometrics and status of Ayres's Hawk-eagle in Zimbabwe. *Journal of Raptor Research*, **37**(1), 44-54.
- Herényi, M., Hegyi, G., Garamszegi, L.Z., Hargitai, R., Michl, G., Rosivall, B. & Török, J. (2012) Lifetime offspring production in relation to breeding lifespan, attractiveness, and mating status in male collared flycatchers. *Oecologia*, **170**(4), 935-942.
- Hetzler, B.C. (2013) Female Peregrine Falcon (*Falco peregrinus*) exploits fish as prey. *Western North American Naturalist*, **73**(1), 107-109.
- Hickey, J.J. (1969) Peregrine Falcon populations: their biology and decline. *Madison Peregrine conference*. Ed by J.J. Hickey, p. 569. Madison.
- Hobbie, J.E., Carpenter, S.R., Grimm, N.B., Gosz, J.R. & Seastedt, T.R. (2003) The US Long Term Ecological Research Program. *BioScience*, **53**(1), 21-32.
- Hoekstra, J.M., Fagan, W.F. & Bradley, J.E. (2002) A Critical Role for Critical Habitat in the Recovery Planning Process? Not Yet. *Ecological Applications* **12**(3), 701-707.
- Hofer, C., Gallagher, F.J. & Holzapfel, C. (2010) Metal accumulation and performance of nestlings of passerine bird species at an urban brownfield site. *Environmental Pollution*, **158**(5), 1207-1213.
- Hofgaard, A., Harper, K.A. & Golubeva, E. (2012) The role of the circumarctic forest-tundra ecotone for Arctic biodiversity. *Biodiversity*, **13**(3-4), 174-181.
- Hogan, F.E., Cooke, R., Burridge, C.P. & Norman, J.A. (2008) Optimizing the use of shed feathers for genetic analysis. *Molecular Ecology Resources*, **8**(3), 561-567.
- Holdsworth, M., Dettmann, B. & Baker, G.B. (2011) Survival in the Orange-bellied Parrot (*Neophema chrysogaster*). *Emu*, **111**(3), 222-228.
- Holthuijzen, A.M.A., Eastland, W.G., Ansell, A.R., KOchert, M.N., Williams, R.D. & Young, L.S. (1990) Effects of blasting on behaviour and productivity of nesting Prairie Falcons. *Wildlife Society Bulletin*, **18**281-1990.
- Hoodless, A.N., Inglis, J.G. & Baines, D. (2006) Effects of weather and timing on counts of breeding Snipe *Gallinago gallinago*. *Bird Study*, **53**(3), 205-212.
- Howitz, J.L. (1981) Determination of total colour band combinations. *Journal of Field Ornithology*, **52**(4), 317-324.
- Hoyt, D.F. (1976) The effect of shape on the surface-volume relationships of birds' eggs. *The Condor*, **78**(3), 343-349.
- Hoyt, D.F. (1979) Practical methods of estimating volume and fresh weight of bird eggs. *The Auk*, **96**(1), 73-77.
- Hurley, V.G., White, J.G. & Cooke, R. (2013) Techniques for optimising long-term, large-scale capture-mark-resighting raptor studies: climb hard, band fast. *Wildlife Research*, **40**(4), 269-280.
- Hurley, V.G., Hogan, F., White, J.G. & Cooke, R. (2007) A morphological model for sexing nestling Peregrine Falcons (*Falco peregrinus macropus*) verified through genetic analysis. *Wildlife Research*, **34**(1), 54-58.
- Ihaka, R. & Gentleman, R. (1996) R: A Language for Data Analysis and Graphics. *Journal of Computational and Graphical Statistics* **5**(3), 299-314.
- James, P.C., Warkentin, I.G. & Oliphant, L.W. (1989) Turnover and dispersal in urban Merlins *Falco columbarius*. *Ibis*, **131**(3), 426-429.
- Jenkins, A. & Avery, G.M. (1999) Diets of breeding Peregrine and Lanner Falcons in South Africa. *Journal of Raptor Research*, **33**(3), 190-206.
- Jenkins, A.R. (1994) Caught in the act: mamba attack on Peregrine brood. *African Wildlife*, **48**(1), 13-15.

- Jenkins, A.R. (2000a) Factors affecting breeding success of Peregrine and Lanner Falcons in South Africa. *Ostrich*, **71**((3&4)), 385-392.
- Jenkins, A.R. (2000b) Hunting mode and success of African Peregrines *Falco peregrinus minor*, does nesting habitat quality affect foraging efficiency? *Ibis*, **142**(2), 235-246.
- Jenkins, A.R. & Benn, G.A. (1998) Home range size and habitat requirements of Peregrine Falcons on the Cape Peninsula, South Africa. *Journal of Raptor Research*, **32**(2), 90-97.
- Jenkins, A.R. & Hockey, P.A.R. (2001) Prey availability influences habitat tolerance: an explanation for the rarity of Peregrine Falcons in the tropics. *Ecography*, **24**(3), 359-367.
- Juillard, M. & Rebetez, M. (1991) Capture of a family of Peregrine Falcons by the Eagle Owl, *Bubo bubo*. *Nos Oiseaux*, **41**(2), 196-1907.
- Juntti, M., Russel, D. & Turnpenny, J. (2009) Evidence, politics and power in public policy for the environment. *Environmental Science and Policy*, **12**(3), 207-215.
- Kahn, N.W., St. John, J. & Quinn, T.W. (1998) Chromosome-specific Intron size differences in the Avian CHD gene provide an efficient method for sex identification in birds. *The Auk*, **115**(4), 1074-1078.
- Kark, S., Allnutt, T.F., Levin, N., Manne, L.L. & Williams, P.H. (2007) The role of transitional areas as avian biodiversity centres. *Global Ecology and Biogeography*, **16**(2), 187-196.
- Karyakin, I.V. & Pazhenov, A.S. (2009) Population trends of the Peregrine Falcon in the Volga-Ural region (Russia) for twenty years. In: *Peregrine Falcon populations: Status and perspectives in the 21st century*. Eds. J. Sielicki and J. Mizera, pp. 335-356. University of Life Sciences Press, Warsaw, Poznan, Poland.
- Kauffman, M.J., Frick, W.F. & Linthicum, J. (2003) Estimation of habitat-specific demography and population growth for Peregrine Falcons in California. *Ecological applications*, **13**(6), 1802-1816.
- Keeling, C.D. (1998) Rewards and penalties of monitoring the earth. *Annual Review of Energy & the Environment*, **23**(1), 25-83.
- Kiff, L. (1988) Changes in the status of the peregrine in North America: an overview. *Peregrine Falcon Populations: Their Management and Recovery*. Ed by T.J. Cade, J.H. Enderson, C.G. Thelander and C.M. White, pp. 123-139. Sacramento, California.
- Kirmse, W. (1991) Zur Wiedereinbürgerung von Baubrütenden Wanderfalken *Falco peregrinus* im Flachland Mitteleuropas. *Populationsökologie Greifvögel und Eulenarten*. Ed. by M. Stubbe, pp. 359-364. Nationalen Wiss. Beitr. Univ., Halle [in German].
- Kirmse, W. (1994) Raptors' plasticity on nest site selection. *Raptor Conservation Today*. Ed. by R.D. Chancellor and B.-U. Meyburg, pp. 143-145. The World Working Group of Birds of Prey and Owls / The Pica Press, Budapest.
- Kirmse, W. (2001) Reintroduction of tree-nesting Peregrines (*Falco peregrinus*) in Central Europe. *Wiedereinbürgerung baumbrütender Wanderfalken (Falco peregrinus) in Mitteleuropa*, **47**(3), 165-177.
- Kirmse, W. (2004) Tree-nesting Peregrines *Falco p. peregrinus* in Europe did not recover. *Raptors worldwide*. Ed. by R.D. Chancellor and B.-U. Meyburg, pp. 271-277. The World Working Group of Birds of Prey and Owls / The Pica Press, Budapest.
- Klein, Á., Nagy, T., Csörgö, T. & Mátics, R. (2007) Exterior nest-boxes may negatively affect Barn Owl *Tyto alba* survival: an ecological trap. *Bird Conservation International*, **17**(3), 273-281.
- Kleinstäuber, G. & Kirmse, W. (2001) Extinction and comeback of the Peregrine Falcon (*Falco peregrinus*) in eastern Germany. *Beiträge zur Jagd- und Wildforschung*, **26**(3), 381-398.
- Kleinstäuber, G. & Kirmse, W. (2009) The return of the Peregrine to eastern Germany: recolonisation in the west and east; the formation of an isolated tree-nesting subpopulation and further management. In: *Peregrine Falcon populations: Status and*

- perspectives in the 21st Century*. Eds. J. Sielicki and J. Mizera, pp. 641-676. Poznan University of Life Sciences Press, Poznan, Poland.
- Kolbe, J.J. & Janzen, F.J. (2002) Impact of nest-site selection on nest success and nest temperature in natural and disturbed habitats. *Ecology*, **83**(1), 269-281.
- Korpimäki, E. (1987) Clutch size, breeding success and brood size experiments in Tengmalm's Owl *Aegolius funereus*: a test of hypotheses. *Ornis Scandinavica*, **18**(4), 277-284.
- Korpimäki, E. (1988) Effects of Territory Quality on Occupancy, Breeding Performance and Breeding Dispersal in Tengmalm's Owl. *Journal of Animal Ecology* **57**(1), 97-108
- Korpimäki, E. & Higgins, P.J. (1985) Clutch size and breeding success in relation to nest-box size in Tengmalm's Owl *Aegolius funereus*. *Holarctic Ecology*, **8**(1), 175-180.
- Korpimäki, E., Norrdahl, K., Huitu, O. & Klemola, T. (2005) Predator-induced synchrony in population oscillations of coexisting small mammal species. *Proceedings of the Royal Society B: Biological Sciences*, **272**(2), 193-202.
- Kovács, A., Mammen, U.C.C. & Wernham, C.V. (2008) European Monitoring for Raptors and Owls: State of the Art and Future Needs. *AMBIO: A Journal of the Human Environment*, **37**(6), 408-412.
- Kross, S.M., McDonald, P.G. & Nelson, X.J. (2013) New Zealand Falcon nests suffer lower predation in agricultural habitat than in natural habitat. *Bird Conservation International*, **FirstView**1-8.
- Krüger, O. (2002) Analysis of nest occupancy and nest reproduction in two sympatric raptors: common buzzard *Buteo buteo* and goshawk *Accipiter gentilis*. *Ecography*, **25**(5), 523-532.
- Krüger, O. (2004) The importance of competition, food, habitat, weather and phenotype for the reproduction of Buzzard *Buteo buteo*. *Bird Study*, **51**(2), 125-132.
- Krüger, O. & Lindström, J. (2001) Lifetime reproductive success in common buzzard, *Buteo buteo*: from individual variation to population demography. *Oikos*, **93**(2), 260-273.
- Laurance, W.F., Koster, H., Grooten, M., Anderson, A.B., Zuidema, P.A., Zwick, S., Zagt, R.J., Lynam, A.J., Linkie, M. & Anten, N.P.R. (2012) Making conservation research more relevant for conservation practitioners. *Biological Conservation*, **153**(0), 164-168.
- Ledger, J.A. & Hobbs, J.C.A. (1999) Raptor use and abuse of powerlines in southern Africa. *Journal of Raptor Research*, **33**(1), 49-52.
- Lehman, R.N. (2001) Raptor electrocution on power lines: current issues and outlook. *Wildlife Society Bulletin*, **29**(3), 804-813.
- Leu, M., Hanser, S.E. & Knick, S.T. (2008) The human footprint in the west: A large-scale analysis of anthropogenic impacts. *Ecological applications*, **18**(5), 1119-1139.
- Libois, E., Gimenez, O., Oro, D., Mínguez, E., Pradel, R. & Sanz-Aguilar, A. (2012) Nest boxes: A successful management tool for the conservation of an endangered seabird. *Biological Conservation*, **155**(0), 39-43.
- Lindberg, P. (2009) Colour-ringing of Swedish Peregrine Falcons: migration and natal dispersal. In: *Peregrine Falcon populations: Status and perspectives in the 21st Century*. Eds. J. Sielicki and J. Mizera, pp. 145-152. Poznan University of Life Sciences Press, Poznan, Poland.
- Lindenmayer, D.B., MacGregor, C. & Gibbons, P. (2002) Comment - Economics of a nest-box program for the conservation of an endangered species: a re-appraisal. *Canadian Journal of Forest Research*, **32**(12), 2244-2247.
- Lindenmayer, D.B., Wood, J.T., McBurney, L., MacGregor, C., Youngentob, K. & Banks, S.C. (2011) How to make a common species rare: A case against conservation complacency. *Biological Conservation*, **144**(5), 1663-1672.

- Lindenmayer, D.B., Welsh, A., Donnelly, C., Crane, M., Michael, D., MacGregor, C., McBurney, L., Montague-Drake, R. & Gibbons, P. (2009) Are nest boxes a viable alternative source of cavities for hollow-dependent animals? Long-term monitoring of nest box occupancy, pest use and attrition. *Biological Conservation*, **142**(1), 33-42.
- Lindenmayer, D.B., Gibbons, P., Bourke, M.A.X., Burgman, M., Dickman, C.R., Ferrier, S., Fitzsimons, J., Freudenberger, D., Garnett, S.T., Groves, C., Hobbs, R.J., Kingsford, R.T., Krebs, C., Legge, S., Lowe, A.J., McLean, R.O.B., Montambault, J., Possingham, H., Radford, J.I.M., Robinson, D., Smallbone, L., Thomas, D., Varcoe, T., Vardon, M., Wardle, G., Woinarski, J. & Zerger, A. (2012) Improving biodiversity monitoring. *Austral Ecology*, **37**(3), 285-294.
- Lindsey, G.D., Wilson, K.A. & Herrmann, C. (1995) Color change in Hughes's celluloid bands. *Journal of Field Ornithology*, **66**(2), 289-295.
- Linkhart, B.D. & Reynolds, R.T. (2006) Lifetime reproduction of Flammulated Owls in Colorado. *Journal of Raptor Research*, **40**(1), 29-37.
- López-López, P., Verdejo, J. & Barba, E. (2009) The role of pigeon consumption in the population dynamics and breeding performance of a Peregrine Falcon (*Falco peregrinus*) population: conservation implications. *European Journal of Wildlife Research*, **55**(2), 125-132.
- Lowe, K.W. (1989) The Australian Bird Bander's Manual. In: Ed. Anpws, pp. 3.1-3.6. Australian Bird and Bat Banding Schemes, Australian National Parks and Wildlife Service, Commonwealth of Australia, Canberra, Australia.
- Lowe, W.H. (2010) Explaining long-distance dispersal: effects of dispersal distance on survival and growth in a stream salamander. *Ecology*, **91**(10), 3008-3015.
- Lowery, G.H. (1974) Louisiana Birds. Louisiana State Univ.,
- Lutmerding, J.A., Rogosky, M., Peterjohn, B., McNicoll, J. & Bystrak, D. (2012) Summary of raptor encounter records at the bird banding lab. *Journal of Raptor Research*, **46**(1), 17-26.
- Macdonald, H. (2006) *Falcon*, 1st Edn. Reaktion Books Ltd, London.
- Macias-Duarte, A., Montoya, A.B. & Hunt, W.G. (2004) Reproduction, prey and habitat of the Aplomado Falcon *Falco femoralis* in desert grasslands of Chihuahua, Mexico. *The Auk*, **121**(4), 1081-1093.
- MacKinnon, M. (2011) *Does diet flexibility facilitate Peregrine Falcon persistence with landuse change?* Deakin University, Melbourne, Melbourne.
- Magurran, A.E., Baillie, S.R., Buckland, S.T., Dick, J.M., Elston, D.A., Scott, E.M., Smith, R.I., Somerfield, P.J. & Watt, A.D. (2010) Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. *Trends in Ecology and Evolution*, **25**(10), 574-582.
- Mänd, R., Tilgar, V., Lõhmus, A. & Leivits, A. (2005) Providing nest boxes for hole-nesting birds - Does habitat matter? *Biodiversity & Conservation*, **14**(8), 1823-1840.
- Marchant, S. & Higgins, P.J. (1993) Handbook of Australian, New Zealand and Antarctic birds: Volume 2 - Raptors to lapwings. Ed. by S. Marchant and P.J. Higgins, p. 984. Oxford University Press, Melbourne.
- Marks, J.B. (1994) Managing active nest sites and territories of the Peregrine Falcon in an urban environment. *Journal of Raptor Research*, **28**(1), 60.
- Martin, T.E. (1993) Nest Predation and Nest Sites. *BioScience*, **43**(8), pp. 523-532.
- Martin, T.E., Morné A du, P., Nalwanga, D. & Penn, L. (2004) The influence of nest-site characteristics on the nesting success of the Karoo Prinia (*Prinia maculosa*). *Ostrich*, **75**(4), 269-274.

- Martindale, S. (1982) Nest defense and central place foraging: A model and experiment. *Behavioral Ecology and Sociobiology*, **10**(2), 85-89.
- Martínez-Abraín, A., Crespo, J., Jiménez, J., Gómez, J.A. & Oro, D. (2009) Is the historical war against wildlife over in southern Europe? *Animal Conservation*, **12**(3), 204-208.
- Martínez, J.E., Pagán, I. & Calvo, J.F. (2006) Factors influencing territorial occupancy and reproductive output in the Booted Eagle *Hieraaetus pennatus*. *Ibis*, **148**(4), 807-819.
- McCulloch, M.A. (1990) Evaluation of leg markers for Bald Eagles. *Wildlife Society Bulletin*, **18**(3), 298-303.
- McDonald-Madden, E., Baxter, P.W.J., Fuller, R.A., Martin, T.G., Game, E.T., Montambault, J. & Possingham, H.P. (2010) Monitoring does not always count. *Trends in Ecology and Evolution*, **25**(10), 547-550.
- McDonald, P.G. (2003) Nestling growth and development in the Brown Falcon, *Falco berigora*: an improved ageing formula and field-based method of sex determination. *Wildlife Research*, **30**(4), 411-418.
- McDonald, P.G., Olsen, P.D. & Cockburn, A. (2004) Weather dictates reproductive success and survival in the Australian brown falcon *Falco berigora*. *Journal of Animal Ecology*, **73**(4), 683-692.
- McGraw, J.B. & Caswell, H. (1996) Estimation of individual fitness from life-history data. *The American Naturalist*, **147**(1), 47-64.
- Mearns, R. & Newton, I. (1984) Turnover and dispersal in a Peregrine *Falco peregrinus* population. *Ibis*, **126**(3), 347-355.
- Mearns, R. & Newton, I. (1988) Factors affecting breeding success of Peregrines in South Scotland. *Journal of Animal Ecology*, **57**(3), 903-916.
- Meijaard, E., Wich, S., Ancrenaz, M. & Marshall, A.J. (2012) Not by science alone: why orangutan conservationists must think outside the box. *Annals of the New York Academy of Sciences*, **1249**(1), 29-44.
- Merilä, J. & Sheldon, B.C. (2000) Lifetime Reproductive Success and Heritability in Nature. *The American Naturalist*, **155**(3), 301-310.
- Midwestern Peregrine Society (2009) *Project history*. Available at: <http://www.midwestperegrine.org/> [accessed 14th March 2013].
- Miller, J.R. & Hobbs, R.J. (2002) Conservation where people live and work. *Conservation Biology*, **16**(2), 330-337.
- Mizera, T. & Sielicki, J. (1995) The Peregrine Falcon *Falco peregrinus* in Poland - its situation and perspectives for reinstatement. *Acta Ornithologica*, **30**(1), 47-52.
- Mizera, T. & Sielicki, J. (2009) Breeding status of the Peregrine Falcon in Poland during the pre- and post- DDT era. In: *Peregrine Falcon populations: Status and perspectives in the 21st century*. Eds. J. Sielicki and J. Mizera, pp. 153-168. University of Life Sciences Press, Warsaw, Poznan, Poland.
- Monneret, R.J. (1983) L'aide à l'élevage chez le Faucon pèlerin. *Aulada*, **4**(2), 241-250.
- Mooney, N.J. (1985) Notes on Tasmanian birds of prey and domestic pigeons. In: *Tasmanian Parks and Wildlife*, Hobart.
- Mooney, N.J. (2013) Predation on Tasmanian Peregrines. *Boobook*, **31**(3), 60.
- Mooney, N.J. & Brothers, N. (1993) Dispersion, nest and pair fidelity of Peregrine Falcons *Falco peregrinus* in Tasmania. *Australian Raptor Studies*. Ed by P.D. Olsen, pp. 33-42. Currumbin, Qld.
- Moritsch, M.Q. (1983) Photographic guide for aging nestling Prairie Falcons. United States Bureau of Land Management, Boise, Idaho.

- Morrison, J.L. & Wood, P.B. (2009) Broadening our approaches to studying dispersal in raptors. *Journal of Raptor Research*, **43**(2), 81-89.
- Moussus, J.-P., Jiguet, F., Clavel, J. & Julliard, R. (2009) A method to estimate phenological variation using data from large-scale abundance monitoring programmes. *Bird Study*, **56**(2), 198-212.
- Mueller, H.C. (1990) Can Saw-whet Owls be sexed by external measurements? *Journal of Field Ornithology*, **61**(3), 339-346.
- Nelson, R.W. (1988) Do large natural broods increase mortality of parent Peregrine Falcons? *Peregrine Falcon populations: Their management and recovery*. Ed by T.J. Cade, J.H. Enderson, C.G. Thelander and C.M. White, pp. 719-728. Sacramento.
- Newsome, S.D., Park, J.S., Henry, B.W., Holden, A., Fogel, M.L., Linthicum, J., Chu, V. & Hooper, K. (2010) Polybrominated diphenyl ether (PBDE) levels in Peregrine Falcon (*Falco peregrinus*) eggs from California correlate with diet and human population density. *Environmental Science and Technology*, **44**(13), 5248-5255.
- Newton, I. (1979a) *Population ecology of raptors*, 1 Edn. T & AD Poyser, Berkhamsted.
- Newton, I. (1979b) Effects of human persecution on European raptors. *Journal of Raptor Research*, **13**(3), 65-78.
- Newton, I. (1985) Lifetime reproductive output of female Sparrowhawks. *Journal of Animal Ecology*, **54**(1), 241-253.
- Newton, I. (1989) *Lifetime reproductive success in birds*. Ed I. Newton 1 Edn. Academic Press, San Diego, CA. USA.
- Newton, I. (1991) Habitat variation and population regulation in Sparrowhawks. *Ibis*, **133**(1), 76-88.
- Newton, I. (1992) Experiments on the limitation of bird numbers by territorial behaviour. *Biological Reviews*, **67**(2), 129-173.
- Newton, I. (1993) Age and site fidelity in female sparrowhawks, *Accipiter nisus*. *Animal Behaviour*, **46**(1), 161-168.
- Newton, I. (2001) Studies of the reproduction, longevity and movements of individual animals. In: *Ecology: achievement and challenge. The 41st Symposium of the British Ecological Society jointly sponsored by the Ecological Society of America*. Eds. M.C. Press, N.J. Huntly and S. Levin, pp. 67-92. Blackwell Science, New York, Orlando, Florida, USA 10-13 April 2000.
- Newton, I. (2003) *Population limitation in birds*. 2 Edn. Academic Press, San Diego, USA.
- Newton, I., Bogan, J.A. & Haas, M.B. (1989) Organochlorines and mercury in the eggs of British Peregrines *Falco peregrinus*. *Ibis*, **131**(3), 355-376.
- Nicholls, J.A., Double, M.C., Rowell, D.M. & Magrath, R.D. (2000) The evolution of cooperative and pair breeding in thornbills *Acanthiza* (*Pardalotidae*). *Journal of Avian Biology*, **31**(2), 165-176.
- Nichols, J.D. & Williams, B.K. (2006) Monitoring for conservation. *Trends in Ecology and Evolution*, **21**(12), 668-673.
- Nisbet, E. (2007) Earth monitoring: Cinderella science. *Nature*, **450**(6), 789-790.
- Nisbet, I.C.T. (1988) Summary. *Peregrine Falcon populations: Their management and recovery*. Ed. by T.J. Cade, J.H. Enderson, C.G. Thelander and C.M. White, pp. 851-856. The Peregrine Fund Inc., Boise, Idaho.
- Norris, K.C., Emison, W.B. & Bren, W.M. (1977) A preliminary survey of the population of Peregrine Falcons in Victoria. *Emu*, **77**(2), 86-87.
- Olendorf, R.R. (1972) Weighing and measuring raptors. *Journal of Raptor Research*, **6**(2), 53-56.

- Ollila, T. (2009) Status of the Peregrine Falcon in Finland 1993-2006. In: *Peregrine Falcon populations: Status and perspectives in the 21st century*. Eds. J. Sielicki and J. Mizera, pp. 189-198. University of Life Sciences Press, Warsaw, Poznan, Poland.
- Olsen, J. & Olsen, P.D. (1978) Alleviating the impact of human disturbance on the breeding Peregrine Falcon II. Public and recreational lands. *Corella*, **4**(3), 54-57.
- Olsen, J. & Olsen, P.D. (1980) Alleviating the impact of human disturbance on the breeding Peregrine Falcon II. Public and recreational lands. *Corella*, **4**(3), 54-57.
- Olsen, J. & Georges, A. (1993) Do Peregrine Falcon fledglings reach independence during peak abundance of their main prey? *Journal of Raptor Research*, **27**(3), 149-153.
- Olsen, J., Fuentes, E., Dykstra, R. & Rose, A.B. (2006) Male Peregrine Falcon *Falco peregrinus* fledged from a cliff-nest found breeding in a stick nest. *Australian Field Ornithology*, **23**(1), 8-14.
- Olsen, J., Judge, D., Fuentes, E., Rose, A.B. & Debus, S.J.S. (2010) Diets of Wedge-tailed Eagles (*Aquila audax*) and Little Eagles (*Hieraaetus morphnoides*) Breeding Near Canberra, Australia. *Journal of Raptor Research*, **44**(1), 50-61.
- Olsen, P.D. (1982) Ecogeographic and Temporal Variation in the Eggs and Nests of the Peregrine, *Falco peregrinus* (Aves: Falconidae) in Australia. *Australian Wildlife Research*, **9**(2), 277-291.
- Olsen, P.D. (1995) *Australian birds of prey*, 1st Edn. University of New South Wales Press, Sydney.
- Olsen, P.D. (1997) Egg weight loss during incubation, and growth and development of captive-bred Southern Boobooks *Ninox novaeseelandiae*. In: *Australian Raptor Studies II. Birds Australia monograph 3*. Eds. G.V. Czechura and S.J.S. Debus, pp. 92-97. Birds Australia, Melbourne, Currumbin, QLD.
- Olsen, P.D. & Olsen, J. (1987a) Sexual size dimorphism in raptors: intrasexual competition in the larger sex for a scarce breeding resource, the smaller sex. *Emu*, **87**(1), 59-62.
- Olsen, P.D. & Olsen, J. (1987b) Estimating the age of nestling raptors. *Australian Bird Watcher*, **12**(4), 130-131.
- Olsen, P.D. & Olsen, J. (1988a) Breeding of the Peregrine Falcon *Falco peregrinus*: I. Weather, Nest Spacing and Territory Occupancy. *Emu*, **88**(4), 195-201.
- Olsen, P.D. & Olsen, J. (1988b) Population trends, distribution, and status of the Peregrine Falcon in Australia. *Peregrine Falcon populations: Their management and recovery*. Ed. by T.J. Cade, J.H. Enderson, C.G. Thelander and C.M. White, pp. 255-274. The Peregrine Fund. Inc., Boise, Idaho.
- Olsen, P.D. & Olsen, J. (1989a) Breeding of the Peregrine Falcon *Falco peregrinus*: II. Weather, Nest Quality and the Timing of Egg Laying. *Emu*, **89**(1), 1-5.
- Olsen, P.D. & Olsen, J. (1989b) Breeding of the Peregrine Falcon *Falco peregrinus*: III. Weather, Nest Quality and Breeding Success. *Emu*, **89**(1), 6-14.
- Olsen, P.D. & Cockburn, A. (1991) Female-biased sex allocation in Peregrine Falcons and other raptors. *Behavioral Ecology and Sociobiology*, **28**(6), 417-423.
- Olsen, P.D. & Olsen, J. (1992) Does Rain Hamper Hunting by Breeding Raptors? *Emu*, **92**(3), 184-187.
- Olsen, P.D., Olsen, J. & Mooney, N.J. (1982) Growth and development of nestling Brown Goshawks *Accipiter fasciatus*, with details of breeding biology. *Emu*, **82**(4), 189-194.
- Olsen, P.D., Olsen, J. & Mason, I. (1993) Breeding and non-breeding season diet of the Peregrine Falcon *Falco peregrinus* near Canberra, prey selection, and the relationship between diet and reproductive success. *Australian Raptor Studies*. Ed by P.D. Olsen, pp. 55-77. Brisbane.

- Olsen, P.D., Doyle, V. & Boulet, M. (1998) Variation in male provisioning in relation to brood size in Peregrine Falcons *Falco peregrinus*. *Emu*, **98**(4), 297-304.
- Olsen, P.D., Emison, W.B., Mooney, N.J. & Brothers, N. (1992) DDT and dieldrin: effects on resident Peregrine Falcon populations in south-eastern Australia. *Ecotoxicology*, **1**(1), 89-100.
- Palmer, A.G., Nordmeyer, D.L. & Roby, D.D. (2004) Nestling provisioning rates of Peregrine Falcons in interior Alaska. *Journal of Raptor Research*, **38**(1), 9-18.
- Park, J.S., Fong, A., Chu, V., Holden, A., Linthicum, J. & Hooper, K. (2011) Prey species as possible sources of PBDE exposures for peregrine falcons (*Falco peregrinus*) nesting in major California cities. *Archives of Environmental Contamination and Toxicology*, **60**(3), 518-523.
- Park, P. (1981) A colour-banding study of Welcome Swallows breeding in Southern Tasmania. *Corella*, **5**(1), 37-41.
- Pärn, H., Jensen, H., Ringsby, T.H. & Sæther, B.-E. (2009) Sex-specific fitness correlates of dispersal in a house sparrow metapopulation. *Journal of Animal Ecology*, **78**(6), 1216-1225.
- Pärt, T. (1990) Natal dispersal in the Collared Flycatcher: Possible causes and reproductive consequences. *Ornis Scandinavica*, **21**(2), pp. 83-88.
- Pärt, T. (1995) The importance of local familiarity and search costs for age- and sex-biased philopatry in the collared flycatcher. *Animal Behaviour*, **49**(4), 1029-1038.
- Peakall, D.B. & Kiff, L.F. (1988) DDE contamination in Peregrines and American Kestrels and its effect on reproduction. *Peregrine Falcon populations: Their recovery and management*. Ed. by T.J. Cade, J.H. Enderson, C.G. Thelander and C.M. White, pp. 337-350. The Peregrine Fund Inc., Boise, Idaho.
- Pedrini, P. & Sergio, F. (2001) Density, productivity, diet, and human persecution of Golden Eagles (*Aquila chrysaetos*) in the central-eastern Italian alps. *Journal of Raptor Research*, **35**(1), 40-48.
- Penteriani, V., Delgado, M.M., Maggio, C., Aradis, A. & Sergio, F. (2005) Development of chicks and predispersal behaviour of young in the Eagle Owl *Bubo bubo*. *Ibis*, **147**(1), 155-168.
- Perrin, N. & Mazalov, V. (2000) Local competition, inbreeding, and the evolution of sex-biased dispersal. *The American Naturalist*, **155**(1), 116.
- Plissner, J.H. & Gowaty, P.A. (1996) Patterns of natal dispersal, turnover and dispersal costs in eastern bluebirds. *Animal Behaviour*, **51**(6), 1307-1322.
- Pokrovsky, I., Lecomte, N., Sokolov, A., Sokolov, V. & Yoccoz, N.G. (2010) Peregrine Falcons kill a Gyrfalcon feeding on their nestling. *Journal of Raptor Research*, **44**(1), 66-69.
- Porter, R.D., Jenkins, A.M. & Gaski, A.L. (1987) *Working Bibliography of the Peregrine Falcon*. Ed M.N. Lefranc Jr. 1 Edn. Institute for Wildlife Research, National Wildlife Federation, Washington, D.C.
- Prestt, I. (1965) An enquiry into the recent breeding status of some smaller birds of prey and crows in Britain. *Bird Study*, **12**(3), 196-221.
- Pruett-Jones, S.G., White, C.M. & Emison, W.B. (1981a) Eggshell thinning and organochlorine residues in eggs and prey of Peregrine Falcons from Victoria, Australia. *Emu*, **80**(Supplement), 281-287.
- Pruett-Jones, S.G., White, C.M. & Devine, W.R. (1981b) Breeding of the Peregrine Falcon in Victoria, Australia. *Emu*, **80**(supplement), 253-269.
- Pulliam, H.R. & Danielson, B.J. (1991) Sources, sinks, and habitat selection: A landscape perspective on population dynamics. *The American Naturalist*, **137**(Supplement: Habitat Selection), S50-S66.

- Pusey, A.E. (1987) Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends in Ecology and Evolution*, **2**(10), 295-299.
- Quader, S. (2006) What makes a good nest? Benefits of nest choice to female Baya Weavers (*Ploceus philippinus*). *The Auk*, **123**(2), 475-486.
- Ratcliffe, D.A. (1993) *The Peregrine Falcon*, 2nd Edn. T & AD Poyser Ltd, London.
- Ratcliffe, D.A. (2003) The Peregrine saga. In: *Birds of prey in a changing environment*. Eds. D.B.A. Thompson, S.M. Redpath, A.H. Fielding, M. Marquiss and C.A. Galbraith, pp. 91-99. The Stationery Office Limited, Edinburgh.
- Redig, P.T. & Tordoff, H.B. (1988) Peregrine Falcon reintroduction in the Upper Mississippi valley and Western Great Lakes Region. *Peregrine Falcon populations: Their Management and Recovery*. Ed. by T.J. Cade, J.H. Enderson, C.G. Thelander and C.M. White, pp. 559-574. The Peregrine Fund, Boise.
- Remeš, V., Matysiuková, B. & Cockburn, A. (2012) Long-term and large-scale analyses of nest predation patterns in Australian songbirds and a global comparison of nest predation rates. *Journal of Avian Biology*, **43**(5), 435-444.
- Remeš, V. (2000) How can maladaptive habitat choice generate source-sink population dynamics? *Oikos*, **91**(3), 579-582.
- Restani, M. & Mattox, W.G. (2000) Natal dispersal of Peregrine Falcons in Greenland. *The Auk*, **117**(2), 500-504.
- Richardson, G.T. & Miller, C.K. (1997) Recommendations for protecting raptors from human disturbance: a review. *Wildlife Society Bulletin*, **25**(8), 634-638.
- Ridgway, R. (1895) Nesting of the duck hawk in trees.
- Ripple, W.J. & Beschta, R.L. (2012) Trophic cascades in Yellowstone: The first 15 years after wolf reintroduction. *Biological Conservation*, **145**(1), 205-213.
- Ritchie, E.G. & Johnson, C.N. (2009) Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, **12**(9), 982-998.
- Robbins, A.M., Stoinski, T., Fawcett, K. & Robbins, M.M. (2011) Lifetime reproductive success of female mountain gorillas. *American Journal of Physical Anthropology*, **146**(4), 582-593.
- Robertson, B.A. & Hutto, R.L. (2006) A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology*, **87**(5), 1075-1085.
- Robertson, G.P., Collins, S.L., Foster, D.R., Brokaw, N., Ducklow, H.W., Gragson, T.L., Gries, C., Hamilton, S.K., McGuire, A.D., Moore, J.C., Stanley, E.H., Waide, R.B. & Williams, M.W. (2012) Long-Term Ecological Research in a Human-Dominated World. *BioScience*, **62**(4), 342-353.
- Rodewald, A.D., Shustack, D.P. & Jones, T.M. (2011) Dynamic selective environments and evolutionary traps in human-dominated landscapes. *Ecology*, **92**(9), 1781-1788.
- Root-Bernstein, M. & Ladle, R.J. (2010) Conservation by design. *Conservation Biology*, **24**(5), 1205-1211.
- Rosenfield, R.N., Grier, J.W. & Fyfe, R., W. (2007) Reducing management and research disturbance, Ch 19. *Raptor Research and Management Techniques*. Ed. by D.M. Bird and K.L. Bildstein, pp. 351-364. Hancock House, Surrey, BC, Canada.
- Rosenfield, R.N., Schneider, J.W., Papp, J.M. & Seegar, W.S. (1995) Prey of Peregrine Falcons breeding in West Greenland. *The Condor*, **97**(3), 763.
- Santana, C.E., Verdugo-Munguía, H., Ibarra-Cerdeña, C., Nuñez-Figueroa, J.J. & Sánchez-Jiménez, O. (2006) Extension of the known breeding range and breeding season of the Peregrine Falcon in western North America. *Journal of Raptor Research*, **40**(3), 238-241.

- Sarasola, J.H. & Negro, J.J. (2004) Gender determination in the Swainson's Hawk (*Buteo swainsoni*) using molecular procedures and discriminant function analysis. *Journal of Raptor Research*, **38**(4), 357-361.
- Saunders, D.A. & Smith, G.T. (1981) Egg dimensions and egg weight loss during incubation in five species of Cockatoo, and the use of measurements to determine the stage of incubation in bird's eggs. *Australian Wildlife Research*, **8**(3), 411-419.
- Saunders, D.A., Smith, G.T. & Campbell, N.A. (1984) The relationship between body weight, egg weight, incubation period, nestling period and nest site in the Psittaciformes, Falconiformes, Strigiformes and Columbiformes. *Australian Journal of Zoology*, **32**(1), 57-65.
- Sayre, N.F. (2012) The politics of the anthropogenic. In, pp. 57-70
- Schoenjahn, J. (2012) A hot environment and one type of prey: investigating why the Grey Falcon (*Falco hypoleucos*) is Australia's rarest falcon. *Emu*, **112**(4),
- Septon, G.A., Bielefeldt, J., Ellestad, T., Marks, J.B. & Rosenfield, R.N. (1996) Bridge use by Peregrine Falcons in the San Francisco Bay area. *Raptors in human landscapes: adaptations to built and cultivated environments*. Ed. by D.M. Bird, D. Varland and J.J. Negro, pp. 145-153. Academic Press Inc., London.
- Sergio, F., Rizzolli, F., Marchesi, L. & Pedrini, P. (2004) The importance of interspecific interactions for breeding-site selection: Peregrine Falcons seek proximity to Raven nests. *Ecography*, **27**(6), 818-829.
- Sergio, F., Caro, T., Brown, D., Clucas, B., Hunter, J., Ketchum, J., McHugh, K. & Hiraldo, F. (2008) Top predators as conservation tools: Ecological rationale, assumptions and efficacy. *The Annual Review of Ecology, Evolution and Systematics*, **39**(1), 1-19.
- Serrano, D. & Tella, J.L. (2012) Lifetime fitness correlates of natal dispersal distance in a colonial bird. *Journal of Animal Ecology*, **81**(1), 97-107.
- Sherrod, S.K. (1983) *Behaviour of fledgling Peregrines*, 1 Edn. Pioneer Impressions, Ft. Collins.
- Sherrod, S.K., Heinrich, W., Burnham, W., Barclay, J. & Cade, T.J. (1982) *Hacking: a method for releasing Peregrine Falcons and other birds of prey*. The Peregrine Fund, Cornell Univ., Ithaca, New York.
- Sielicki, J. & Mizera, J. (2009) *Peregrine Falcon Populations: Status and perspectives in the 21st Century*. Turul Publishing & Poznan University of Life Sciences Press, Warsaw, Poland.
- Silvy, N.J., Lopez, R.R. & Peterson, M.J. (2005) Wildlife marking techniques. *Research and management techniques for wildlife and habitats*. Ed. by C.E. Braun, pp. 339-376. The Wildlife Society Inc., Bethesda, MD U.S.A.
- Silvy, N.J., Lopez, R.R. & Peterson, M.J. (2012) Techniques for Marking Wildlife Ch 9. *The wildlife techniques manual - research*. Ed. by N.J. Silvy, pp. pp 230-257. Published in affiliation with The Wildlife Society, The John Hopkins University Press, Baltimore, USA.
- Sinclair, A.R.E., Mduma, S.A.R., Hopcraft, J.G.C., Fryxell, J.M., Hilborn, R.A.Y. & Thirgood, S. (2007) Long-Term Ecosystem Dynamics in the Serengeti: Lessons for Conservation. *Conservation Biology*, **21**(3), 580-590.
- Smart, J., Amar, A., Sim, I.M.W., Etheridge, B., Cameron, D., Christie, G. & Wilson, J.D. (2010) Illegal killing slows population recovery of a re-introduced raptor of high conservation concern - The red kite *Milvus milvus*. *Biological Conservation*, **143**(5), 1278-1286.
- Smith, G.D. & McGrady, M. (2009) Using passive integrated transponder (PIT) tags to better understanding Peregrine Falcon population in South Scotland and North East England. In: *Peregrine Falcon populations: Status and perspectives in the 21st Century*. Eds. J. Sielicki and T. Mizera, pp. 245-258. Turul Publishing & Poznan University of Life Sciences Press, Poznan, Poland.

- Smits, J.E.G. & Fernie, K.J. (2012) Avian wildlife as sentinels of ecosystem health. *Comparative Immunology, Microbiology and Infectious Diseases*, **36**(3), 333-342.
- Solonen, T. & Ursin, K.A. (2008) Breeding of Tawny Owls *Strix aluco* in rural and urban habitats in southern Finland. *Bird Study*, **55**(2), 216-221.
- Sonne, C. (2010) Health effects from long-range transported contaminants in Arctic top predators: An integrated review based on studies of polar bears and relevant model species. *Environment International*, **36**(5), 461-491.
- Spear, L.B., Pyle, P. & Nur, N. (1998) Natal dispersal in the western gull: proximal factors and fitness consequences. *Journal of Animal Ecology*, **67**(2), 165-179.
- Spofford, W.R. (1947) Another tree-nesting peregrine falcon record for Tennessee. *Migrant* **8**(1), 60.
- Spring, D.A., Bevers, M., Kennedy, J.O.S. & Harley, D. (2001) Economics of a nest-box programme for the conservation of an endangered species: a reappraisal. *Canadian Journal of Forest Research*, **31**(11), 1992-2003.
- Squires, R. & Kennedy, P.L. (2006) Northern Goshawk ecology: an assessment of current knowledge and information needs for conservation and management. *Studies in Avian Biology*, **31**(1), 8-62.
- Stamps, J.A. & Swaisgood, R.R. (2007) Someplace like home: Experience, habitat selection and conservation biology. *Applied Animal Behaviour Science*, **102**(3), 392-409.
- Stamps, J.A., Krishnan, V.V. & Reid, M.L. (2005) Search costs and habitat selection by dispersers. *Ecology*, **86**(2), 510-518.
- Stearns, S.C. (1976) Life-History Tactics: A Review of the Ideas. *The Quarterly Review of Biology* **51**(1), 3-47.
- Steenhof, K. & Kochert, M.N. (1982) An Evaluation of methods used to estimate raptor nesting success. *The Journal of Wildlife Management*, **46**(4), 885-893.
- Steenhof, K. & Newton, I. (2007) Assessing nesting success and productivity. *Raptor research and management techniques*. Ed. by D.M. Bird and K.L. Bildstein, pp. 181-192. Hancock House Publishers, Surrey, British Columbia, Canada.
- Steenhof, K., Kochert, M.N. & Roppe, J.A. (1993) Nesting by raptors and common ravens on electrical transmission line towers. *The Journal of Wildlife Management*, **57**(2), 271-281.
- Strasser, E.H. & Heath, J.A. (2013 *in press*) Reproductive failure of a human-tolerant species, the American Kestrel, is associated with stress and human disturbance. *Journal of Applied Ecology*, **50**(4), 912-919.
- Strydom, W.F., Funke, N., Nienaber, S., Nortje, K. & Steyn, M. (2010) Evidence-based policymaking: A review. *South African Journal of Science*, **106**(5-6),
- Suárez, E., Morales, M., Cueva, R., Bucheli, U.V., Zapata-Ríos, G., Toral, E., Torres, J., Prado, W. & Olalla, V.J. (2009) Oil industry, wild meat trade and roads: Indirect effects of oil extraction activities in a protected area in north-eastern Ecuador. *Animal Conservation*, **12**(4), 364-373.
- Sutherland, G.D., Harestad, A.S., Price, K. & Lertzman, K. (2000) Scaling of natal dispersal distances in terrestrial birds and mammals. *Ecology and Society*, **4**(1),
- Tanner, L. (2011) *Sideshow: Dumbing Down Democracy*. Scribe, Melbourne, Australia.
- Taranto, P. (2009) Patterns of urbanisation and hunting strategies of urban Peregrine Falcons in Italy. In: *Peregrine Falcon populations: Status and perspectives in the 21st Century*. Eds. J. Sielicki and J. Mizera, pp. 725-728. Poznan University of Life Sciences Press, Poznan, Poland.
- Taranto, P., Sielicki, J. & Mizera, T. (2008) Patterns of urbanisation and hunting strategies of urban Peregrine Falcons in Italy. *Peregrine Falcon populations: Status and perspectives*

- in the 21st century. pp. 725-728. Turul Publishing and Poznan University of Life Sciences Press, Poznan, Poland.
- Thomas, B., Holland, J.D. & Minot, E.O. (2011) Wildlife tracking technology options and cost considerations. *Wildlife Research*, **38**(5), 653-663.
- Thompson, B.C., Knadle, G.F., Brubaker, D.L. & Brubaker, K.S. (2001) Nest success is not an adequate comparative estimate of avian reproduction. *Journal of Field Ornithology*, **72**(4), 527-536.
- Thompson, D.B.A., Redpath, S.M., Fielding, A.H., Marquiss, M. & Galbraith, C.A. (2003) *Birds of prey in a changing environment*. The Stationery Office Limited, Edinburgh, Scotland.
- Tint, A., Real, J. & Mañosa, S. (2010) Predicting and correcting electrocution of birds in Mediterranean areas. *Journal of Wildlife Management*, **74**(8), 1852-1862.
- Tordoff, H.B. & Redig, P.T. (1997) Midwest Peregrine Falcon demography, 1982-1995. *Journal of Raptor Research*, **31**(4), 339-346.
- Tordoff, H.B., Martell, M.S. & Redig, P.T. (1998) Effect of fledge site on choice of nest site by midwestern Peregrine Falcons. *The Loon*, **70**(2), 127-129.
- Tukey, J.W. (1991) The Philosophy of Multiple Comparisons. *Statistical Science* **6**(1), 100-116.
- Turner, J. (2005) Tree-nesting Peregrines. In: *RSPB Birds*. p. 7. Royal Society for the Preservation of Birds, London.
- United Nations (2012) Population Division World Urbanisation Prospects: The 2011 Revision highlights. (http://esa.un.org/unpd/wup/pdf/WUP2011_Highlights.pdf).
- Varland, D.E., Smallwood, J.A., Young, L.S. & Kochert, M.N. (2007) Marking techniques Ch. 13. *Raptor Research and Management Techniques*. Ed. by D.M. Bird and K.L. Bildstein, pp. pp 221-236. Hancock House Publisher, Ltd, Surrey, BC, Canada.
- Verdejo, J. & López-López, P. (2008) Long-term monitoring of a peregrine falcon population: Size, breeding performance and nest-site characteristics. *Ardeola*, **55**(1), 87-96.
- Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. (1997) Human Domination of Earth's Ecosystems. *Science*, **277**(5325), 494-499.
- Vora, G.J., Meador, C.E., Stenger, D.A. & Andreadis, J.D. (2004) Nucleic acid amplification strategies for DNA microarray-based pathogen detection. *Applied and environmental microbiology*, **70**(5), 3047-3054.
- Waits, L.P. & Paetkau, D. (2005) Non-invasive genetic sampling tools for wildlife biologists: a review of applications and recommendations for accurate data collection. *The Journal of Wildlife Management*, **69**(4), 1419-1433.
- Wakamiya, S.M. & Roy, C.L. (2009) Use of monitoring data and population viability analysis to inform reintroduction decisions: Peregrine Falcons in the Midwestern United States. *Biological Conservation*, **142**, 1767-1776.
- Walsh, J.C., Wilson, K.A., Benshemesh, J. & Possingham, H.P. (2012) Integrating research, monitoring and management into an adaptive management framework to achieve effective conservation outcomes. *Animal Conservation*, **15**(4), 334-336.
- Warkentin, I.G. & James, P.C. (1988) Nest-Site Selection by Urban Merlins. *The Condor*, **90**(3), 734-738.
- Watson, J.W. (2004) Response of nesting Bald Eagles to experimental pedestrian activity. *Journal of Raptor Research*, **38**(4), 295-303.
- Wegner, P. & Fürst, P. (2009) Long-term investigation of the degree of exposure of German Peregrine Falcons to damaging chemicals from the environment and recent results. In: *Peregrine Falcon populations: Status and perspectives in the 21st century*. Eds. J. Sielicki and J. Mizera, pp. 625-630. University of Life Sciences Press, Warsaw, Poznan, Poland.

- Wegner, P., Brücher, H., Brücher, S., Höller, T., Jödes, M., Kladny, M., Linder, M., Sell, G., Speer, G., Thomas, T. & Volkhausen, J. (2009) Development of an urban population of Peregrine Falcons in North Rhine-Westphalia, Germany: population status nest site selection and some biological results. In: *Peregrine Falcon populations: Status and perspectives in the 21st century*. Ed. J.S.a.T. Mizera, pp. 729-746. Turul/Poznan University of Life Sciences Press, Warsaw, Poznan, Poland.
- White, C.M. (1987) The Peregrine: systematics and evolution. *Working bibliography of the Peregrine Falcon*. Ed. by R.D. Porter, A. Jenkins and A. Gaski, pp. xii-xxx. National Wildlife Federation Science Technical Series no. 9, Washington D.C.
- White, C.M. (2009) Peregrine Falcons and the literature. In: *Peregrine Falcon populations: Status and perspectives in the 21st Century*. Eds. J. Sielicki and J. Mizera, pp. 8-9. Turul Publishing & Poznan University of Life Sciences Press, Poznan, Poland.
- White, C.M. & Roseneau, D.G. (1970) Observations on food, nesting, and winter populations of large North American Falcons. *The Condor*, **72**(1), 113-115.
- White, C.M. & Jones, S.G. (1977) Distribution and ecology of the Peregrine Falcon in Victoria. Fisheries and Wildlife Division, Ministry for Conservation, Government of Victoria.
- White, C.M. & Thurow, T.L. (1985) Reproduction of Ferruginous Hawks exposed to controlled disturbance. *The Condor*, **87**(1), 14-22.
- White, C.M. & Boyce, D.A. (1988) An overview of Peregrine Falcon subspecies. *Peregrine Falcon populations: Their Management and Recovery*. Ed. by T.J. Cade, J.H. Enderson, C.G. Thelander and C.M. White, pp. 789-810. The Peregrine Fund, Boise.
- White, C.M. & Brimm, D.J. (1990) Insect hawking by a Peregrine Falcon (*Falco peregrinus*) in Fiji. *Notornis*, **37**140.
- White, C.M., Pruett-Jones, S.G. & Emison, W.B. (1981) The status and distribution of the Peregrine Falcon in Victoria, Australia. *Emu*, **80**(Supplement), 270-280.
- White, C.M., Emison, W.B. & Bren, W.M. (1988) Atypical nesting habitat of the Peregrine Falcon *Falco peregrinus* in Victoria, Australia. *Journal of Raptor Research*, **22**(2), 37-43.
- White, C.M., Sonsthagen, S.A., Sage, G.K., Anderson, C. & Talbot, S.L. (2013) Genetic relationships among some subspecies of the Peregrine Falcon (*Falco peregrinus* L.), inferred from mitochondrial DNA control-region sequences. *The Auk*, **130**(1), 78-87.
- Whitlock, M.C. (2011) Data archiving in ecology and evolution: best practices. *Trends in Ecology and Evolution*, **26**(2), 61-65.
- Whitman, J.S. & Caikoski, J.R. (2008) Peregrine Falcon nesting in tree stick-nest in Alaska. *Journal of Raptor Research*, **42**(4), 300-302.
- Wiersma, J., Nermut, W. & Shephard, J.M. (2001) A variation on the 'noosed fish' method and its suitability for trapping the White-bellied Sea-eagle *Haliaeetus leucogaster*. *Corella*, **25**(4), 97-99.
- Wightman, C.S. & Fuller, M. (2006) Influence of habitat heterogeneity on distribution, occupancy patterns, and productivity of breeding Peregrine Falcons in central west Greenland. *The Condor*, **108**(2), 270-281.
- Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A. & Losos, E. (1998) Quantifying threats to imperiled species in the United States. *BioScience*, **48**(8), 607-615.
- Zhu, X., Srivastava, D.S., Smith, J.N.M. & Martin, K. (2012) Habitat Selection and Reproductive Success of Lewis's Woodpecker (*Melanerpes lewis*) at its Northern Limit. *Plos One*, **7**(9), (e44346) 1-10.
- Zuberogitia, I., Ruiz Moneo, J.F. & Torres, J.J. (2002) *El Halcón Peregrino*. Dpto Agricultura, Diputación Foral de Bizkaia, Bilbao.

- Zuberogoitia, I., Martínez, J., Azkona, A., Castillo, I. & Zabala, J. (2009) Using recruitment age, territorial fidelity and dispersal as decisive tools in the conservation and management of Peregrine Falcon (*Falco peregrinus*) populations: the case of a healthy population in Northern Spain. *Journal of Ornithology*, **150**(1), 95-101.
- Zuberogoitia, I., Martínez, J.E., González-Oreja, J.A., Calvo, J.F. & Zabala, J. (2013) The relationship between brood size and prey selection in a Peregrine Falcon population located in a strategic region on the Western European Flyway. *Journal of Ornithology*, **154**(1), 73-82.

Appendices



Humphrey Bogart (Haunted Studios ©)

Detective Tom Polhaus (picks up falcon statue): "Heavy. What is it?"

Sam Spade: "The, uh, stuff that dreams are made of."

(Closing lines of *The Maltese Falcon*, 1941)

Appendix I – 1st Peregrine Falcon band recovery

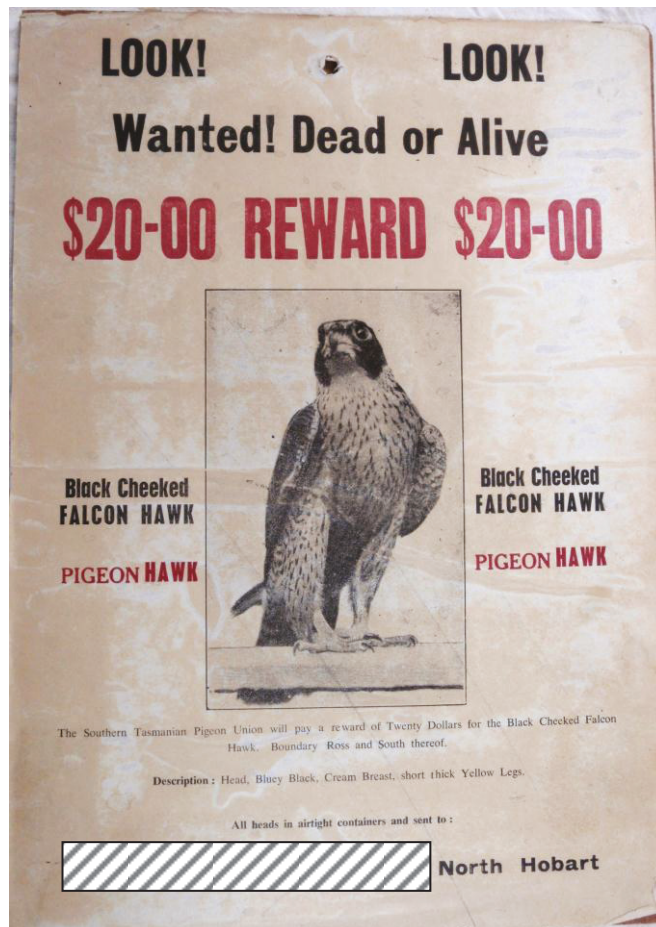
COMMONWEALTH SCIENTIFIC AND INDUSTRIAL RESEARCH ORGANISATION	
WILDLIFE SURVEY SECTION	
AUSTRALIAN BIRD BANDING SCHEME	
<u>RECOVERY REPORT</u>	
BAND NUMBER:	120 - 02615
R.A.O.U.NO.:	237
SPECIES :	Peregrine Falcon
RECOVERED AT:	Cavendish, c. 18 m. N of Hamilton, Vic. 37.31 142.62
ON (date) :	8 May 58
HOW RECOVERED:	Found dead
OTHER DETAILS:	Appeared to have been shot
Banded by S.B.Hood Banded 20/1/50 Ad.F. 27/1/50 miles D+D 73/ESC	
RETURNED BY:	R.F.Munn, Cavendish, Vic.
FILE NUMBER:	B4/6
RECEIVED:	14 May 58
BAND CARD NUMBER:	
BAND SCHEDULE NO.:	237/4/2
WLS/B-BS/16	

With the Compliments
of
The Secretary
Australian Bird-Banding Scheme
Division of Wildlife Research
Commonwealth Scientific and
Industrial Research
Organization

3.0 / Copy as provided
2/3

P.O. Box 34
Lyndham, Canberra
A.C.T. 2602
Australia

Appendix II – Peregrine persecution



Pigeon club poster from Tasmania, circa 1970, (supplied by N.J. Mooney).



Old pigeon bands dating back to 1905 found in an active Peregrine Falcon nest, 2005.

Appendix III – Banding data sheet



FIELD DATA SHEET - 2012

Page

 of

Bander : _____

LOCATION: _____ LOCODE:

TIME: _____ AM / PM DATE: ____ / ____ / 2012

WEIGHT		AGE		SEX	
Bird + bag = _____		J / / A		M / F	
- Bag = _____		WING LENGTH			
Bird = _____ g		TAIL LENGTH			
TARSUS LENGTH		HEAD + BILL			
_____ mm		_____ cm			
Hind Talon LENGTH		TIP-CERE			
_____ mm		_____ mm			
Hind Talon DEPTH		EXPOSED CULMEN			
_____ mm		_____ mm			
Hind Talon WIDTH		LEG BANDS			
_____ mm		_____ mm			
LEFT		LEG BANDS		RIGHT	
Colour	ID Code	Colour	ID Code	Colour	ID Code
_____	_____	Place band sticker inside this dotted line box		_____	_____
Pins Broken ?	No. of Eggs	No. of Chicks	Hatch Order	Sex ratio	
Y / N	_____	_____	_____	_____	
Adult ♂ Band Numbers		Adult ♀ Band Numbers		Comments	
_____		_____		_____	

Appendix IV – Adult band monitoring data sheet



COLOUR BAND RECORD SHEET - 2012

V 17.1

LOCODE:

LOCATION: _____

LOCODE: _____

Observer(s): _____ DATE: ____ / ____ / 2012

Leg Bands Identified by:		Telescope	Binoculars	Naked Eye	Trapped	Camera
Reason for delay:		Bird present and would not settle	Waiting for incubation change over	Adult away hunting/feeding	weather	
ADULT	FEMALE banded?	Agro Index*	Age	Clutch size	Hatch Order	
FEMALE	Y / N / 0					
LEFT LEG BAND		RIGHT LEG BAND				
Colour	ID Code	Colour		ID Code		
_____	_____	_____		_____		

Origin: _____ Distance: _____ Direction: _____ Bearing: _____

Reason for delay:		Bird present and would not settle	Waiting for incubation change over	Adult away hunting/feeding	weather	
ADULT	MALE banded?	Agro Index*	Age	Clutch size	Hatch Order	
MALE	Y / N / 0					
LEFT LEG BAND		RIGHT LEG BAND				
Colour	ID Code	Colour		ID Code		
_____	_____	_____		_____		
Eggs	Chicks	Comments				
_____	_____	_____				

Origin: _____ Distance: _____ Direction: _____ Bearing: _____

All Adults must be monitored for leg bands!

*Agro Index, only to be used when someone climbs or abseils into the nest.

0 = not seen, 1 = present but not defending, 2 = calling and agitated but not flying

3 = calling, flying & not stooping, 4 = stooping without hitting, 5 = hit climber!

Data Sheet - Season 2012

Site: _____ LOCODE _____

Time: _____ Date: _____

	Egg 1	Egg 2	Egg 3	Egg 4
Length				
Width				
Weight				
Laying date				
Hatch date				
Band date (24d)				

General notes on site, breeding activity etc.

Appendix VI – Banding Manual

VICTORIAN PEREGRINE PROJECT

Colour Banding Manual

2013



23/7/2013

A banding manual for use by volunteers of the Victorian Peregrine Project.

Title: "Victorian Peregrine Project: Colour banding manual, Version 22.1".

Prepared by: Victor G. Hurley
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Produced for: Volunteers of the Victorian Peregrine Project

Report Status: Final - 23 July 2013

Citation: Hurley, V.G. (2013) "Victorian Peregrine Project: Colour banding manual, Version 22.1". Mildura, Australia.

Cover photograph: An adult ♀ Peregrine Falcon flying 200 m above Collins St, Melbourne. (Photo by VG Hurley ©)

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Introduction

Not all banding projects follow the measuring standards used in this project. So do not be concerned if the following protocols vary from what you may be used to. As this project has been running for 10+ years it is important to maintain and not to vary from the protocols used from the beginning.

Please read the following manual carefully before going out in the field and have it with you on your first few trips as a reference until the measuring techniques become quite familiar to you.

Filling in the Field Data Sheet

Notes to the person acting as data recorder

Where two or more people are involved in processing a bird, one person should be dedicated to taking the measurements and another to recording the details. Accurate record keeping is essential. In order to minimise the chances for recording incorrect data, the measurer should read out aloud the measurements and the scientific units used. The recorder should enter the data and read out, aloud back to the measurer the figures written down so both people agree on what the data is. This procedure must be followed for each and every data point.

Page Numbering

Each data sheet relates to the banding data for one bird. So starting with the first data sheet circle only one number on each sheet in the top row for each bird banded. Circle the lower number (on every sheet) to represent how many birds in total are being banded at that site on that particular day.

The example below shows this data sheet holds information on the second of three birds to be banded at that site for that day.

Page	1	2	3	4	5
of	1	2	3	4	5

Bander

Print clearly the name of the bander and the data recorder in the space provided.

LOCATION

Enter the name from the VPP Locode list provided. Where the banding is being done at a site not listed, enter a new location name in the space provided and then record on the back of the data sheet a Melways or Vic Roads map or GPS map grid reference and don't forget the map datum! Provide as much detail as possible. Include a site description indicating whether the site is a tree, cliff or other structure and contact details of the responsible land manager as well as a mud map so others can find the site.

LOCODE

The Locode is a location code that identifies the site for the Australian Bird and Bat Banding Scheme office in Canberra. Each Locode is made up of two alpha/numeric characters and are listed on the VPP laminated Locode sheet provided.

TIME

Enter the time and circle AM or PM as appropriate. This is important to record, as chicks banded in the afternoon will have been fed (usually) and may weigh 20g+ heavier than first thing in the morning. This may be important later on when aging or sexing young chicks and in determining condition.

DATE

Record date in the following format: DD/MM/YYYY e.g. the sixth of September 2000 would read 06/09/2000. The banding date is essential to assist with determining the laying date.

Weight

Bird & Bag

Using a Pesola spring balance scale weigh first the bag when it is empty and record this in the box labelled "**Bag =**". Then place the bird in the bag and record their combined weight (**Bird + bag**). Finally subtract the weight of the bag from the combined weight to determine the weight of the bird. Weight is often the only measure needed to determine the sex of a Peregrine. Males tend to peak at 700gm in the nest and are usually closer to 600gm after fledging. Females have been recorded over 1kg. Healthy females at the same age (*which can be determined from the wing length*) are heavier than males.

WEIGHT
Bird + bag =
- Bag =
Bird = g

Other Measurements

All other measurements should be recorded in millimetres using first the digital callipers and then the stainless steel ruler for wing and tail measurements. With all of the calliper measurements be sure to remove the callipers very carefully away from the bird before reading the measurements.

Exposed Culmen

This measurement measures the cord of the arc (ie shortest or net distance) from the tip of the beak to its' base, where it grows out of the yellow cere.

This measurement is best done by resting the top arm of an opened pair of callipers at the base on the front edge of the cere and then gently closing the callipers so the lower arm just touches the tip of the beak.



Tip-Cere

This measurement measures the cord of the arch (ie shortest or net distance) of the whole beak including the width of the cere. Measure the tip of the beak to the point at which feathers start growing from the base of the yellow cere.

This measurement is best done by resting the top arm of an opened pair of callipers at the point where the feathers start growing out of the cere and then gently closing the callipers so the lower arm just touches the tip of the beak. As with all calliper measurements gently and slowly remove the callipers away from the bird before reading out the measurement to the recorder.



Head + Bill

This measurement measures the distance from the back of the skull to the tip of the beak.

This measurement is best done by resting the top arm of an opened pair of callipers at the back of the skull near the occipital condyles. There is a notch at the base of the skull formed by the top of the condyles which is the recommended point to place the top calliper arm. Then gently closing the callipers so the lower arm just touches the tip of the beak. Carefully remove the callipers away from the bird before reading out the measurement.



TAIL LENGTH

This measurement is to determine the length of the longest tail feathers (*which normally are the central two feathers*). This measurement can be done using either callipers or more easily by using a steel ruler. First count the number of pairs of feathers starting from the outer two on either side of the tail. Upon arriving at the central pair gently slide an end of the ruler down to the base in between these two feathers. Then press one of the feathers against the ruler and read off the length. Remember that all measurements are to be in millimetres.

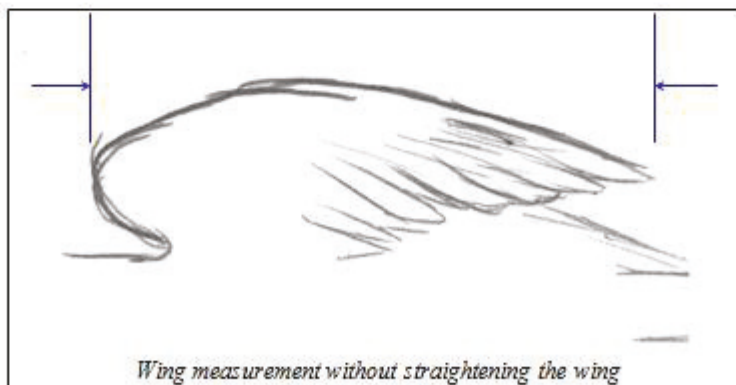
WING LENGTH

This is one of the most important measurements as it provides the only measure we have of the age of the individual. So care must be taken and it can be measured on both wings using the second measure to calibrate the consistency of measurements.

There are three recognised measures of wing length. All can be taken with a butt ended ruler. This is a rule which has been cut so that one end starts at the zero measurement without any border or gap before the end of the ruler. At this end there should be a right angled piece of metal (the butt) welded to the ruler. The carpal joint (wrist joint or leading bend in the wing) is placed against the butt of the ruler with the wing in the naturally folded position resting on top of the ruler. The length of the longest primary is then recorded straight from the ruler without straightening or flattening the feathers and without lifting the wing from the ruler. This is referred to as measuring the wing cord as it is measuring the straight line from the wrist joint to the tip of the longest primary without straightening or flattening the wing at all. This measurement should be taken with the wing sitting folded as it sits naturally against the body of the bird.



The bird's 'wrist joint' is pushed up against the butt of the ruler on the right in this photos.



Wing measurement without straightening the wing

TARSUS LENGTH

This is one of the more difficult measurements to take and is easiest done if an assistant is holding the bird whilst the bander is taking this measurement.

This is measured from the intertarsal joint (*knee joint*) to the lower edge of the last undivided scute (*scale*) before the toes diverge. The leg to be measured should be held out from the body of the bird so as to form an 's' bend with two right angles in it. One is at the knee joint and the second is formed by folding the toes backwards at right angles to the body.

As with previous measurements using an open pair of calipers the top arm of the calipers should be rested in the prominent notch at the back of the knee joint. The lower arm of the calipers should then be gently closed into the notch between the longest central toe and the tarsus. By locating both of these notches with your fingers before you start measuring the tarsus it will make this measurement much easier to do.



AGE

We are using a very simplified age classification system. Chicks in the nest are referred to as 'J' for juveniles and all others 'A' for adult. Just circle which option applies to the bird you are measuring.

For a more accurate estimate of age, the following formula provides a good estimate within 1-2 days for nestlings up to fledging.

$$\text{Age (in days)} = \frac{(WL + 0.84)}{0.69}$$

WL = Wing Length

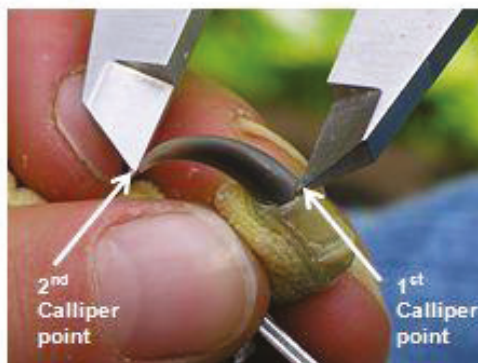
Any individual with a wing length less than 9.0 cm is NOT to be banded.

Halux Volume Vs Wing Chord Length

The Halux is the claw on the hind talon on each foot of a Peregrine. The halux volume is a reliable index of sex and nestling condition. Again an open pair of callipers is required for this set of measurements. Three measurements are taken in all and these are simply multiplied together to give the volume of this feature.

Halux Length

The callipers are rested one point at the outer most edge of the base of the claw with the second calliper point just touching the tip of the halux. This measurement is best taken with the second calliper point able to move just clear of the halux tip.



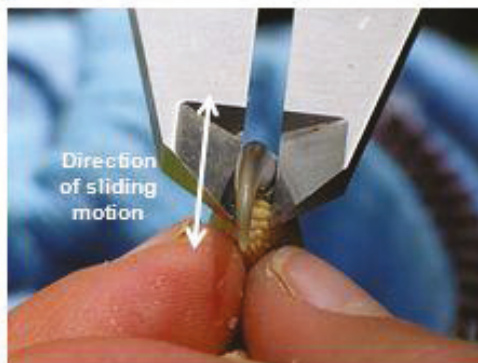
Halux Depth

Halux depth is measured by resting the two calliper points on the base of the halux where it emerges from the yellow skin of the talon. There should be just enough gap width between the callipers and the halux so that the callipers can be gently slid back and forth without scratching the surface of the halux.



Halux Width

Halux width is also measured by resting the two calliper points on the base of the halux where it emerges from the yellow skin of the talon. Again gently slide the callipers back and forth along the base of the halux without scratching the surface of the halux.



PINS BROKEN?

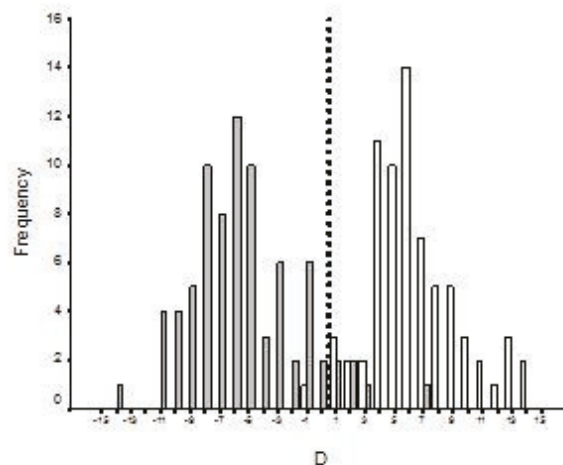
Are the flight feather pins broken? Nestlings are aged by the wing length. There are two formulas that can be applied and one uses feathers that are still completely contained within the growth pins and is used for peregrines less than 10 days old. The other formula is used for any nestling which has growing feathers that have erupted from the feather pins. Circling 'Y' or 'N' will determine which formula we use.

SEX

Some of the measurements you have been taking can be used with much certainty to determine the sex of the bird. This is important because females being bigger than males take larger leg bands. Adult male Peregrines will not be over 700gm and mostly be between 550 and 650gm. A healthy adult female will not normally be below 800gm. Males take ABBBS size 11 and females take size 27 or even 12 for really big birds!

The following formula is to be used to determine the sex of the nestling prior to banding:

$$D_i = -39.930 - 16.830 (\text{wing} (\log_{10} \text{ cm})) + 12.128 (\text{weight} (\log_{10})) + 0.124 (\text{head+bill} (\text{mm})) + 0.130 (\text{tarsus} (\text{mm})) + 0.502 (\text{culmen} (\text{mm}))$$



Discriminant scores for male and female Peregrine Falcon *F.p. macropus* nestlings. Grey bars represent males and white bars represent females as determined by genetic analysis (71♂, 79♀). The reference line is at zero to indicate the pivot point between male and female classification.

BANDING

Bands are applied to both the left and right legs of all peregrines in this study. Refer to the VPP Colour Band Charts for a fuller explanation of the banding scheme. The data recorder and the bander must agree on the codes and the colours of all bands before they are applied to the bird.

As stated there are two bands to be applied, one is an aluminium band with a dual character code of silver letters repeated four times around the band. This band is applied by using two pop-rivets inserted into pre-drilled holes. This band is applied to the right leg of males and the left leg of females.

Before the band is riveted closed the data recorder must confirm for the bander that the band is sitting at the right orientation so that the code is not upside down when the birds stands up. Once agreement has been made close the band around the leg with your fingers and then insert the pop-rivets and close each one at a time. It may take more than one go to fully close the pop-rivet gun so be patient! Remember if the rivet has not taken on the first go then open the gun fully and push it forward so the head of the rivet gun sits the end of the pop-rivet and completely flush with the flange of the band.

On the other leg place one of the single colour powder coated stainless steel ABBBS bands.

Step 1: Place the band on the leg of the bird and then fit the band in the appropriate hole of the banding pliers with the gap of the band aligned facing in from the open jaws of the banding pliers. Close the band by gently squeezing the handles of the pliers so that the two ends of the band are brought together.

Step 2: Once the initial closure of the pliers has been completed, the band should now be rotated so that the band gap is aligned at right angles to the open jaws. By squeezing the pliers with increasing pressure, the band should become fully closed and completely circularised.

In step 1 bands may become out of shape and not completely closed in step 2. Usually in this situation one side of the band is sitting either overlapping the other or out of alignment to form an uneven join. If this happens rotate the band again so that it's gap is aligned at 45° to the open jaws of the pliers. In this way the pliers can be closed so as to push the outlying band edge under the other edge. Close the pliers so that the outer band edge slides under the other edge. Once you release the pliers the band will spring back to form a tight closed join. Remember when using stainless steel the bands won't move over time and so do not leave either a gap or allow for any overlap of the band once plier pressure has been removed. If the band becomes distorted and badly out of shape then remove it and use a fresh one. Banders will be provided with circlip pliers that can remove these stainless steel bands. Remember to record the new band code before applying to the bird.

Double check now that both the bander and the data recorder agree on the colours and codes recorded for both bands and which leg each is on.

All adults must be monitored for leg bands!

These last two rows of data relate to the resident adult pair at whose eyrie you are banding chicks. You may have noticed them whilst abseiling into the eyrie...! If not they are sure to appear when you attempt to return the chicks. For each adult record each of the following details:

MALE / FEMALE BANDED?

Whilst one person is abseiling down to the eyrie the remaining person should have binoculars or a telescope and watch the adults. Once one of them perches you will have an opportunity to observe if there is any dark object (ie a band) on their legs. Bands are easiest to read on a bird standing in shadow. Be sure to check both legs as a very small number of Peregrines have only one band on their leg. To make matters more challenging this band may be an uncoloured stainless steel band which can be very hard to detect!

To record that you have monitored each adult circle one of the following for each.

- 'Y' If you did observe that the adult was wearing one or more bands. Then proceed to the next row to fill out what details you can.
- 'N' Only if you clearly saw both legs and the bird was definitely not wearing a leg band on either leg.
- '0' If the bird does not appear or you could not determine if it was wearing any bands. Then make a note to that effect on the back of the data sheet as to why you could not determine if it was banded. Rarely one or other adult will not appear the whole time you are in the area.

When recording band details on wild adults start with the colours and be sure to correctly identify which leg has which band!

Once all of the colours have been recorded then focus on identifying the dual code on the aluminium band. Usually the lower character is the first to be seen because the leg feathers tend to hang down obscuring both the top colour and the top character. From a distance bands are easiest read when the bird has just landed and is perched in shadow or at least out of direct sunlight. Bright sunlight on the legs is a good way to determine if the bird is banded but the light tends to then make reading the bands very difficult. The phenomenon called "heat haze" also greatly reduces the visibility of even the best telescopes!

Agro Index

Usually this is arrived at after banding has finished and the bander and the data recorder can discuss and compare perceptions of the behaviour of each adult. The data recorder might give a score first and then compare notes! Only use the Agro index if someone enters the nest.

- 0 That particular adult was not seen. Sometimes the male will be off hunting and does not appear the whole time you are there. You will need to be both lucky and very fast for this to happen!
- 1 Present and not defending. Some times the male and very rarely the female will fly away to a far off perch or not respond at all aggressively.
- 2 Calling and agitated and but flying.
- 3 Calling, flying and not stooping. May be keeping some distance off without coming in. Not seen as any threat to the climber.
- 4 Calling, flying and stooping with intent! This bird means no good! However, it may not be game enough to actually make contact.
- 5 Calling, flying, stooping and hitting! Birds (usually the female) hit on only 5% of occasions. These birds really mean business and your helmet alone may not be enough to prevent bloodshed! Once a bird starts striking then you can reasonably expect it to continue!

Conclusion

Banding should not be seen as an overly complicated task and this manual has been prepared to give a clear understanding of the techniques involved in banding Peregrine Falcons. Many of these can be applied to other raptors and owls. If however, the individual cannot be banded correctly then it should be left in the nest unbanded.

Colour Band - field identification chart

Two styles of colour bands are used on Peregrines by the VPP. The first group pictured below are stainless steel which are issued by the Australian Bird and Bat Banding Schemes' office in Canberra. These are powder coated. The colour of these allows us to identify the year of birth of a bird. The second group are anodised aluminium bands specially made by Acraft and imported from Edmonton, Canada. The combination of the codes and colours identify who the individual is.



Field Banding data sheet



FIELD DATA SHEET - 2013

Page
of

1	2	3	4	5
1	2	3	4	5

Bander: _____

LOCATION: _____

LOCODE: _____

TIME: _____ AM / PM DATE: ____ / ____ / 2013

WEIGHT		AGE		SEX	
Bird + bag =		J / / A		M / F	
- Bag =		WING LENGTH			
Bird = g		cm			
TARSUS LENGTH		TAIL LENGTH			
mm		cm			
Hind Talon	LENGTH	HEAD + BILL			
mm		mm			
Hind Talon	DEPTH	TIP-CERE			
mm		mm			
Hind Talon	WIDTH	EXPOSED CULMEN			
mm		mm			
LEFT		LEG BANDS		RIGHT	
Colour	ID Code	Colour	ID Code	Colour	ID Code
		Place band sticker inside this dotted line box			
Pins Broken ?	No. of Eggs	No. of Chicks	Hatch Order	Sex ratio	
Y / N					
Adult ♂ Band Numbers		Adult ♀ Band Numbers		Comments	

Appendix VIII – Band Recovery (public report)

 Band Recovery Report - Alive / Breeding Recoveries		Office use only
Where data is inaccurate, please correct and return to the VPP (VPP 36 Wirraway Drive, Mildura, VIC 3500)		
1 Band finder's details		
Name	Primary contact (full name) Via Jim O'Brien, DEPI Ballarat	
Postal address		
Phone number	Town or suburb	Postcode
	Primary contact number	Email
2 Fledge nest site details		
Location name	Pt Addis	Locode 74
Land tenure	Parks Victoria	
Nest site origin	Origin type Natural	Nest subtype Cliff
Nest site	Nest type Cliff	Nest substrate Sandstone
Nest height	Above ground (m) 15	% Distance from cliff top 33%
Exposure	Vertical Degrees above horizontal 75°	Exposure horizontal degrees 120°
Nest area	Surface area of nest (m²) 0.25m²	Date nest site first described 1978
3 Banding details		
Date 23/10/2010	Band No. 27010518	
Sex F	Age at banding Nestling	
Fatness Index	Relative body weight for age n.a.	Statewide Figures
Clutch size	Eggs laid 3	Eggs 2.9
	Chicks hatched 3	chicks 2.4
	Hatch rate 100	Hatch rate 83%
Sex ratio of clutch	% males produced 66%	% males produced 48%
Hatch order	* Indicates the hatch order of this individual 1 st F 2 nd F* 3 rd F 4 th -	
4 Recovery details		
Date 18/07/2013	Location name/description Anthony's cutting, heading west on Western H'way, Bacchus Marsh.	
Sighting	Brief description of situation Found dead inside plastic bag on side of road. Carcass was not fresh. Date of death unknown at this stage.	
Behaviours	Description of injuries Thought to have been shot.	
Time since banding	years 2	months 8 days 26
Distance moved since banding	(km) 80.1	Direction moved 9° (N)
5 General comments		
This female was coming into her 3rd year and would have been searching for a mate and nest site at this time of year. There are no records of this bird having been sighted between banding in 2010 and now. Pigeon breeders in and around Bacchus Marsh are known to have persecuted Peregrines and other raptors for many years.		

Page 1 of band recovery report issued to public



Band Recovery Report - Alive / Breeding Recoveries

Where data is inaccurate, please correct and return to the VPP
(VPP 36 Wirraway Drive, Mildura, VIC 3500)

Office use only

1 Band finder's details



View of nest site 2009



Band attached to tarsus bones (discovered July 2013)

-- End --

