

**Reproductive success, dimorphism and sex allocation
in the brown falcon *Falco berigora***

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Declaration

The research presented in this thesis is my original and independent work. No part of it has been submitted for any previous degree.

Paul G. M^cDonald

Title Page: An adult male brown falcon from the focal population; note colour bands. Photo courtesy of Ian Montgomery.

Table of Contents

Declaration	<i>ii</i>
Acknowledgments	<i>iv</i>
Abstract	<i>vii</i>
Chapter 1 – General introduction	<i>1</i>
Chapter 2 – Variable plumage and bare part colouration in the brown falcon <i>Falco berigora</i>: the influence of age and sex	<i>11</i>
Chapter 3 – Nestling growth and development in the brown falcon <i>Falco berigora</i>: an improved ageing formula and field-based method of sex determination	<i>40</i>
Chapter 4 – The breeding ecology and behaviour of a colour-marked population of brown falcons <i>Falco berigora</i>	<i>66</i>
Chapter 5 – Territory fidelity, reproductive success and prey choice in the brown falcon <i>Falco berigora</i>: a flexible bet-hedger?	<i>88</i>
Chapter 6 – Weather dictates reproductive success and survival in the Australian brown falcon <i>Falco berigora</i>	<i>121</i>
Chapter 7 – Selection on body size in a raptor with pronounced reversed sexual size dimorphism: is bigger better?	<i>151</i>
Chapter 8 – Sex allocation and nestling survival in a dimorphic raptor: does size matter?	<i>187</i>
Chapter 9 – Appendices	<i>219</i>
9.1. The number taken and mean biomass of different prey items recorded in the diet of brown falcons sampled at the study site	<i>219</i>
9.2. Brown falcon <i>Falco berigora</i> pair successfully raise Australian hobby <i>F. longipennis</i> nestlings	<i>222</i>

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Abstract

This project describes various aspects of the breeding ecology and behaviour of the brown falcon *Falco berigora*, a common but poorly study Australian raptor. In particular it examines (a) the main influences on reproductive success; (b) tests predictions of theories proposed to explain the evolution and maintenance of sexual size dimorphism (RSD; females the larger sex) in raptors; and (c) investigates sex allocation patterns in the light of current sex ratio and parental investment theory. The study was conducted between July 1999 and June 2002 approximately 35 km southwest of Melbourne, at the Western Treatment Plant (WTP), Werribee (38°0'S 144°34'E) and surrounds, a total area of approximately 150 km².

- In all plumage and bare part colouration of 160 free-flying falcons was described. The majority of variation in these characters could be attributed to distinct age and/or sex differences as opposed to previously described colour 'morphs'.
- Nestling chronology and development is described and formulae based on wing length derived for determining nestling age. An accurate field-based test for determining nestling sex at banding age is also presented.
- Strong sex role differentiation was apparent during breeding; typical of falcons females performed most parental duties whilst males predominantly hunted for their brood and partner. Based on observations of marked individuals, both sexes of brown falcons aggressively defended mutual territories throughout the year, with just 10% of each sex changing territories during the entire study period. Males performed territorial displays more frequently than females, the latter rarely displaying alone.
- The diet of the population as a whole was very broad, but within pairs both sexes predominantly specialised on either lagomorphs, small ground prey (e.g. house mice *Mus musculus*), small birds, large birds or reptiles, according to availability.

- Reproductive parameters such as clutch size and the duration of parental care were constant across all years, however marked annual differences in brood size and the proportion of pairs breeding were evident.
- Age was an important influence upon reproductive success and survival, with immature birds inferior to adults in both areas. However, interannual differences were by far the most influential factor on breeding success and female survival. Heavy rain downpours were implicated as the main determinant of reproductive success and adult female mortality in a population largely devoid of predation or human interference.
- Female-female competition for territorial vacancies was intense; larger adult females were more likely to be recruited and once breeding fledged more offspring. In contrast, male recruitment and breeding success was unrelated to either body size or condition indices, although smaller immature males were more likely to survive to the next breeding season. This directional selection is consistent only with the predictions of the intrasexual competition hypothesis.
- Despite marked RSD (males c. 75% of female body mass), throughout the nestling phase female nestlings did not require greater quantities of food than their male siblings. However, female parents fed their last-hatched sons but not daughters, resulting in the complete mortality of all last-hatched female offspring in focal nests. Given last-hatched nestlings suffered markedly reduced growth rates and female, but not male, body size is important in determining recruitment patterns, the biased allocation amongst last-hatched offspring is likely to reflect differing benefits associated with investing in small members of each sex, consistent with broad-scale Trivers-Willard effects. Recruitment patterns support this, with surviving last-hatched females, in contrast to males, unable to gain recruitment into the breeding population upon their return to the study site.

Thus selection appears to act at the nestling, immature and adult stages to maintain RSD in the focal population. Larger females were favoured in the nestling phase, at recruitment and once breeding had greater reproductive success. In contrast, selection favoured a reduction or maintenance of immature male size as smaller birds had a greater chance of survival in the year following recruitment than their larger counterparts; thereafter male size was unimportant. Together, this directional selection favouring increased female competitive ability is consistent only with the predictions of the intrasexual competition hypothesis, which appears the most probable in explaining the maintenance and perhaps evolution of RSD in raptors.

Chapter 1 – General introduction

Raptors, an unrelated group of predatory birds comprised of the Falconiformes (eagles, hawks and falcons) and Strigiformes (owls), have attracted much research interest. Life history traits such as the re-use of regular nesting areas, distinct sex role differentiation during breeding and the production of ‘pellets’ (regurgitated indigestible material useful in dietary analyses) make this group ideal for examining many aspects of evolutionary and applied ecology (Newton 1979; Olsen 1995). Despite this, many Australian raptors remain poorly studied (Marchant and Higgins 1993).

The brown falcon *Falco berigora*, one of Australia’s most frequently encountered birds (Blakers *et al.* 1984), is an ideal model for use in testing various aspects of ecological theory. It occurs in high densities, is readily observed and robust to disturbance, however, much of its basic ecology remains poorly understood. In an attempt to rectify these shortcomings this study had two main aims. Firstly, to attempt to redress the current lack of knowledge about this unusual falcon and second, to investigate areas of evolutionary ecology for which the brown falcon was an ideal focal species. An overview of each chapter is presented below. Several chapters are presented with co-authors, however, in each case the work carried out was substantially my own. Co-authors provided guidance throughout the project, however, responsibility for the ideas and conclusions presented in this thesis lies with me.

The study was conducted between July 1999 and June 2002 approximately 35 km southwest of Melbourne, at the Western Treatment Plant, Werribee (38°0’S

144°34'E), adjacent Avalon Airport (38°2'S 144°28'E) and small areas of surrounding private land, a total area of approximately 150 km² (Fig. 1.1).

Throughout the study period as many individuals as possible were captured on-site and fitted with coloured leg bands. Whilst conducting fieldwork marked individuals were sought and their location plotted to facilitate the recognition of pairs, territory boundaries and the status of individual birds.

Although the brown falcon is common throughout most of Australia, considerable confusion remains over the influence of geography, age and sex on plumage and bare part colouration in this species. To address this issue, 160 immature and adult falcons from the focal population were examined (Chapter 2). In contrast to previous studies, the marking regime of this study ensured that all individuals were of known sex and age-group. Adult males had significantly lighter upperpart, cap, ventral and underwing covert plumage in comparison with other birds; closely resembling what has previously been described as a 'rufous morph' (see Marchant and Higgins 1993 for descriptions of proposed colour morphs). Immature females were significantly darker than other ages and sexes in upperpart and underwing covert plumage, resembling descriptions of 'dark morphs'. In contrast, plumage of immature males and adult females tended to be similar and intermediate between these extremes, resembling the 'brown morph'. The buff-tinged, not white, ventral plumage and darker underwing covert plumage of immature males separated them from adult females. Cere and orbital ring colour also differed with sex and age; immature females had the dullest facial bare parts and adult males the brightest. Adult females and immature males were again intermediate between the two. The results indicate

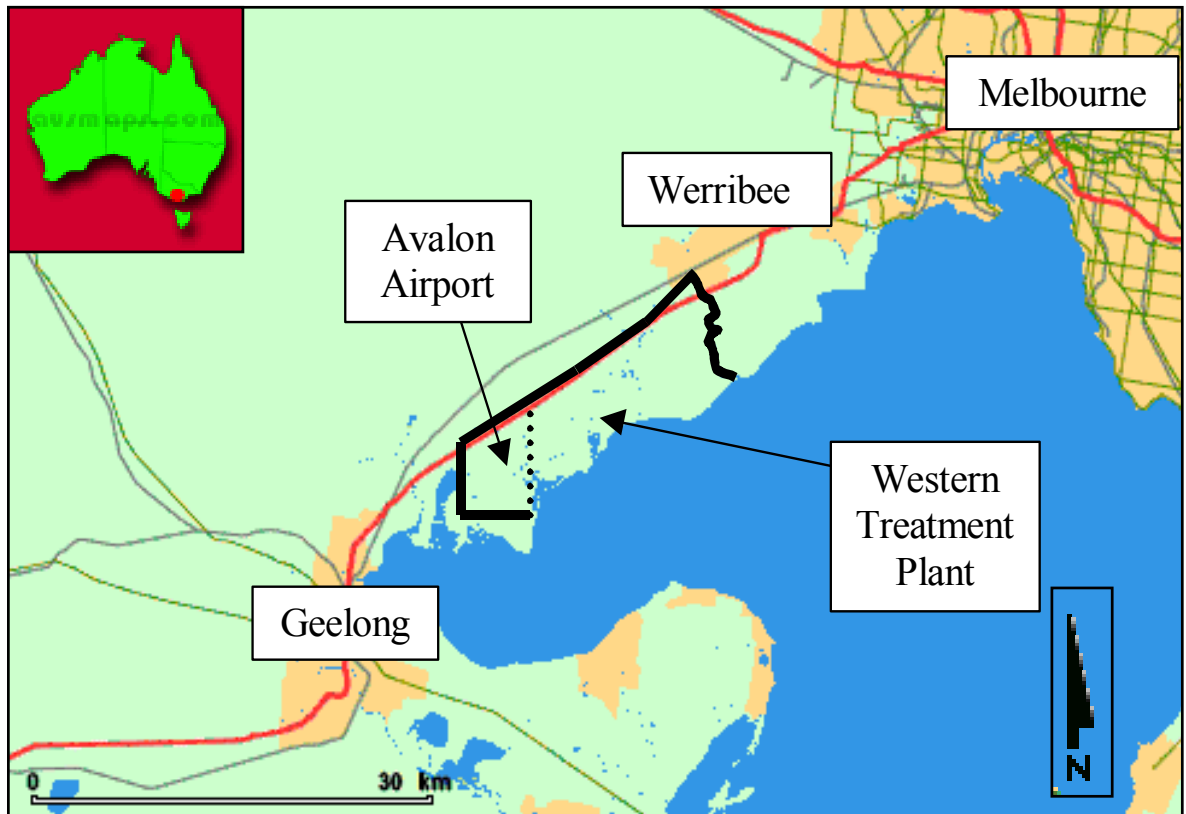


Figure 1.1. The study site, bounded by solid black lines. Broken line indicates approximate boundary between Avalon Airport and the Western Treatment Plant.

that the majority of variation in plumage and facial bare part colouration observed in the population could be attributed to age and sex differences as opposed to racial clines or the existence of colour morphs. Moreover, the brighter colours of adult falcons may function as honest signals of quality.

The accurate determination of nestling age and sex is an important tool for studies examining life history traits and ecological interactions, and was critical to many aspects addressed in the latter chapters of this thesis. A range of measurements from a large sample of free-living nestlings were analysed and the most reliable measure for ageing nestlings was found to be wing length (Chapter 3). Wing length increased in a linear manner with chick age, independent of seven potentially confounding factors examined such as sex, brood size and hatch order. Ageing formulae based on wing length before and after remiges emerge are presented. In addition, an accurate test for determining nestling sex at banding age, based on tarsus width, is proposed. Further, the development of brown falcon nestlings is described in detail for the first time. Nestling development was similar to that described for other Falconiformes, however the chronology of nestling development was too variable to be useful in assigning chick age. Despite this, within six days of the eldest chick hatching the relative brightness of down and the degree to which chick's eyes had opened were useful in assigning hatch order within broods of similar wing lengths.

By monitoring known individuals over the course of the study behavioural interactions could be quantified and placed in the correct context (Chapter 4). Both pair members aggressively defended territories throughout the year from conspecifics and other species alike. Males performed territorial displays more

frequently than females, which rarely displayed unprompted. Strong differences in the types of parental care provided by each sex were evident, with females contributing to the bulk of incubation, brooding and feeding of nestlings and fledglings. Males, on the other hand, provided the majority of food to both females and broods, from well before the first eggs were laid until nestlings were 2 - 3 weeks old. Prey deliveries were more frequent early in the morning and late in the evening; however, remains of larger prey were cached, presumably to provision the offspring more regularly throughout the day. Nestlings were fed prey either whole or, in the case of larger items, piecemeal.

During the study the breeding biology of the population was also recorded and this was used to describe the life-history strategy of brown falcons (Chapter 5).

Reproductive parameters such as clutch size and the duration of parental care were constant across years, despite marked annual differences in brood size and the proportion of pairs breeding. Both sexes of falcons were found to have high territory and mate fidelity, with only 10% of members of each sex changing territories during the entire study. Falcons were flexible in their choice of nest sites, using a variety of tree species and even isolated nest trees, allowing them to breed in several areas of the study site devoid of other breeding raptors. Nest sites and territories were regularly distributed throughout the study area, with the density of the population the highest on record for this species, averaging 3.2 to 3.6 km² per pair. The diet of the population as a whole was very broad, but each pair predominantly specialised on either lagomorphs, small ground prey (e.g. insects, house mice *Mus musculus*), small birds (e.g. European starlings *Sturnus vulgaris*, Richard's pipit *Anthus novaeseelandiae*), large birds (e.g. silver gulls *Larus novaehollandiae*) or reptiles

(e.g. Eastern tiger snake *Notechis scutatus*, blue-tongued lizard *Tiliqua scincoides*). Each dietary group was captured with a different hunting technique. Individuals that changed territory within the study area also switched their diet according to the predominant land-use within the new territory and thus prey availability. It is argued that, at the population level, broad dietary breadth, flexibility in choice of nest site, and a conservative, static breeding strategy allows the species to persist in a broad range of environments, possibly through ‘bet-hedging’ (*sensu* Philippi and Seger 1989). At the individual level, changeable dietary specialisation, high territory fidelity, strong year-round territorial defence, confining breeding to years when individual conditions were favourable and adjusting brood sizes when required appear to be the main strategies enabling brown falcons to thrive under a variety of, often unpredictable, conditions across their range.

The focal population was virtually free from predation and human persecution, facilitating examination of the influence of other factors such as parental age, pair-bond duration, prey size and weather conditions upon reproductive success (Chapter 6). Pairs on territories that enabled them to capture large prey items were more likely to initiate breeding attempts. Females taking larger prey items experienced higher mortality rates when they bred late in the season, whereas those taking smaller prey had a greater probability of survival when laying later in the season — relationships likely linked to opposing seasonal differences in prey availability. Mean egg size and the duration of pair bonds had no influence upon any aspect of reproductive success examined.

In contrast, interannual differences influenced almost every reproductive success parameter and female survival. Pairs on-site in the first year of the study (1999) were more successful breeders and had greater survival prospects than those present in the latter two seasons (2000 and 2001). This pattern corresponded strongly to the observed frequency of heavy rain downpours and implicated these events as the main cause of reproductive failure and mortality amongst adult females. These detrimental effects were likely due to an increased chance of chilling, exposure and starvation for chicks and parents alike. The importance of unpredictable climatic variables in shaping the reproductive success and survival of brown falcons and raptors from other regions indicates that, in the absence of significant nest predation, weather, in this case in the form of heavy rain, may well be the most important factor influencing long-term reproductive success in this group.

One of the most active areas of research involving raptors has been the investigation of reversed sexual size dimorphism (RSD; females the larger sex), with well over 20 hypotheses proposed to account for this trait. Previous research has principally focused on interspecific patterns of RSD, rarely testing predictions of various hypotheses within populations. To redress this, data collated from both sexes of the large brown falcon population studied were used to evaluate the importance of size and body condition indices upon the hunting prowess of males and the reproductive success, recruitment and survival probabilities of both sexes (Chapter 7). The brown falcon is a medium sized raptor exhibiting moderate levels of RSD (Males: $486 \text{ g} \pm 5\text{SE}$, $n = 69$; Females: $658 \text{ g} \pm 7\text{SE}$, $n = 91$). Female-female competition for territorial vacancies was likely to be intense as the floating population was female-biased and intrasexual agonistic interactions were frequently observed (Chapter 4).

In this competitive population larger adult females were more likely to be recruited, indicating directional selection favouring increased female body size. Further, after recruitment larger females were more likely to successfully fledge offspring, providing a mechanism by which RSD is maintained in the population. In contrast, male recruitment was unrelated to either body size or condition indices. Larger immature males more often lost their territories from one breeding season to the next in comparison with their smaller counterparts, however they also took large prey more frequently, a diet facilitating greater reproductive success (Chapter 6). Male competition for access to high quality territories may explain the presence, and indeed high turnover, of larger males on these territories. Alternatively, larger prey is more dangerous and difficult to capture than smaller prey items; immature males relying upon large prey may therefore be exposed to higher mortality rates associated with hunting mishaps or starvation.

It is argued that, together, these results are indicative of selection favouring an increase in female body size and a reduction or maintenance of male body size. Of all the hypotheses proposed to account for the maintenance and evolution of RSD in raptors, this scenario is consistent only with the predictions of the intrasexual competition hypothesis. This hypothesis posits that intrasexual competition amongst females for males favours an increase in female body size, whereas male body size is shaped by natural selection pressure (Olsen and Olsen 1987).

Fisher's theory (1930) predicts equal sex ratios at the end of parental care if the costs and benefits associated with raising each sex of offspring are equal. In raptors, which display various degrees of RSD, sex ratios biased in favour of smaller males, which

are expected based upon size differences alone, are not universally reported. This suggests either that offspring of each sex may confer different fitness advantages to parents or that body size differences alone are not a reliable indicator of the potential costs to parents in raising each sex. To investigate this further, the relative potential costs and benefits of raising brown falcon nestlings of each sex were examined (Chapter 8). Female nestlings did not require more food, nor did they hatch from larger eggs or remain dependent upon parents for longer periods than male offspring. Together with previous studies this result indicates that even in markedly dimorphic species the relative costs of raising the larger sex are likely to be less than that predicted by body size differences alone. Moreover, focal mothers fed their last-hatched sons but not daughters, resulting in the complete mortality of all last-hatched female nestlings in focal nests. Last-hatched nestlings suffer a reduced growth rate in this asynchronously hatching species, resulting in smaller final body size. As larger females, but males of any size, are more likely to be recruited in this species (Chapter 7), the biased sex allocation and subsequent post-hatch sex ratio manipulation of last-hatched offspring is likely to reflect differing benefits of investing in smaller members of each sex. This pattern of differential investment in offspring is most consistent with broad-scale Trivers-Willard (1973) effects.

Together, these results indicate that large females have a better chance of fledging, are more likely to be recruited into the breeding population and once there are more successful breeders. In contrast, male nestlings of all sizes fledged, but smaller immatures were more likely to survive in the breeding population in the year following initial recruitment. Male size had no influence upon recruitment probabilities, survival after initial recruitment or reproductive success. Selection

therefore appears to be favouring an increase in female size and a decrease or stabilisation of male size in this species. In concert, these results provide strong support for the intrasexual competition hypothesis (Olsen and Olsen 1987) as the main factor maintaining RSD in raptors.

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Chapter 2 – Variable plumage and bare part colouration in the brown falcon *Falco berigora*: the influence of age and sex



Plate 2.1 Close-up views of an adult male (above) and adult female (below) brown falcon. Note differences in facial bare part colouration. Photos courtesy of Doris Graham.

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Abstract

The brown falcon *Falco berigora* is one of Australasia's most common raptors, yet considerable confusion remains over the influence of geography, age and sex on plumage and bare part colouration in this species. To address this issue, 160 immature and adult falcons from an individually marked, closely monitored population were examined. In contrast to previous studies, all were of known sex, age-group and part of the resident population or their offspring. Adult males had significantly lighter upperpart, cap, ventral and underwing covert plumage in comparison with other birds; closely resembling what has previously been described as a 'rufous morph'. Immature females were significantly darker than other ages and sexes in upperpart and underwing covert plumage, resembling descriptions of 'dark morphs'. In contrast, plumage of immature males and adult females tended to be similar and intermediate between these extremes, resembling the 'brown morph'. The buff-tinged, not white, ventral plumage and darker underwing covert plumage of immature males separated them from adult females. Cere and orbital ring colour also differed with sex and age, immature females had the dullest facial bare parts and adult males the brightest. Adult females and immature males were again intermediate between the two. The results indicate that the majority of variation in plumage and facial bare part colouration observed in the population could be attributed to age and sex differences as opposed to racial clines or the existence of colour morphs. Moreover, the brighter colours of adult falcons may function as honest signals of quality.

Introduction

The brown falcon *Falco berigora* exhibits one of the most varied plumages of all falcons, with birds ranging in colour from a very dark brown, almost black plumage through to a light red ‘phase’ reminiscent of Australian Kestrels *F. cenchroides* (Marchant and Higgins 1993; Olsen 1995). Despite its ubiquitous nature (Blakers *et al.* 1984), the marked variation that exists in plumage colouration remains poorly understood in this species. As many as seven races have been described, with many more plumage types or phases (Condon 1951). To date, uncertainties associated with individual, sexual and regional differences in plumage colouration have led some to raise doubts over the validity of many proposed subspecific splits (Baker-Gabb 1986; Marchant and Higgins 1993). The most recent review has rejected all but the nominate *berigora* race of Australia and the *novaeguinae* race of New Guinea, subject to the attainment of more information on plumage variation (Marchant and Higgins 1993).

Several authors have described geographic variation principally through examination of museum skins (Amadon 1941; Condon 1951; Marchant and Higgins 1993), while McDonald (in press *a*) described plumage and development characteristics of nestlings. Weatherly *et al.* (1985) identified features of juvenile plumage through observations of known-age captives and examination of skins. In doing so, Weatherly and colleagues identified age-related plumage traits that had clearly been mistaken for individual variation in other studies (e.g. Amadon 1941), such as mottled markings on flank feathers and buff plumage.

While the initial plumage of juveniles is now apparently well described and applicable throughout much of the species range (Weatherly *et al.* 1985), the procession of subsequent moults between juvenile and attainment of adult plumage remains poorly understood. Weatherly *et al.* (1985) suggest ventral surfaces progressively whiten with age and that this, along with the presence of spotted flank feathers, enables birds to be aged ‘with considerable accuracy’ to adulthood. Despite this, details of intermediate plumages were not provided, making this claim difficult to assess. The number of moults required to obtain adult plumage also remains debatable, variously listed as 4 or 6 years (Weatherly *et al.* 1985; Baker-Gabb 1986). While Weatherly *et al.* (1985) described plumage maturation in an unknown number of captive birds, they were all sourced from Tasmania, a population reputed to show little plumage variation in comparison with mainland birds (Marchant and Higgins 1993). Moreover, Olsen (in Marchant and Higgins 1993), in contrast to Weatherly *et al.* (1985), reports little comparative change in three captive birds from southeastern Australia following their initial moult, further clouding the sequence of transition from juvenile to adult plumage.

Sexual differences in plumage also remain poorly described. Weatherly *et al.* (1985) suggest females of equivalent age were darker than their male counterparts, as progressive whitening of ventral surfaces proceeded faster in males. Some females also retained a yellow speckled breast band, although this too was apparently lost with age (Weatherly *et al.* 1985). These sexual differences were not quantified and the extent to which they are applicable to mainland populations is yet to be assessed.

On top of this uncertainty with plumage colouration, differences in bare part colouration also remain poorly understood. In general bare part colours of the orbital ring, cere, feet and legs are usually described as grey or bluish-grey, however a consistent proportion of records list specimens with varying degrees of yellow in these areas (Condon 1951; Weatherly *et al.* 1985; Marchant and Higgins 1993). Given the importance of both non-plumage (Picozzi 1981; Rosenfield and Bielefeldt 1997), and plumage characters (e.g. Village 1990), in ageing and sexing other raptor species, some of the confusion arising from these varied reports may be due to age and/or sex-related differences. Thus the aim of this study was to examine plumage and bare part characteristics of a closely monitored, colour-marked population of brown falcons during the course of a long-term investigation of their breeding biology and ecology. This chapter reports on preliminary results obtained during the first three years of the study.

Methods

Study site and general methods

Fieldwork began in July 1999 and remains ongoing; data collection for results presented ceased in January 2002. The study site is situated approximately 35 km southwest of Melbourne, at the Western Treatment Plant, Werribee (38°0'S 144°34'E), adjacent Avalon Airport (38°2'S 144°28'E) and small areas of surrounding private land, a total area of approximately 150 km². Additional details of the study site have been described elsewhere (Baker-Gabb 1984a). The study site was visited regularly (6 - 7 days a week during late winter-early summer, 2 days per week at other times), with bal-chatri and modified goshawk traps (Bloom 1987) utilised to capture falcons. All birds were fitted with a unique

combination of colour bands and a service band supplied by the Australian Bird and Bat Banding Scheme (ABBBS). Following data collection birds were released at the point of capture. Nestlings raised in the study area were also colour-banded at an appropriate age (M^cDonald in press *a*). At all times when present on the study site I actively searched for banded birds and plotted their location on maps to identify territorial and pair relationships. Attempts were made to capture all unbanded birds and offspring returning to the study site.

Assigning falcon age and sex

Following capture markings on flank feathers were used to assign relative age (Weatherly *et al.* 1985). In adult birds (plumage not acquired until at least 4 years old) of both sexes these feathers appear with numerous cream spots either side of the midrib, in immature birds (2 - 4 years old) these feathers are normally mottled with buff blotches or occasionally a mixture of buff spots and blotches. Novel juveniles (unbanded birds hatched the same year they were captured) from outside the study area were easily identified by their buff front, buff undertail coverts and dark upperparts (Weatherly *et al.* 1985). The terms adult, immature and juvenile refer to birds aged in this manner. Sex was assigned to free-flying individuals captured using behavioural observations and a variety of morphometric characters that show little overlap in fully-grown brown falcons (Baker-Gabb 1984*b*; pers. obs.). Molecular data were used to confirm the accuracy of this procedure; in a sub-sample of 20 males and 20 females sex was correctly assigned in every case (M^cDonald in press *a*).

Plumage and bare part descriptions

Throughout this chapter, on first use of a colour (except black and white), descriptions are followed by a number and name in parentheses, corresponding to standard colours in Smithe (1975). Following capture detailed descriptions of plumage characteristics were obtained and a photograph taken of each falcon. Before release, each bird's upperparts, cap and underwing coverts were scored as one of four colours, in order of increasing lightness: dark chocolate brown (21; Fuscous), chocolate brown (33; Cinnamon-brown), rufous-brown (c. 38; Tawny) and rufous (c. 140-40; Pratt's/Cinnamon-rufous). Markings either side of the rachis of underwing coverts were also recorded as either cream (c. 54; Cream) or buff (124; Buff) spots or blotches, the latter being imperfect irregular markings in comparison with the regular circles of spotted feathers. Ventral plumage colouration was scored according to the percentage of various shades of brown present in both the breast and belly region. Birds which completely lacked brown on these feathers (i.e. ventral plumage was white) were given a score of 0, whereas birds with completely brown feathers were given a score of 100. Variations in between were assigned an appropriate value to the nearest 10%. Facial bare parts were assigned a value between 0 and 3 based on the degree of yellow present in the cere and orbital ring; 0: both cere and orbital ring blue-grey (86; Pale neutral grey), 1: lower half of orbital ring pale yellow (157; Sulfur yellow), 2: Both cere (usually top half) and orbital ring partially pale yellow, 3: both cere and orbital ring completely bright yellow (55; Spectrum yellow).

Statistical analyses

Falcons captured on multiple occasions were included in analyses using data from their initial capture only. Differences in plumage and facial bare part colouration according to sex and age were assessed with generalised linear models (GLM; M^cCullagh and Nelder 1989). In analyses explanatory factors ‘age’ and ‘sex’ were assessed for statistical significance, as was ‘adulthood’, a factor that compared adult males with all other falcons sampled. Significance of terms was assessed as they were added in a step-wise fashion using the change in deviance statistic. This statistic approximates a chi-square distribution (M^cCullagh and Nelder 1989). Where necessary differences between two ages and/or sexes were determined using *z* statistics. Ventral plumage colour was assessed using an ANOVA with ‘age’ and ‘sex’ as factors. All statistical tests were carried out using Genstat 5 release 6.1. Means are reported \pm one standard deviation. The methodology utilised in this project was approved by the Australian National University Animal Experimentation Ethics Committee (Registration No. F.BTZ.02.99).

Results

In total, 178 falcons were captured, consisting of 48 adult, 43 immature and nine juvenile females and 41 adult, 28 immature and nine juvenile males. Eight adult and seven immature females and three adult and four immature males were also recaptured during the course of the study. A total of 209 plumage descriptions were therefore recorded, including eight recruited offspring and three birds banded by others prior to this study, both of these latter groups were of known age.

General plumage descriptions

Plumage descriptions of each bird fitted the very broad range given in Marchant and Higgins (1993). Falcons with dark chocolate brown upperparts were similar to the ‘dark’ morph, birds with chocolate brown or rufous-brown upperparts were similar to the ‘brown’ morph and falcons with rufous upperparts the ‘rufous’ morph (Marchant and Higgins 1993). Plumage of juveniles closely conformed to that provided by Weatherly *et al.* (1985) and as such is not considered further here.

Upperpart, cap and underwing covert plumage

Adult male falcons had significantly lighter upperpart plumage than all other groups ($\chi^2_1 = 77.2, p < 0.001$; Table 2.1a); 86.7% of birds scored as rufous were adult males. In addition, significant age ($\chi^2_1 = 12.0, p < 0.001$) and sex effects ($\chi^2_1 = 7.4, p = 0.01$) were apparent when added to the model. When these relationships were examined further, immature females were significantly darker than immature males (z statistic = 2.7, $p < 0.01$) and thus adult females (Table 2.1a); 59.4% of dark chocolate-brown birds were immature females. Adult females and immature males tended to be intermediate in colour between the other groups and did not differ significantly from each other (z statistic = -1.0, $p > 0.05$).

Cap colouration tended to be similar to upperpart plumage, in that 80.6% of rufous falcons were adult males and 54.5% of dark chocolate brown birds were immature females (Table 2.1b). Cap colours of adult males were significantly lighter than all other groups ($\chi^2_1 = 82.3, p < 0.001$; Table 2.1b), however no

Table 2.1. Distribution of colours of (a) upperpart, (b) cap and (c) underwing covert plumage recorded in brown falcons of different sex and age classes. Groups significantly different ($p < 0.05$) are marked with different letters.

Age and Sex Class	Dark Chocolate Brown	Chocolate Brown	Rufous-brown	Rufous
<i>a) Upperparts colour</i>				
Adult males ^A	1	4	8	26
Adult females ^B	4	28	10	3
Immature males ^B	8	11	8	1
Immature females ^C	19	22	1	-
<i>b) Cap colour</i>				
Adult males ^A	-	-	9	29
Adult females ^B	3	16	7	4
Immature males ^B	7	8	12	1
Immature females ^B	12	19	6	2
<i>c) Colour of underwing coverts</i>				
Adult males ^A	1	2	2	24
Adult females ^B	3	13	9	13
Immature males ^C	5	15	1	3
Immature females ^C	13	19	1	5

additional age ($\chi^2_1 = 2.5, p > 0.05$) or sex effects were apparent ($\chi^2_1 = 2.75, p > 0.05$).

Adult males had significantly lighter underwing coverts than all other groups ($\chi^2_1 = 38.6, p < 0.001$; Table 2.1c); 53.3% of falcons with rufous underwing coverts were adult males. The addition of age to this model was also significant ($\chi^2_1 = 17.2, p < 0.001$), indicating adult females had lighter underwing coverts than immature birds (Table 2.1c), but darker coverts than adult males (z statistic = 3.5, $p < 0.001$). The addition of sex to this model was not significant ($\chi^2_1 = 0.7, p > 0.05$), as both male and female immature birds had chocolate brown to dark chocolate brown underwing coverts (Table 2.1c).

Clear age effects were apparent in the colours and shape of underwing covert markings (Table 2.2). Immature birds of both sexes tended to have buff blotched markings whereas adults had cream spots. In every bird which did not conform to this pattern a mixture of both markings was observed, these birds probably reflect individuals that have either just obtained or were on the verge of obtaining adult plumage. Once again, adult males had markings of a significantly different colour ($\chi^2_1 = 37.3, p < 0.001$) and shape ($\chi^2_1 = 5.0, p = 0.03$) to the other groups. Adult males always had cream markings, 78.6% of which were spots (Table 2.2). Significant age effects were also apparent for both colour ($\chi^2_1 = 80.7, p < 0.001$) and shape ($\chi^2_1 = 5.0, p = 0.03$), indicating adult females differed significantly from both immature sexes. All but one adult female possessed cream spotted underwing covert markings. Immature falcons did not differ significantly from

Table 2.2. Distribution of colours and patterns of markings on underwing covert feathers in brown falcons according to sex and age classes. Groups

significantly different ($p < 0.05$) are marked with different letters.

Age and Sex Class	Buff		Cream	
	Blotches	Spots	Blotches	Spots
Adult males ^A	-	-	6	22
Adult females ^B	1	-	-	37
Immature males ^C	20	1	2	1
Immature females ^C	31	2	-	5

each other in colour or shape of markings, tending to both be buff blotched (colour: $\chi^2_1 = 1.3, p > 0.05$; shape: $\chi^2_1 = 1.3, p > 0.05$; Table 2.2).

Ventral plumage

A significant age and sex interaction existed in the total proportion of brown evident in the ventral plumage of falcons ($F_{1,156} = 5.0, p = 0.03$). This interaction arose as males possessed lighter fronts than females of the same age, however immature males did not have lighter fronts than adult females (Fig. 2.1). The same interaction and patterns were evident when the percentage of brown in the breast alone was examined ($F_{1,156} = 4.4, p = 0.04$; Fig. 2.1). In contrast, the interaction between sex and age was not significant for belly scores ($F_{1,156} = 3.5, p > 0.05$), however significant age ($F_{1,156} = 86.9, p < 0.001$) and sex ($F_{1,156} = 37.6, p < 0.001$) effects were apparent (Fig. 2.1). Thus immatures of both sexes (relative to adults) and females of both ages (relative to males) were the darkest birds.

Every adult female except one possessed a broad band of chocolate or rufous-brown across the breast (Plate 2.2; pp. 29). This breast band lead to breast scores of adult females being significantly darker than their belly scores ($t_{0.05(2),47} = 5.5, p < 0.005$; Fig. 2.1), an effect that was conspicuous in the field in comparison with the more evenly coloured ventral surfaces of the other groups.

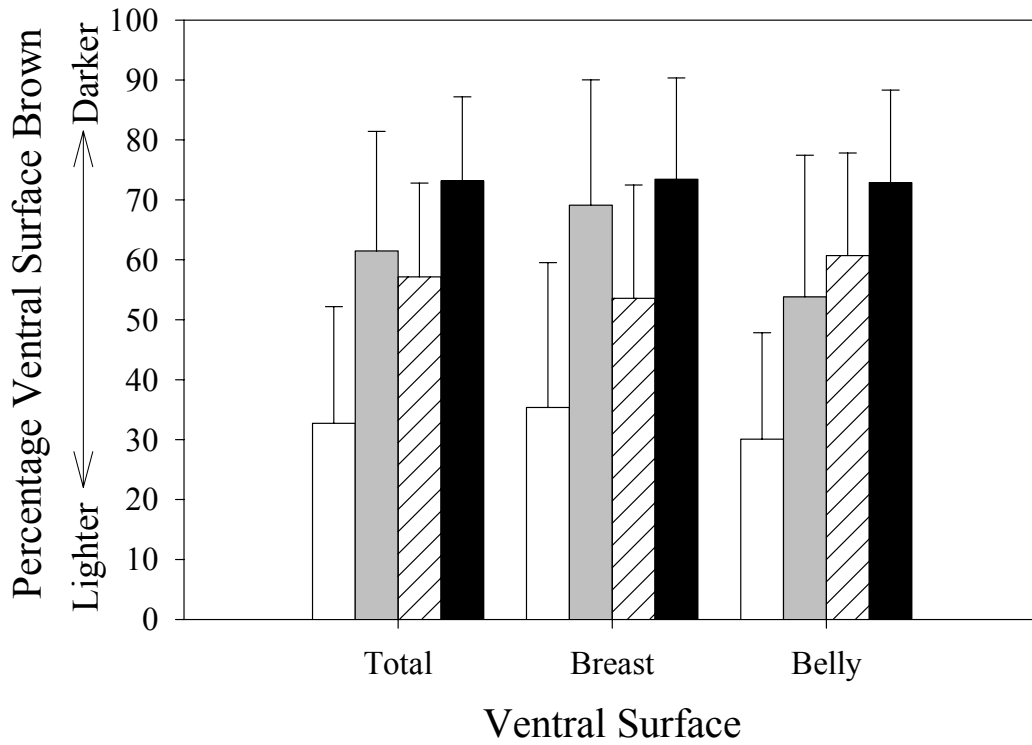


Figure 2.1. The percentage of brown present in two regions (breast, belly and total) of the ventral plumage of brown falcons. Mean scores for adult males (white bars, $n = 41$), adult females (grey bars, $n = 48$), immature males (striped bars, $n = 28$) and immature females (black bars, $n = 43$) are displayed. Error bars indicate one standard deviation.

Bare part colouration

Facial bare part colouration of adult males was significantly brighter than in other groups ($\chi^2_1 = 92.1, p < 0.001$); only adult males developed fully yellow ceres and orbital rings and every adult male had at least some yellow in both these areas (Table 2.3). Both age ($\chi^2_1 = 19.2, p < 0.001$) and sex effects ($\chi^2_1 = 43.0, p < 0.001$) were significant when added to this model. Further examination of this pattern revealed that immature females had darker, more blue-grey facial bare parts than immature males (z statistic = 5.8, $p < 0.001$; Table 2.3). However, while immature males tended to have brighter facial bare parts than adult females this difference was not significant (z statistic = 0.5, $p > 0.05$; Table 2.3). Leg and feet scales were a blue-grey colour in all birds examined.

Tail characteristics

Incomplete barring of rectrices was observed in immatures significantly more often than adults ($\chi^2_1 = 19.8, p < 0.001$), with just one adult female (2.1%) and no adult males possessing the characteristic. A weak sex effect also existed, with more immatures females (27.9%) having incomplete barring of the rectrices than immature males (10.7%; $\chi^2_1 = 4.0, p = 0.045$). Moreover, barring of rectrices in immatures tended to begin c. 20% along the rachis; in adults barring usually began at the base of the feather.

In contrast, barred undertail coverts were more frequently recorded in adults (46.1%) than immatures (25.4%; $\chi^2_1 = 7.4, p = 0.01$), with adult females 60.4% significantly more likely than adult males to possess the character (29.3%; $\chi^2_1 = 8.8, p = 0.003$).

Table 2.3. Distribution of facial bare part colouration scores of brown falcons according to sex and age class. Groups significantly different ($p < 0.05$) are marked with different letters. Higher scores indicate brighter (more yellow) facial bare parts, see methods for details.

Age and Sex Class	Facial Bare Part Score			
	0	1	2	3
Adult male ^A	-	-	24	17
Adult female ^B	1	21	26	-
Immature male ^B	3	7	18	-
Immature female ^C	27	14	2	-

Characteristics of known-aged falcons

The plumage colour of the eight nestlings recaptured on the study site at two ($n = 7$) or one year of age (1 male) followed the patterns described above, with females tending to be darker (Table 2.4). As proposed by Weatherly *et al.* (1985), the inner flank feathers of these immatures were never fully spotted, although some individuals had developed spots in a minority of feathers, verifying the ageing technique used in this study. In a similar pattern to flank feathers, all but one male had buff blotched underwing coverts.

The broad patterns identified above indicate the occurrence of a progressive lightening of plumage and brightening of facial bare parts with increasing age, particularly in males. Excluding returned offspring and falcons recaptured without moulting, multiple descriptions were obtained for 14 birds. Of these, eight had lighter ventral plumage (Plate 2.2*a,b*) and six (all adults) received the same score as on initial capture. Based on the photographs taken at capture, many birds that were not recaptured also lightened considerably during the study. Again this effect was more prominent in males, although these differences could not be quantified. Some adult females however did not change appreciably after moult (Plate 2.2*c,d*). Similarly, facial bare part colouration either remained the same ($n = 12$) or was scored as more yellow ($n = 10$) in recaptured birds. In no case was the reverse, a loss of yellow colouration, observed.

The three older birds initially banded prior to this study commencing supported this pattern. One adult female was recaptured at 13+ years of age with plumage typical of other adult females on the study site, a chocolate brown breast band,

Table 2.4. Colours of (a) upperpart, (b) cap and (c) underwing covert plumage and (d) colour and pattern of underwing covert markings of immature brown falcons either 2 (4 females, 3 males) or 1 year old (1 male).

Sex and Age Class	Females	Males
<i>a) Upperparts colour</i>		
Dark Chocolate Brown	1	-
Chocolate Brown	3	2
Rufous-brown	-	2
<i>b) Cap colour</i>		
Dark Chocolate Brown	2	-
Chocolate Brown	2	3
Rufous-brown	-	1
<i>c) Colour of underwing coverts</i>		
Dark Chocolate Brown	2	-
Chocolate Brown	1	3
Rufous-brown	-	-
Rufous	1	1
<i>d) Underwing covert feather markings</i>		
Buff blotches	4	3
Cream spots	-	1

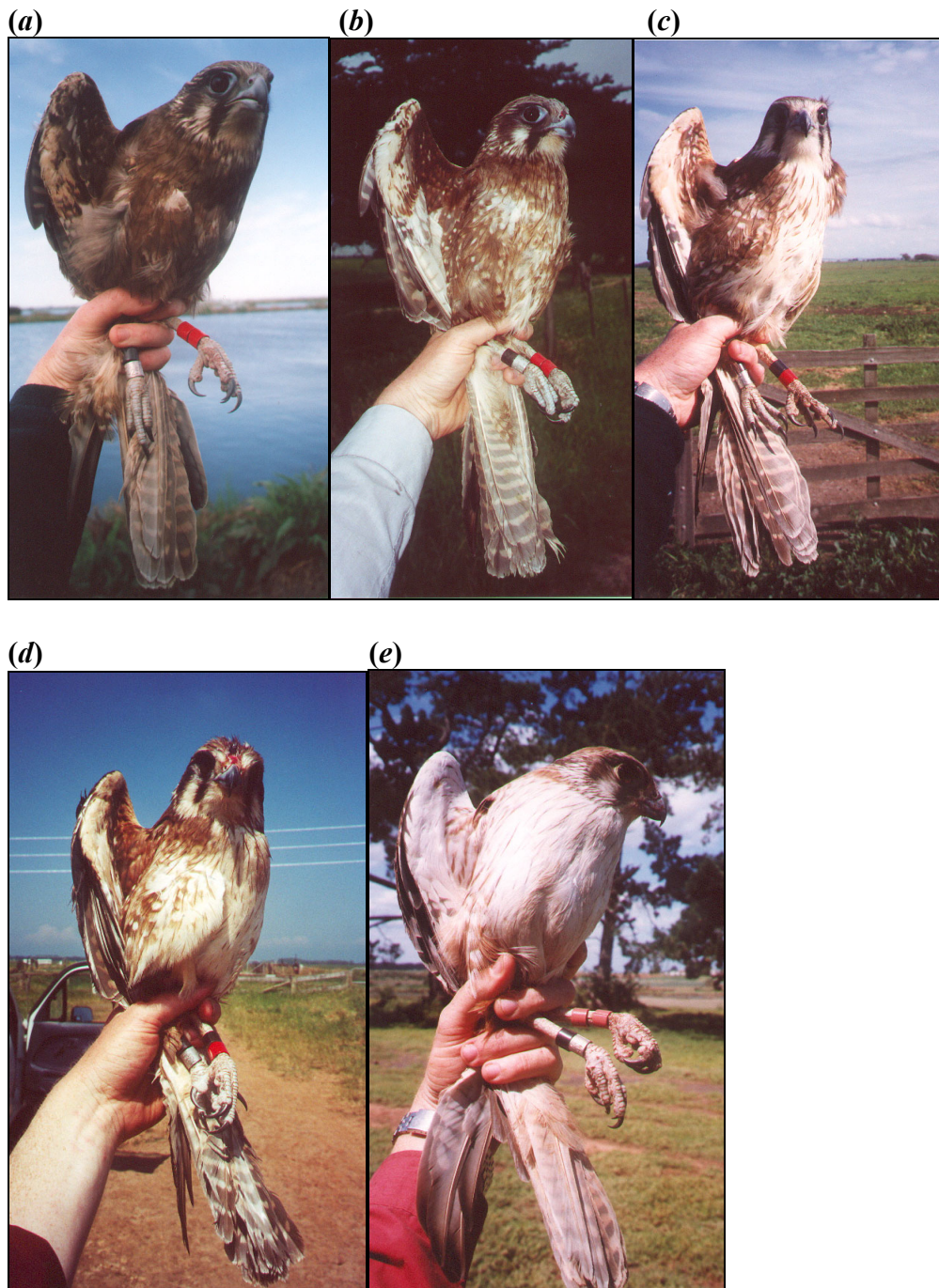


Plate 2.2. (a) Adult female 111-25115, 15th September 1999 and (b) 9th November 2000, 420 days later. (c) Adult female 111-25122, 4th October 1999 and (d) 19th November 2000, 411 days later. (e) Adult male, 100-86344, 13th November 1999, 16 years and 23 days old.

white belly and chocolate brown upperparts (e.g. Plate 2.2c). Two males were recaptured at 16 and 18 years of age, respectively. Both had bright yellow facial bare parts, rufous upperparts and over 90% of their ventral plumage was white, the lightest recorded in the study. Underwing coverts of these individuals were also white with only a few rufous markings (Plate 2.2e). This further supports the result that as falcons age, particularly males, ventral and upperpart plumage became lighter and the proportion of yellow in facial bare parts increased.

Discussion

Based on quantified data, as opposed to more usual qualitative descriptions, the results clearly indicate that much of the variation in brown falcon plumage and facial bare part colouration in southern Victoria can be attributed to differences according to sex and/or age (Table 2.5). Birds with the darkest plumage were generally immature females and the lightest adult males. The plumage colours of these birds closely matched what others (e.g. Marchant and Higgins 1993) have termed dark (immature females) and rufous morphs (adult males). Immature males and adult females tended to be intermediate and of similar colouration to these two extremes, closely matching plumage descriptions of the 'brown morph' (Marchant and Higgins 1993). Facial bare part colouration followed a similar pattern; immature females tended to have blue-grey facial bare parts lacking yellow colouration, immature males and adult females usually had pale yellow in portions of both the cere and the orbital ring; adult males always had some yellow and, in many cases, completely bright yellow facial bare parts. Adult females could be readily distinguished from immatures by a distinct breast band,

Table 2.5. Summary of the main differences in brown falcon plumage and facial bare part characteristics according to age and sex.

Character	Adult		Immature	
	Male	Female	Male	Female
Orbital ring and cere	Both at least some yellow, often completely bright yellow	Usually some yellow in both, never completely yellow	Usually some yellow in both, never completely yellow	Blue-grey, occasionally some yellow in lower-half of orbital ring
Upperparts	Rufous to rufous-brown	Chocolate to rufous-brown	Chocolate to rufous-brown	Dark chocolate to chocolate brown
Underwing coverts	Rufous with cream spots	Chocolate to rufous-brown with cream spots	Dark chocolate to chocolate brown with buff blotches	Dark chocolate to chocolate brown with buff blotches
Ventral plumage	Breast and belly with similar, limited amounts of brown, mainly cream	Cream belly with distinct brown breast band	Brown markings with irregular buff blotches	Brown markings with irregular buff blotches

cream ventral plumage in areas that were not brown, lighter underwing coverts and cream not buff markings on these feathers (Table 2.5).

Age effects on the frequency of incomplete barring in rectrices were also found (*contra* Marchant and Higgins 1993). However, these differences were not consistent enough to utilise as the sole criterion for assigning age as suggested by Condon (1951). The preponderance of barring in the undertail coverts of adult females was unexpected and has not been noted elsewhere. This barring lead to adult females having generally darker undertail coverts than adult males, as fitted the trend for other plumage characteristics, whereas in both sexes of immatures barred undertail coverts were encountered in similar frequencies.

In brown falcons both sexes defend territories and breed in immature plumage (M^cDonald in press *b*; M^cDonald *et al.* in press), engaging in ‘side-slipping’ displays (Baker-Gabb 1982; Debus 1991; Marchant and Higgins 1993), alternatively displaying their ventral and dorsal surfaces. While both sexes regularly perform this display, only males do so alone with regularity (M^cDonald in press *b*). The lighter ventral surface of males of both ages compared with females results in greater contrast between dorsal and ventral surfaces during these displays. Further, the lighter almost white ventral and underwing coverts and rufous upperparts of the apparently oldest males maximises this effect, leading to these birds performing displays of the greatest contrast to my eye. White feathers reflect much greater amounts of ultra-violet light than reddish-brown feathers while both buff and brown feathers reflect similar, comparatively small proportions of UV light (Burkhardt 1989). Therefore, differences in the

contrast between dorsal and ventral plumage of brown falcons evident to humans are also likely to be apparent throughout the entire spectrum visible to falcons. Moreover, facial bare parts of adult birds contain more yellow and are brighter than their younger counterparts, particularly in males, a feature that could quickly and easily be assessed by either sex. As these features appear age-related and are likely to be difficult to 'fake', ventral plumage and facial bare part colouration may be honest signals of quality (Zahavi 1975; Simmons 1988; Palokangas *et al.* 1994), particularly as adult raptors are usually better breeders than younger birds (see Newton 1989; Sæther 1990; Martin 1995 for reviews). These aspects will be investigated elsewhere (Chapter 6).

The frequency of yellow in facial bare parts of brown falcons was far more common than the 1% of birds suggested by Weatherly *et al.* (1985). In this study every adult male and 98% of adult females had at least some yellow in their facial bare parts, with 41% of adult males having complete bright yellow orbital rings and ceres. While age differences in facial bare part colouration have been observed in most falcons, sexual differences are far less frequently reported (e.g. Marchant and Higgins 1993; Negro *et al.* 1998; Ferguson-Lees and Christie 2001; this study), perhaps due to poor recording of facial bare part colour on museum labels and the rapid fading of this character following death (Condon 1951). In any case, the supposition of Weatherly and colleagues (1985) that the presence of yellow in facial bare parts of brown falcons increases with age was confirmed by this study. Despite this, for both age groups males exhibited more yellow in their facial bare parts than equivalent aged females and only adult males obtained fully bright yellow ceres and orbital rings. Seasonal variations in

the colouration of these areas were not observed, in contrast to patterns reported for finches (Burley *et al.* 1992) and the American kestrel (*Falco sparverius*; Negro *et al.* 1998), although repeated intensive sampling of individuals over a season is required to confirm this result.

The fact that adult birds had significantly lighter ventral plumage in comparison with same-sexed immatures also supports the findings of Weatherly *et al.* (1985). Weatherly and colleagues suggested that this process was faster and more complete in males based on observations of captive birds. Quantified data from this study support this; adult females nearly always had a breast band whereas in most males the entire ventral surface was of a similar colour. The extreme condition of an entire white ventral surface was found in only the oldest adult males. Marchant and Higgins (1993) rejected differences in plumage according to sex, however the concurrence of this study and previous work indicates, at least for falcons in Tasmania and southern Victoria, that sexual differences in plumage are considerable and repeatable. Weatherly *et al.* (1985) found that breast bands were yellow in some females and were eventually lost as bird's aged. In this study, female breast bands were a variant of brown in colour over cream to white ventral plumage, and were present in all but one female, including a bird over 13 years old. Further, adult females recaptured retained breast bands over multiple moults, indicating it is unlikely that breast bands are routinely lost in older females.

As the exact ages of all birds sampled were not known, it is possible that the sexual differences in adult plumage described have arisen through biased

sampling, that is comparatively older and thus lighter males were assessed in comparison with females. This appears extremely unlikely however due to the large numbers of falcons scored and the fact that recruitment of both sexes occurred at the same age (two years old for 4 females and 3 males) or was even younger for males (1 male one year old).

Despite the progress in understanding variation in plumage outlined above, the age at which adult plumage is attained in brown falcons remains unclear, as recaptured nestlings had yet to acquire adult plumage. Further assessment of known-age falcons over the coming years will provide clues to this process. Descriptions of the sequence of plumages exhibited by birds until the attainment of adult plumage, and the precise timing of this event, remain the last stumbling blocks to a more complete understanding of plumage variation in this species, at least for populations in southern Victoria.

Distinct differences in the proportion of colour ‘morphs’ of the brown falcon have been reported in other areas, for example the preponderance of ‘red’ morphs in central Australia and ‘dark’ morphs in the tropical north (Amadon 1941; Marchant and Higgins 1993). Despite this, at least for the large population studied, the majority of variation in plumage colouration observed could be attributed to differences resulting from sex and age-specific influences, not the presence of different colour morphs within the population. Indeed, each age and sex class resembled the colour ‘morphs’ described by others (Amadon 1941; Marchant and Higgins 1993). This relationship casts doubt upon descriptions of races and morphs based solely on collections of falcons of uncertain age, sex and

provenance. Clearly, further research of known individuals from other parts of the falcon's range is warranted. This information is critical to our understanding of the supposed marked plumage variation in this species, and thus the interpretation of the validity of proposed subspecies.

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Chapter 3 – Nestling growth and development in the brown falcon

Falco berigora: an improved ageing formula and field-based method of sex determination



Plate 3.1 A brown falcon nest containing a 2 day old nestling and two unhatched eggs. Note front egg is pipped and hatched later the same day.

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Abstract

The accurate determination of nestling age and sex is an important tool for studies that examine life-history traits and ecological interactions. Despite the widespread distribution of the brown falcon *Falco berigora* in Australia, morphological criteria for sexing nestlings of this species have yet to be published and nestling development has yet to be intensively studied. While an ageing formula for the species exists, the small sample from which it was derived precluded appropriate statistical assessment of independence problems and other potentially confounding variables such as hatch order and sex. This study used a larger sample of free-living nestlings to account for these factors and found the most reliable measure for ageing nestlings to be wing length. Wing length increased in a linear manner with chick age, independent of seven other potentially confounding factors examined. Ageing formulae based on wing length before and after remiges emerge are presented. In addition, an accurate test for determining nestling sex at banding age, based on tarsus width, is proposed. Nestling chronology of this species is also described in detail for the first time. Nestling development was similar to that described for other Falconiformes; however the chronology of nestling development was too variable to be useful in assigning chick age. Despite this, within six days of the eldest chick hatching the relative brightness of down and the degree to which chicks' eyes had opened were useful in assigning hatch order amongst nestlings of similar wing lengths.

Introduction

The accurate determination of nestling age is an important tool for studies investigating species management or ecological interactions between reproductive phenology and life-history traits; for example, relating various stages of a predator's reproductive cycle to prey abundance (Ridpath and Brooker 1986; Simmons *et al.* 1986; Korpimäki and Norrdahl 1991; Steenhof *et al.* 1999), examining within-brood variables such as hatching asynchrony (Wiebe and Bortolotti 1995), or the impact of environmental variables such as weather on nestling growth (Olsen and Olsen 1992; Dawson and Bortolotti 2000). From a more practical viewpoint, ornithologists and wildlife managers can use ageing formulae to accurately determine appropriate time frames for banding offspring, hence minimising nest disturbance and the logistical costs of frequent nest visits.

Correct assignment of nestling sex is also important for population studies and management practises, particularly for sexually dimorphic species. From a theoretical point of view, incorrect sexing can lead to biased conclusions about many traits such as growth rates (Ricklefs 1968), population sex ratios (Clutton-Brock 1986) and intersexual differences in survival or dispersal (Newton and Moss 1986). From a more practical viewpoint the correct sexing of many size dimorphic species is important as the sexes may require different sized leg bands; the fitting of incorrect sized bands may harm the recipient (Lowe 1989). While molecular techniques are now available for sexing nestlings of most bird species (Griffiths *et al.* 1998), they are costly, may not be compatible with the logistical constraints of fieldwork and are often beyond the scope of many projects.

The determination of nestling age and sex in raptors is often hampered by the development of size hierarchies associated with hatching asynchrony and comparatively long nestling periods, which can in turn lead to errors in the estimation of nestling age. Previous workers have utilised apparent linear relationships between nestling age and various size measures to generate formulae for ageing nestlings (Moss 1979; Bortolotti 1984a; Olsen and Olsen 1987).

However, avian growth rates are potentially limited by a variety of proximate parental and environmental factors which influence food supply to offspring (Drent and Daan 1980), such as hatch order, sex, brood size, hatching date, parental age/experience and various environmental variables unique to the year of measurement (Moss 1979; Ricklefs and Peters 1981; Ricklefs 1982; Picozzi 1983; Richter 1983; Bortolotti 1986; Olsen and Olsen 1992; Scharf 1992; Olsen 1995; Viñuela 1996).

As part of a long-term study on parental investment and mate choice in the brown falcon *Falco berigora* (M^cDonald 2003, in press; M^cDonald *et al.* in press), accurate methods for ageing and sexing nestlings were required. The brown falcon is a moderately dimorphic raptor and little overlap exists between the sexes for a variety of adult measurements (Baker-Gabb 1984a). However, for much of the early to mid-nestling cycle, nestlings show considerable sexual size overlap (M^cDonald unpubl. data). As older nestlings of this species are the most likely Australian *Falco* to prematurely fledge and potentially be injured if disturbed (Baker-Gabb in Marchant and Higgins 1993), they must be banded relatively early in comparison with other *Falco*. This presents a problem for researchers wishing to fit the correct band size and record the appropriate sex ratio of a brood.

An ageing formula based on nestling wing length has been published for brown falcons by Olsen and Olsen (1987). However, this formula was calculated with a limited sample of measurements from both wild and captive birds and did not account for statistical independence problems associated with sampling multiple chicks per brood. Furthermore, the nestling chronology of the brown falcon has yet to be described in detail, other than anecdotally (Olsen in Marchant and Higgins 1993). This information may also be of use in assigning age and sex of nestlings (e.g. Bortolotti 1984b).

Thus, the aims of this chapter are three-fold: first, to describe in detail the nestling chronology of developing brown falcons; second, to determine an appropriate ageing formula; and third, to identify an accurate field-based method for sexing nestlings. They are published here to assist other researchers and banders.

Methods

Study area

The study was conducted between July 1999 and June 2002, approximately 35 km southwest of Melbourne in southeast Australia, at the Western Treatment Plant (WTP), Werribee (38°0'S 144°34'E), adjacent Avalon Airport (38°2'S 144°28'E) and small areas of surrounding private land. Details of the study site have been provided elsewhere (Baker-Gabb 1984b). Briefly, the area can be divided into four main habitat types defined by the principal land-use, with artificial windbreaks of various pines (*Pinus spp.* and *Cupressus macrocarpa*), sugar gums *Eucalyptus cladocalyx* and occasional river red gums *E. camaldulensis* scattered throughout. The airport, private land and much of the northern section of the WTP are covered by

Untreated Pasture, areas dominated by introduced pasture species and heavily grazed by sheep *Ovis aries* and cattle *Bos taurus*. The remaining three habitats are restricted to the WTP, a long-established sewage treatment area. Most is subject to *Land Filtration*, where fields are irrigated with wastewater and grazed in a rotational manner to keep grasses short. *Grass Filtration* occurs in the western section of the WTP, tall grasses dominate these areas, reaching 1 m or more in height following irrigation. Finally, a series of *Lagoons* used for managing peak daily and inclement weather flows exist throughout the WTP.

General field methods

Falcons began laying clutches from the last week of August through to the end of October. During these times all nests were actively searched for by monitoring the behaviour of resident colour-banded territory owners. Once found, nest trees were climbed where possible and eggs measured to estimate approximate hatching dates. Nests were then visited every 2 days close to hatching to assign a hatch date and order for each chick. Nestlings still damp when first found were classified as hatching on the day of the visit, dry chicks were recorded as hatching the previous day, given most nest visits near hatching were conducted early in the morning. Generally eggs that were just pipped (i.e. the chick had made the first crack in the egg shell), hatched 48 h later; eggs in which a substantial hole existed, allowing nestlings' bills to be seen, hatched within 24 h. Hatch date was scored as age 0. After hatching, nestlings were marked with a small piece of Micropore tape (3M; Pymble, New South Wales) loosely folded around either the left or right humerus until they reached an appropriate age for banding (Plate 3.2*a-c*). This tape was

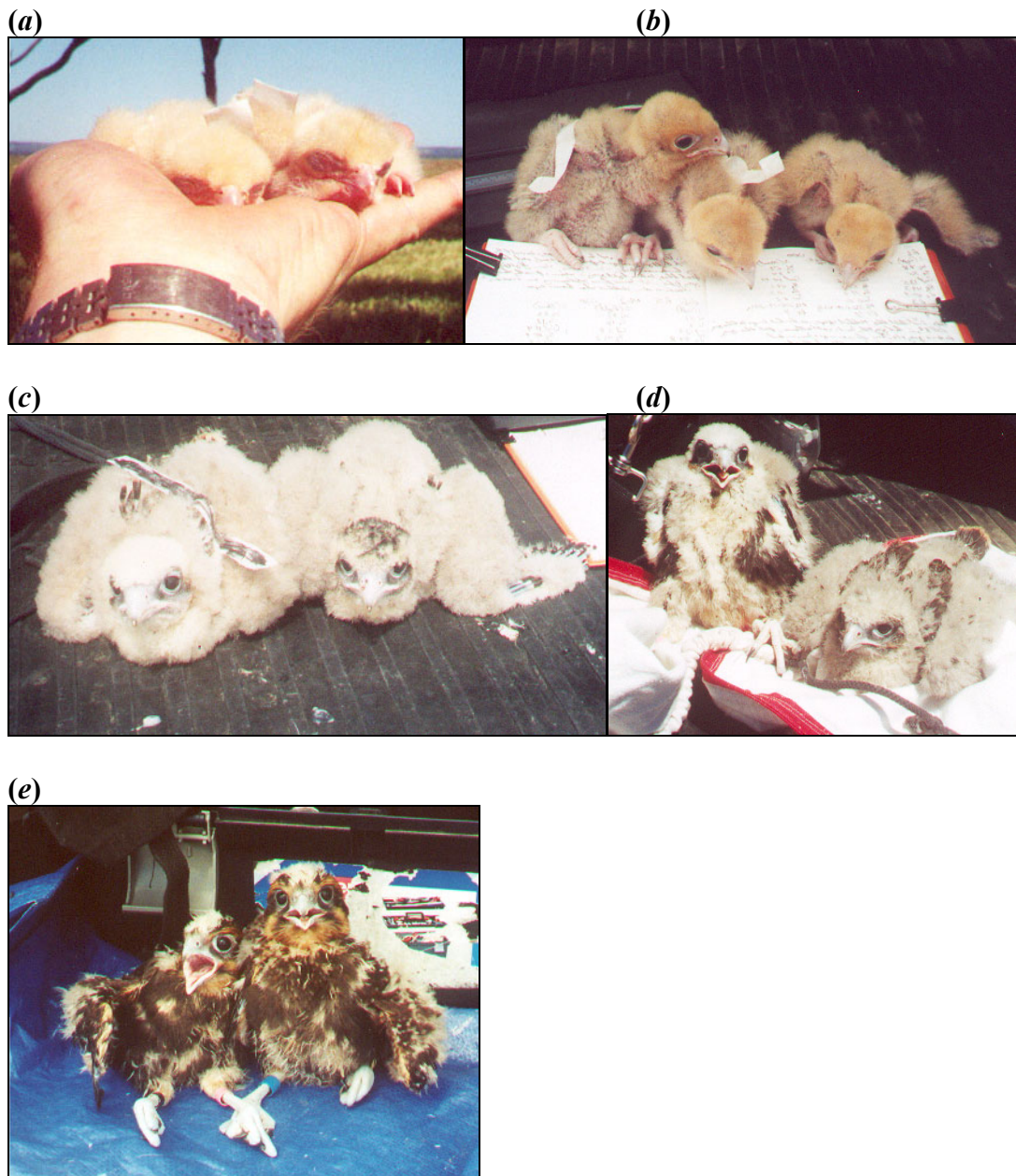


Plate 3.2. Brown falcon nestlings, at ages (left to right) (a) 2 and 1, (b) 9, 9 and 8, (c) 14 and 12, (d) 21 and 17, (e) 29 and 28 days. The oldest birds are male, the youngest female for (a,c-e). Sex of nestlings in (b), (left to right) male, female, male. Note tape around wings to identify nestlings prior to banding (a-c). Crown of youngest bird in (c) has also been marked.

replaced with each visit to allow for growth, and did not leave behind adhesive residue or interfere with growing humerals or remiges.

Morphometric data collection

Following hatching, nests were visited and chicks were measured at approximately weekly intervals (mean: 7.7 days \pm 2.2 SD, range: 3 - 15). Visits to the nest generally ceased when the oldest nestling was 30 days old (range: 0 - 36 days), as older nestlings readily 'branch' and may prematurely fledge if the nest tree is climbed. When each chick was measured, a description of its appearance was recorded and in many cases a photograph taken. At the first mention of a colour in the text, a number and name in parentheses is given that corresponds to standard colours in Smithe (1975).

In total, seven characters were measured for each nestling; four of these were investigated as having potential for use as an ageing or sexing tool. While most researchers have used wing length for developing ageing formulae, the suitability of culmen length and body mass was also examined. Tarsus width was chosen as a variable with which to sex nestlings, as the most obvious difference between sexes are the larger feet and legs of female nestlings (pers. obs.).

Wing length was taken as the chord between the carpal joint and the tip of the 8th (longest) primary (sheath and emerged vane) when flattened along a rule. Prior to the emergence of pins the chord between the carpal joint and the tip of the radius-ulna at the elbow was measured. Culmen length was taken as the chord between the anterior margin of the cere and the tip of the upper mandible. Tarsus width was measured at

the tarsus' midpoint as the chord between the anterior and posterior diameter of the tarsus. Care was taken not to depress any tissue around the tarsus with pressure from callipers when measuring this feature (see Lowe 1989 for details). Wing length was measured to the nearest millimetre using a 400 mm butted steel rule marked in millimetre increments; culmen and tarsus width were measured to the nearest tenth of a millimetre using 150 mm Kinchrome vernier callipers accurate to 0.001 mm. Where applicable these measurements were taken on the right side of nestlings. Body mass was obtained using spring pesolas accurate to 0.5 g, 2 g and 5 g for nestlings weighing up to 60, 300 and 600 g, respectively. No correction was made for crop contents. Each chord was measured during each nest visit, except for tarsus width in 2000, which was generally only taken during the final measurement of nestlings in that year.

Measurements used to generate formulae and assess chronological development were restricted to those taken from nestlings that subsequently fledged and for which hatch date were known (± 24 h). In total 163 measurements/observations of 39 nestlings from 20 broods satisfied these criteria, with 10 broods each raised in 2000 and 2001, respectively.

Sexing nestlings

To correctly assign sex to each nestling a Polymerase chain reaction (PCR)/*HaeIII* digest reaction was used (see Griffiths *et al.* 1998 for detailed methods). A small blood sample (c. 10 - 20 μ L) from the alar vein was obtained from each chick following hatching. PCR primers (P2 and P3) were then used to amplify a gene (*CHD*) on the W-chromosome. The resulting product was then restricted using an

enzyme (*HaeIII*). When run on agarose gels, females could be identified by the presence of two bands, whereas males had only one.

Statistical analyses

To determine the relationship between nestling size and age, I used a statistical modelling approach with Genstat 5 Release 4.21 (Genstat Committee 1993). To account for the unbalanced nature of the measurements and potentially non-independent data, such as measures from multiple nestlings within-broods, I utilised restricted maximum likelihood (REML) procedures. These allow the incorporation of a random model including brood, chick and year of measurement. Effects of the additional fixed factors age, brood size, sex, hatch order, hatch date, parental age and land-use on the response variables body mass, wing and culmen length could then be assessed. Each response variable was used in a separate analysis. The initial model fitted included all explanatory terms and biologically meaningful two-way interactions. Interactions and then terms were then dropped in a step-wise fashion by examining the change in deviance between the full model and the sub-model fitted. This change in deviance statistic approximates a Chi-square distribution. The procedure was repeated until only significant terms remained in the model. For simplicity, interaction terms are not presented unless significant. Land-use was assigned by identifying the principal habitat surrounding each nest. Male age, immature or adult, was used as a simple estimate of parental age, as males are responsible for providing the bulk of food to nestlings (M^cDonald in press). The ageing criteria of Weatherly *et al.* (1985) and M^cDonald (2003) were used to assign this variable.

Student's t-tests were used to assess differences in tarsus width between the sexes for a given age. ANOVAs were used to assess differences in the age at which the egg tooth was lost according to hatch order and sex. All data presented are means \pm one standard deviation. The methodology utilised in this project was approved by the Australian National University Animal Experimentation Ethics Committee (Registration No. F.BTZ.02.99).

Results

Chronology of nestling development: feathers

Nestlings hatched in a sparse orange-buff down (121D; Pale pinkish buff) covering the body which was usually darker on the crown (153; Trogon yellow; Plate 3.2*a,b*). The pink skin (3; Vinaceous) was easily visible through this down (Plate 3.2*b*); the latter quickly fading in colour. Chicks hatched with their eyes fully closed. By the second day their eyes had begun to open, with most chicks having fully open eyes by 6 days (range: 4 - 7 days). The degree to which nestlings' eyes had opened and down colour faded reliably indicated hatch order of broods up until the eldest nestling was 6 days old. Nestling pupils were a reddish chocolate-brown colour (221A; Warm sepia) throughout the nestling period.

By day 9 nestlings had developed a thick, light grey down (c. 44; Smoke grey) over the body (Plate 3.2*c*), however the down on the head retained a buff-orange tinge until nestlings were 14 - 18 days old, by which time the entire body was covered in the grey down. The remiges were the first pins to emerge, typically by day 8 but on day 5 in one individual. Rectrices emerged the day after remiges. Timing of pin emergence of other feather tracts was more variable, however, pins around a bird's

cheeks normally emerged at 14 - 18 days, followed by pins either side of the breast at day 17 - 21 (Plate 3.2*c,d*). Pins along the scapulars were first observed in one bird aged 13 days, although more typically they emerged at day 18. Pins along the crown were the last to develop and were first observed at day 18, but were not found on most birds until day 25 (range 18 - 28). By day 28 pins were present over all areas of nestlings (Plate 3.2*e*). Down on the crown and along the flanks underneath the area covered by folded wings was the last to be lost; many nestlings fledged with down remaining in these areas. No differences according to sex or hatch order were apparent in feather development, however the level of variation in the timing of feather emergence made this an unreliable method of assigning age.

In their first week nestlings tired easily and could raise their head for short periods only, begging with a soft chirping. When 14 days old chicks could briefly stand, but preferred to lie on their chest and tarsi (Plate 3.2). At this age chicks began using louder, higher pitched 'kakk-kakk-kakk-kakk.....' calls when approached. By the time chicks were 21 days old they could stand readily and tried to walk away when released, occasionally defending themselves with their feet, rarely rolling onto their back to do so.

Bare parts

Female nestlings lost their egg tooth significantly later 19.9 ± 4.7 days than males, 17.1 ± 3.7 days, however the relationship was weak ($F_{1,39} = 4.215$, $p = 0.047$) and

overlap between the sexes was common. No other differences associated with sex or hatch order were identified in bare part colour or growth.

On hatching, nestlings' legs, bill, talons and cere were a soft pink colour (108D; Rose pink), although the latter was occasionally creamy white (c. 92; Pale horn colour). At this early stage the tip of the upper mandible and talons were usually dark grey (83; Dark neutral grey) and orbital rings were blue-grey (86; Pale neutral grey) with a pink tinge. By 8 - 9 days nestlings' legs and feet had developed a blue-grey tinge, by day 14 all trace of pink was gone, and by day 20 nestlings' legs had developed the distinctive blue with a grey tinge (c. 88; Pratt's Payne's grey) typical of newly fledged birds. Within a few days of hatching, talons had developed a black tip, by 6 - 7 days most birds had steel blue-grey (85; Light neutral grey) talons tipped black. Birds obtained the typical full black talon colouration of adults by 25 days old. By the second day some birds had a blue-grey base to the upper mandible, this being prominent in all birds by day 9, along with the development of a dark grey tip. The typical steel blue-grey bill with a black tip was obtained by days 13 - 15. Upper halves of nestling ceres had developed a blue-grey tinge by day 5 in some birds, and this was common by day 10. Ceres were the typical blue-grey of fledglings by day 14 in some birds, and in all by day 20. Orbital rings rapidly lost any sign of pink and by day 5 they were the typical blue to blue-grey of fledglings, although the brightness of this blue tended to intensify over the nestling period. As with feather development, the timing of changes in bare part colouration was not consistent enough among chicks to be useful in assigning age.

Nestling size and age

Three potential measures were assessed for their use as an ageing tool: body mass, wing and culmen length. When the measurements of body mass, wing and culmen length were plotted for all known-age nestlings that fledged, large differences in the growth patterns of each measure emerged (Fig. 3.1). Wing length was linear in growth prior to the emergence of remiges, usually at day 8, with growth rates increasing following feathers emerging (Fig. 3.1a). Hence, wing length measurements were split into those taken before and after emergence of remiges. In contrast, culmen length was linear throughout the ranges measured (Fig. 3.1b). Body mass accumulation on the other hand was more variable (Fig. 3.1). In contrast to the other two measurements it displayed a sigmoidal growth curve and appeared to have reached its plateau by day 30 (Fig. 3.1c). Clear sexual differences emerged early in the nestling phase, indicating a separate model for each sex would be required to generate ageing formulae. This was clearly undesirable and, as such, body mass was excluded from further analysis.

Development of ageing formulae

A significant relationship existed between wing length prior to the emergence of pins and age using a REML model ($\chi^2 = 37$, $df = 1$, $p < 0.001$; Table 3.1a). None of the other variables or two-way interactions included in the model affected the rate of wing length growth (Table 3.1a), with the age of nestlings prior to the emergence of remiges described by the following linear relationship:

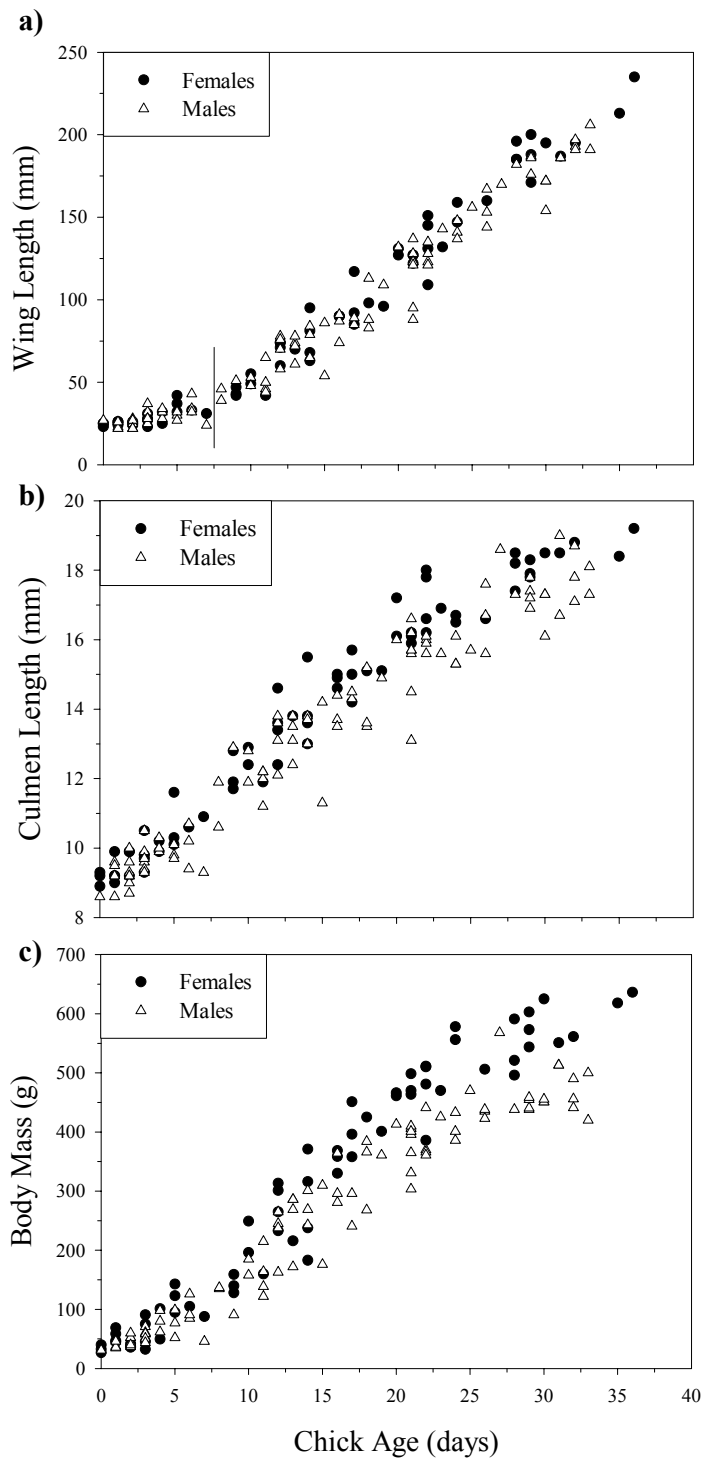


Figure 3.1. Measurements of (a) wing length, (b) culmen length and (c) body mass for 163 measurements of 39 known-age brown falcon nestlings that survived to fledging. Line in wing length graph represents the average age at which remiges first emerge and where the data were split for further analyses (see Results).

Table 3.1. Summary of analyses of nestling size using the REML modelling procedure. In all models random terms included were brood, chick and year. Change in deviance statistics for each term initially included in the model are presented, bold values indicate $p < 0.05$. Biologically meaningful two-way interactions were initially included in all models, but are presented only if statistically significant.

Explanatory variable	Change in deviance (χ^2)	Degrees of freedom	<i>p</i> value
<i>a) Wing length prior to emergence of remiges (n = 50)</i>			
Age (days)	37	1	<0.001
Brood size	2.15	1	0.143
Land-use type	3.56	2	0.169
Hatch date	1.87	1	0.171
Presence of brood reduction	0.85	1	0.357
Male age	0.37	1	0.541
Hatch order	0.81	2	0.667
Sex	0.03	1	0.873
<i>b) Wing length following emergence of remiges (n = 113)</i>			
Age (days)	6914.58	1	<0.001
Brood size	3.16	1	0.075
Sex	2.88	1	0.09
Hatch date	2.81	1	0.093
Male age	1.31	1	0.253
Hatch order	1.07	2	0.585
Presence of brood reduction	0.06	1	0.805
Land-use type	0.18	2	0.914
<i>c) Culmen length throughout the nestling phase (n = 163)</i>			
Age (days) *Sex	6.99	1	0.008
Sex	21.77	1	<0.001
Age (days)	3825.07	1	<0.001
Brood size	2.96	1	0.085
Land-use type	3.48	2	0.176
Hatch date	1.32	1	0.250
Presence of brood reduction	0.1	1	0.747
Hatch order	0.51	2	0.775
Male age	0.01	1	0.942

$$\text{Age (days)} = [\text{Wing length (mm)} - 23.22] \div 1.584$$

A similar relationship emerged between wing length and age following the emergence of remiges ($\chi^2 = 6914.6$, $df = 1$, $p < 0.001$; Table 3.1*b*). Age of nestlings with emerged pins could therefore be determined by:

$$\text{Age (days)} = [\text{Wing length (mm)} + 19.4] \div 6.812$$

In contrast to the two wing length measures, a significant interaction between age and sex existed when culmen length was assessed ($\chi^2 = 7.2$, $df = 1$, $p = 0.007$; Table 3.1*c*). Slopes explaining male culmen growth rates were 0.292 in contrast to 0.318 for females; culmens grew more slowly in males. Further analysis of culmen length was therefore excluded, as having separate ageing formulae for each sex was undesirable.

Sexing nestlings

To identify an appropriate method of sexing nestlings, chicks were grouped into 5 - day age intervals from hatching, with nestlings 25 - 36 days old grouped to increase sample sizes. Using the results from PCR sexing, 112 measurements of tarsus width from 37 known-sex individuals were obtained. By the age of 15 - 19 days, male nestlings had significantly smaller tarsus widths than did their female counterparts ($t_{0.05(1),14} = 2.23$, $p < 0.05$; Fig. 3.2), but 95% confidence intervals of the mean for each sex still overlapped. This overlap ceased by 20 - 24 days and 25 - 36 days old, as tarsus width of nestlings became more sexually dimorphic ($t_{0.05(1),21} = 1.721$; $t_{0.05(1),26} = 1.706$, respectively, both $p < 0.005$; Fig. 3.2). Tarsus width did not reach

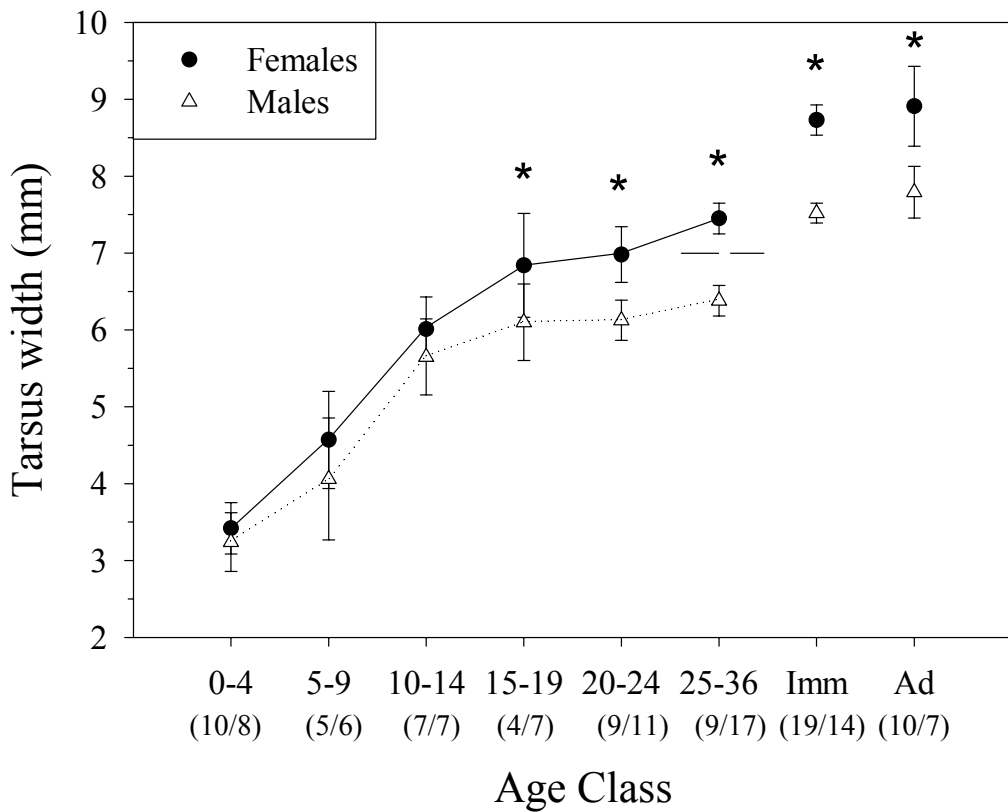


Figure 3.2. Mean tarsus width of female (closed circles and solid line) and male (open triangles and dotted line) nestlings, immature and adult brown falcons. Error bars indicate 95% confidence intervals of means, numbers under x-axis indicate sample sizes for females/males, respectively. Broken line indicates cut-off point for determining nestling sex at age 25 - 30 days, inclusive. Asterisks indicate significant ($p < 0.05$) sexual differences.

full size in the nestling period measured, since adult and immature birds both had wider tarsi than the nestlings measured (Fig. 3.2). Thus, criteria for sexing individuals should be restricted to age classes. The ideal age for banding individuals is between 25 and 30 days old, as chicks are then almost fully grown and have yet to develop a tendency to leave the nest (pers. obs.). At this age the tarsus width of all males was less than 7 mm, with those of females greater than or equal to 7 mm. By this criterion 18 birds within this age group (12 males and 6 females) were sexed correctly, as indicated by molecular data. Further, an additional six males and four females were measured at 31 - 36 days old; all of these birds were again correctly sexed by the tarsus-width relationship described above. Using the ageing formula for chicks with emerged remiges, nestlings with wing lengths between 150.9 and 185 mm (ages 25 - 30 days inclusive) can be correctly sexed as female if tarsus width is greater than or equal to 7 mm (Fig. 3.2). Moreover, no male measured throughout the entire nestling phase had a tarsus width greater than 6.9 mm, thus any bird which is larger than this measurement up to 36 days old (wing length 226 mm) could be reliably sexed as female.

Discussion

This study is the first detailed report of the nestling chronology of the brown falcon, with development of chicks found to be similar to that described for other Falconiformes (Roest 1957; Newton 1979; Olsen and Olsen 1980; Olsen *et al.* 1982; Marchant and Higgins 1993), although the first orange-buff down present in newly hatched chicks is atypical in comparison with a more usual cream or white down in most other species. While some historical records have reported brown falcon nestlings with an initial white down (see Condon 1951 for review), most reports

describe various shades of orange-buff down as observed in this study (Condon 1951; Weatherly *et al.* 1985; Marchant and Higgins 1993). The timing of nestling development was also similar to that in previous reports, although this study identified a longer period for chicks eyes to open fully (6 cf. 4 days) and faster development of pins over the entire body (25 days cf. 27+) than described in Marchant and Higgins (1993). This study also found a longer age to the acquisition of the second grey down by nestlings, in comparison with that previously reported (9 cf. 5 days; Weatherly *et al.* 1985).

Unlike in previous studies, the relationships between nestling age and wing length presented took into account the potential confounding effects associated with sampling multiple nestlings within-broods, and other factors previously demonstrated to have important influences on growth, such as sex and hatch order. Despite this, wing length was again found to be the best variable for use in formulae to determine nestling age, as it remained independent of nestling sex, as suggested by Olsen and Olsen (1987). Wing length was also found to be independent of all other variables assessed, some of which affect food supply to nestlings (Chapter 8). Given this, it appears that wing length is resilient to short-term food shortages in the brown falcon, as has been noted in American kestrels *F. sparverius* (Negro *et al.* 1994) and previously suggested by Olsen and Olsen (1987). Thus the two easily applied formulae generated will be useful tools in assigning nestling age in future studies of brown falcons.

In contrast to wing length, nestling development was generally too variable to be used as a reliable tool for ageing young brown falcons. However, a combination of

the relative brightness of down colour and the proportion of a chick's eye that was open can be useful for assigning hatch order among young broods with similar wing lengths.

During this study, disturbance was minimised at nest sites by handling nestlings for the smallest time possible. Hence, the repeatability of each measurement could not be determined. In other raptor studies wing and culmen length have both been found to be highly repeatable measurements (Bortolotti 1984*a*). Given that these measurements are easily made and familiar to researchers, measurement error is unlikely to be a source of significant bias in the ageing formulae presented. Tarsus width was more prone to measurement error in Bortolotti (1984*a*), who used the mean of two measurements just above the phalanges. The mensural character suggested here involves only one measurement at the midpoint of the tarsus. In brown falcons of the recommended age, tissue surrounding this area is quite hard and the chord easy to measure, as nestlings can be allowed to sit in their preferred position. Nevertheless, great care must be taken to avoid depressing the tissue around the tarsus with calliper ends during measurement. If this were not done, results obtained would be unreliable.

The sexing criterion presented in this paper has the advantage of utilising one character (cf. Bortolotti 1984*a*), and as such is a simple and easily applied method. Despite its simplicity, application of the formula correctly identified the sex of every nestling in the study, as verified by molecular analysis. The proposed method was, at least in this case, as reliable as expensive molecular techniques and can be easily and quickly carried out in the field. Where populations of smaller brown falcons occur

however, such as southwest Australia and Papua New Guinea (Marchant and Higgins 1993), these formulae should be modified accordingly.

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Chapter 4 – The breeding ecology and behaviour of a colour-marked population of brown falcons *Falco berigora*



Plate 4.1. An adult female brown falcon from the focal population. Photo courtesy of Ian Montgomery.

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Abstract

This study took advantage of a large, closely monitored colour-banded population of brown falcons to describe aspects of this species breeding ecology and behaviour over three consecutive years. Both pair members aggressively defended territories throughout the year from conspecifics and other species alike. Males performed territorial displays more frequently than females, which rarely displayed unprompted. Strong differences in the types of parental care provided by each sex were evident, with females contributing to the bulk of incubation, brooding and feeding of nestlings and fledglings. Males, on the other hand, provided the majority of food to both females and broods, from well before the first eggs were laid until nestlings were two to three weeks old. Prey deliveries were more frequent early in the morning and late in the evening; however, remains of larger prey were cached, presumably to provision the offspring more regularly throughout the day.

Introduction

Despite being one of Australia's most commonly encountered raptors (Blakers *et al.* 1984), the behaviour and breeding biology of the brown falcon *Falco berigora* has received little scientific attention. In the most comprehensive studies to date, Baker-Gabb (1982) monitored up to 25 pairs in southern Victoria over three seasons and Mooney (1976) described several aspects of the behaviour of captive individuals. However, this work is largely confined to unpublished theses. Bollen (1993) published descriptions of the behaviour from one pair, while Debus (1991) described two displays of a single male and Olsen and Olsen (1980) have described nest defence behaviour in response to human intruders. Additional information on the Tasmanian population has been provided by Mooney in Cade (1982) and Marchant and Higgins (1993). The latter also contains a review of additional anecdotal evidence.

This study, as part of a larger investigation into the breeding biology and life history strategies of brown falcons, took advantage of a large, colour-banded population to investigate and describe additional behaviours of birds of known sex and background. In addition, footage from nest surveillance cameras over two seasons allowed a detailed examination of the degree of sex role partitioning during parental care.

Methods

The study was conducted between July 1999 and June 2002 approximately 35 km southwest of Melbourne, at the Western Treatment Plant, Werribee (38°0'S 144°34'E), adjacent Avalon Airport (38°2'S 144°28'E) and small areas of

surrounding private land, a total area of approximately 150 km². Details of the study site (Baker-Gabb 1982, 1984a) and population, which included 44 to 49 breeding pairs each season, have been described elsewhere (M^cDonald 2003, in press; M^cDonald *et al.* in press).

Falcons were captured with bal-chatri and modified goshawk traps (see Bloom 1987 for details), fitted with a unique combination of colour bands approved by the Australian Bird and Bat Banding Scheme and released at the point of capture. During frequent visits to the study site banded birds were actively sought, identified and their behaviour noted. When found, nest trees were climbed daily until clutches were complete. If not observed directly, laying date of first eggs were estimated using either a formula based on egg weight (P. Olsen unpubl. data) or, if eggs hatched, by backdating using an average incubation period of 36 days (this study) and estimating chick age from formulas based on wing length (M^cDonald in press). Nests were visited weekly after hatching to determine nestling periods and the number of birds successfully fledged from each nest. At approximately four weeks of age nestlings were fitted with colour bands. Following fledging, the length of post-fledging parental care was determined by visiting the nest area bi-weekly. If fledglings could not be located in three successive visits they were deemed to have successfully reached independence. During the breeding seasons of 2000 and 2001 intensive assessments of parental roles at the nest were conducted using surveillance cameras throughout the nestling stage. Small cameras with infrared lights (Model 43150674; Radio Parts Group, Melbourne) were placed at nests for 48 h periods throughout the nestling phase. Cameras were powered by deep cycle batteries (Besco N70T; Battery World, Canberra) and connected to time-lapse video recorders (Hitachi VT1200E;

Radio Parts Group, Melbourne) run at 1/8 normal speed; this minimised visits to the nest tree to 24 h intervals to change batteries and tapes. The behaviour of parent birds and offspring was then noted on subsequent viewing of video footage.

Statistical analyses

Goodness of fit tests were used to assess the significance of differences in prey delivery rates throughout the day as well as sexual differences in the recorded frequency of each display type. Where appropriate Yates corrections for continuity were used (Zar 1996). One-way ANOVAs and linear regressions were used to assess yearly differences in the duration of various phases of parental care. The methodology utilised in this project was approved by the Australian National University Animal Experimentation Ethics Committee (F.BTZ.02.99).

Results

Agonistic interactions

Both members of brown falcon pairs aggressively defended territories from intraspecific intruders of either sex throughout the year, although agonistic interactions were more common and were of a longer duration between July and November (the breeding season, see below). Interactions often escalated into physical contact between birds, with perched combatants observed jumping to the ground to avoid being struck by conspecifics on seven occasions. Talon presentation displays were also common and, in one extreme case, two females locked talons and spiralled downwards 20 m in a 'cartwheeling' flight, completing four full revolutions before releasing their grip close to the ground.

Territorial and courtship displays

Displays were also frequently encountered throughout the year, becoming more frequent from July to November. Of a total of 126 displays given by banded birds, 'side-slipping' was the most frequently observed (62.7%). During this display birds would rotate rapidly from side-to-side while in a gliding descent, often from great height, with wings held stiffly behind their back, alternatively displaying their dorsal and ventral plumage. Males were usually more exaggerated than females in their movements, often using strong winds to perform the display in a stationary position above their eventual perch, rotating through an axis of up to 270° with each turn. This display was usually given by both sexes upon landing near the nest tree or returning to perches following agonistic interactions. Females (40.5%) were observed giving this display less frequently than males (59.5%; $n = 79$; $\chi^2_c = 2.86$, $p = 0.09$). In all cases females were prompted in some manner before giving the display, whereas males often performed displays alone. For example, following territorial disputes, females would usually follow males back to perches, usually 3 - 5 m behind. Upon landing, males routinely gave the side-slipping display, with females following suit with fewer, smaller rotations. The only other occasions females were recorded side-slipping was after they were flushed from nests or released following capture (both these contrived situations were not included in figures presented above). In contrast, males frequently gave this display outside of these situations and in areas away from the nest.

Other displays observed include mutual soaring (16.7%, total $n = 126$), where both members of a pair would soar within 50 m of each other, and a variety of stoops and soaring displays accompanied by quick, flickering wing beats while the birds rolled

from side to side in flight (9.5%, total $n = 126$). This faster wingbeat seemed to be confined to territorial disputes, usually given with much calling. Equal numbers of males and females were observed performing this display. Another apparently territorial display was observed in 11.1% ($n = 126$) of observations, with falcons flying in a series of large, undulating 'U' shapes, giving quick wingbeats during upsurges, again with much calling and usually while rolling from side to side with the wings held in a half closed position, particularly during descents. More rarely, this display was performed while flying at a constant elevation in a figure-of-eight pattern. U-displays were given significantly more often by males (85.7%, total $n = 14$; $\chi^2_c = 5.21, p = 0.02$); females were observed giving this display on just two occasions (both times in the company of a displaying male). U-displays were usually performed over an owners territory during/following agonistic interactions, with neighbouring males observed giving this display while soaring 200 m apart. Typically, U-displays were given at great height, often culminating in spectacular, steep and rapid descents to nest trees, with marked side-slipping and frequent calling throughout. After birds returned to perches following territorial disputes, occasionally both members of a pair would continue to call, raising their wings above their back, fully outstretched, while facing the direction from which the intrusion came. At dusk males would fly around their territory with fast wing beats giving single, sharp 'ack' calls, with the 'arrrrrk-ark-ark' call often heard during this and all other displays.

Courtship feeds and copulation behaviour

The first courtship feeds of the season were recorded in mid-July each year. Males would bring prey, house mice *Mus musculus* in all cases identified ($n = 13$), towards

females with fast, exaggerated wing beats, frequently giving ‘arrrrk-ark-ark’ calls and performing the side-slipping display before landing. Females responded with trilling calls or occasionally a sharp ‘kark’, taking the prey from males’ beak to beak or less often with her talons. Copulation was only observed following a courtship feed on one occasion (6.7%, total $n = 15$). Females initiated copulation on 27.8% of all occasions it was witnessed ($n = 18$), by giving short, sharp monosyllable calls, bowing their heads forward and lifting up their tail and rump. After this behaviour males would approach the female and land upon her back before copulation for 5 - 7 sec ensued. Less often, both sexes would perform this bowing display prior to and immediately following copulation.

Duration of and the partitioning of parental care among the sexes

Incubation lasted $35.8 \text{ days} \pm 0.8$, based on six eggs found on the day that they were laid and subsequently hatched. Nestling periods were obtained for 60 nestlings and did not differ between the 2000 and 2001 breeding seasons ($F_{1,58} = 0.77, p = 0.39$), averaging $41.5 \text{ days} \pm 0.5\text{SE}$. Nestling periods were unaffected by nestling sex ($F_{1,54} = 1.08, p = 0.30$), hatch order ($F_{2,54} = 0.35, p = 0.71$) or the interaction between the two ($F_{2,54} = 0.43, p = 0.65$). Likewise, post-fledging parental care periods were not influenced by sex ($F_{1,37} = 0.21, p = 0.65$), hatch order ($F_{2,37} = 0.09, p = 0.92$) or this interaction ($F_{2,37} = 1.11, p = 0.34$). The duration of post-fledging parental care was identified for 46 fledglings, being quite variable (range: 7 - 70 days), lasting on average $27.9 \text{ days} \pm 2.3\text{SE}$. Yearly differences were again not apparent ($F_{1,44} = 0.46, p = 0.83$), however chicks which fledged later in a given season received shorter periods of post-fledging parental care ($R^2 = 0.29, F_{1,44} = 18.30, p < 0.0005$; parental care duration [days] = $227.9 - 0.6[\text{Julian date fledged}]$). No such seasonal decline

was apparent for the nestling period ($F_{1,58} = 1.26, p = 0.27$). Over one quarter of fledged young failed to reach independence (28.1%, $n = 64$), all remains recovered indicated predation by either red foxes *Vulpes vulpes* or feral cats *Felis catus* was responsible for these deaths.

Strong sex role partitioning was apparent throughout the breeding season. Females rarely hunted from approximately two weeks prior to laying the first egg, staying close to the eventual nest site. In this period males supplied females with most of their food with courtship feeds as described above. Following laying, females assumed the bulk of incubation duties and in all cases observed except one incubated/brooded during the night. Three males were observed incubating clutches, in one of these nests incubation was monitored over a 24 h period with a surveillance camera. During this time, the male provided 45.4% of 610 min incubation during daylight hours, with the longest stint lasting 92 min. However, at the other nest monitored the resident male did not incubate at all, indicating considerable individual variation in this trait.

After hatching, males occasionally brooded young, but at a much lower frequency than during incubation. Instead, males supplied most of the food for both the brood and the female until chicks were 2 - 3 weeks old, when females again resumed hunting. Males usually brought prey to a tree next to the nest site with similar behaviour to that observed during courtship feeds. When a male arrived with food, which was usually decapitated, females retrieved prey directly from their partner, usually in a tree close to the nest, before distributing food amongst the brood. If prey remained after chicks were satiated, remains were usually either eaten by the female

or cached, often in a disused corvid nest near where transfers took place. If females were absent from the nest area males would drop the prey item into the nest and leave; if chicks were unable to break up the prey themselves, females would usually retrieve it upon their return. Only one male was ever observed feeding nestlings; this occurred when a male brought prey to the nest while the female was already feeding one nestling. After unsuccessfully offering the prey to the occupied female, the male proceeded to feed the second nestling himself.

Prey delivery and the feeding of nestlings

Prey delivery to nests displayed two distinct peaks in frequency over the course of the day (Fig. 4.1): the first at 0600 - 0800 h, just after sunrise and the second just prior to sunset. Deliveries during the middle of the day were less frequent.

Differences in the number of prey items delivered to nests throughout the day differed significantly ($\chi^2_{16} = 87.5, p < 0.0005$). Deliveries of four of the five different dietary groups taken by pairs within the study site – Lagomorphs, Small ground prey, Small birds, Large birds and Reptiles (See M^cDonald *et al.* in press for definitions), as well as prey which could not be identified, followed the same general daily pattern (all $p < 0.05$; Fig. 4.1). Large birds were the exception ($\chi^2_7 = 10.7, p = 0.15$), although this is likely an artefact of low sample size. Nestlings were often fed from cached prey remains before sunrise; final daily feeds were often conducted after sunset. During rain periods prey deliveries were rare.

First hatched birds were not fed until the day after hatching, although nestlings hatched later in the sequence were fed earlier, as they received food during the eldest

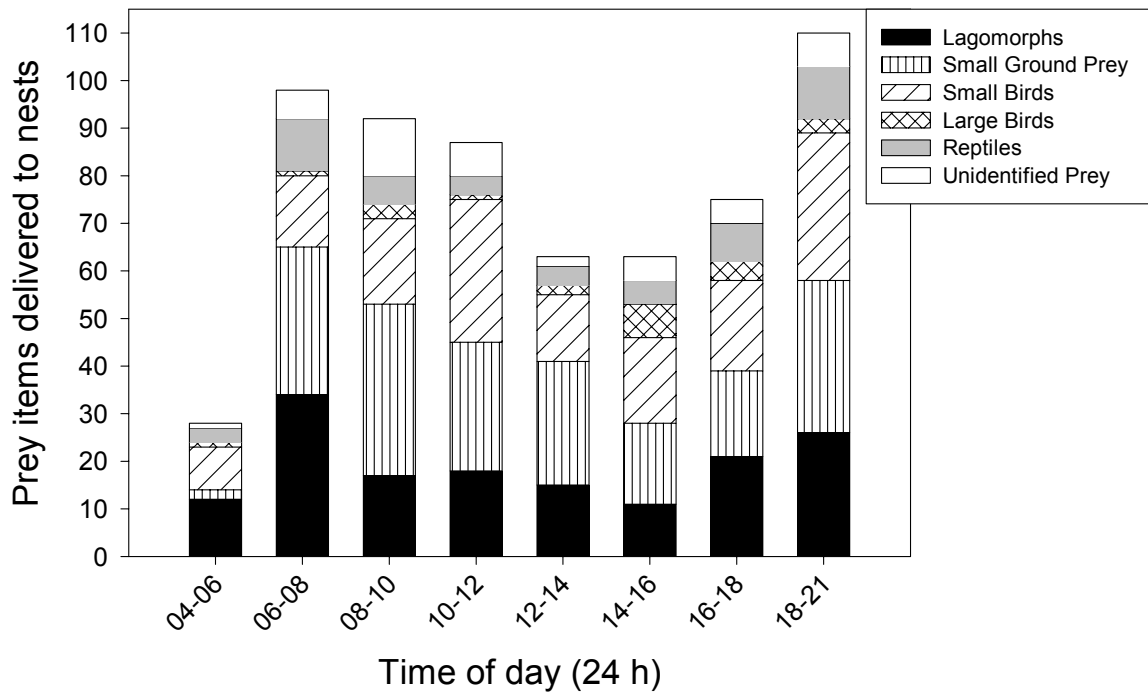


Figure 4.1. The number and timing of 616 prey deliveries made to 27 brown falcon nests monitored for 48 h with nest surveillance cameras. Legend indicates category of prey item delivered, according to five dietary groups defined by M^cDonald *et al.* (in press) and unidentified prey. Numbers in parentheses indicate total number of prey items recorded.

chick's first feed. When feeding young, females generally ate the intestines, feet, fur, large bones and feathers of prey items, giving progressively larger and coarser pieces of prey to nestlings as they grew. Once nestlings were two weeks old females began giving smaller prey items to them whole. At this age chicks could either swallow the prey in its entirety or break off smaller pieces unaided. Chicks were brooded constantly until 10 - 14 days old, coincident with the development of a thick woolly down (M^cDonald in press). When not brooding, females usually remained perched within 100 m of the nest, although this distance increased as nestlings' aged. Females were generally within site of young right up until independence was gained, responding to perceived threats, such as my presence, more quickly than males. Nestlings were still brooded overnight until about 25 days old, when feathers had emerged over much of their bodies (M^cDonald in press). Females slept in the nest until their chicks fledged. Once fledged, young on several occasions roosted in a corvid nest close to their nest tree, however fledged offspring were not observed returning to the natal nest.

When females arrived at the edge of the nest with prey, nestlings older than seven days would jostle for position closest to the female, with birds older than three weeks generally holding out their wings to keep brood mates away from food. In larger broods nestlings at the back of nests pushed their way forward closer to the female, however, bills or talons were not used against other siblings. Older nestlings intercepted food from the female more easily than younger nestlings as they had a longer reach. Once satiated, chicks would sit back down on their tarsi, allowing hungrier chicks to move forward and receive any remaining food. When nestlings began breaking prey up into manageable pieces by themselves, nestmates would use

their bills and talons to attempt to grab prey from each other. Once all prey was consumed, nestlings which were not being brooded huddled together during periods of cool weather or lay on their side with legs stretched out during hotter parts of the day.

When begging, fledglings assumed a similar posture to females receiving courtship feeds, with the head and shoulders held low and forward, wings slightly open, the body parallel to the ground and the tail lowered, giving a trilling call throughout. Both sexes delivered prey to fledged young, but males did so more often. Most food was given to fledglings whole, however, occasionally large prey would still be broken up for recently fledged birds. In one case a fledgling, recently independent, begged with fledglings from another brood and received food from the male territory holder. This brood parasitism was observed over several days without any sign of aggression from the territory owners. Likewise, recently independent young were also observed begging from territory holding birds other than their parents in December and January, without any sign of aggression towards the intruding young.

Fledglings normally drifted further and further away from the nest area before obtaining independence of their own accord, however, parental aggression was observed in two cases. An adult female tail-chased and swooped her young in the week prior to independence, striking them on two occasions. In another instance, an adult male flew very fast and straight at his begging fledgling 300 m away. A tail chase ensued, with the adult bird pulling out of the chase after the fledgling landed in a small tree.

Interspecific interactions

An area of up to 500 m from the nest site was aggressively defended by both sexes against corvids and other raptors breeding on the study site, namely, black-shouldered kites *Elanus axillaris*, black kites *Milvus migrans*, whistling kites *Haliastur sphenurus*, brown goshawks *Accipiter fasciatus*, little eagles *Hieraaetus morphnoides*, swamp harriers *Circus approximans*, nankeen kestrels *F. cenchroides* and Australian hobbies *F. longipennis*. Defence was most intense and prolonged against wedge-tailed eagles *Aquila audax*. This latter species was often swooped at by both sexes with much calling and fast wing beats, similar to those used in territorial interactions with other brown falcons. Often, when eagles soared to a height of 100 m or so, as many as three pairs of falcons would display and direct swoops at them. Despite this interspecific aggression, nests of Australian hobbies and whistling kites were both observed within 50 m of brown falcon nests and that of a wedge-tailed eagle within 250 m. Interspecific agonistic interactions between these close nesting pairs were rarely observed unless intruders flew directly at the falcon's nest. Of the other raptor species on-site, only black-shouldered kites were observed initiating attacks against brown falcons. This species did so frequently throughout the entire year. One brown falcon was observed taking a recently caught house mouse from a kite in an act of mid-air kleptoparasitism.

Discussion

Displays, aggression and breeding behaviour

Throughout the entire year both sexes of brown falcon pairs aggressively maintained territorial boundaries, with physical contact between combatants frequently recorded. The high level of agonistic interactions in this population may reflect the high

density of breeding birds present in the study area; in two out of the three years this population was monitored densities were the highest on record (McDonald *et al.* in press). Given this, territories on-site are likely to be highly sought after and this perhaps may explain the level of agonistic interactions observed. The intersexual displays observed were similar to those that have been described previously (Baker-Gabb 1982; Debus 1991; Bollen 1993; Marchant and Higgins 1993). However, by monitoring a population of banded birds this study was able to determine that females displayed less frequently than males. This was particularly evident in examination of side-slipping and U-displays, with females rarely giving these displays unprompted.

In contrast, females were frequently involved in agonistic disputes, with the one case of a 'cartwheeling' flight involving two females. These flights in raptors are considered by some researchers to be primarily aggressive in nature (Simmons and Mendelsohn 1993). This was apparently so in two recorded cases of male Tasmanian brown falcons cartwheeling (Mooney in Simmons and Mendelsohn 1993), although Hollands (1984) reported one instance involving a male and female apparently related to courtship. The incident reported in this paper appears aggressive in nature as it involved two females from adjacent territories, occurred in the approximate area where these territorial boundaries met and both individuals returned to the centre of their respective territories after the interaction.

Courtship feeding was commonly observed prior to the laying of eggs in this population, and this behaviour has been described previously by Baker-Gabb (1982). The sole use of house mice as prey during courtship feeds is interesting given the

wide range of prey taken by the population (M^cDonald *et al.* in press). Perhaps heavier prey items do not allow males to perform the side-slipping display when delivering prey to females, overriding any advantage of delivering a larger biomass. Alternatively, delivering smaller amounts of food more frequently throughout the day, thus increasing the number of interactions between members of a pair, may cement pair bonds and help coordinate reproductive activities more efficiently than less frequent deliveries of larger prey (Hamerstrom 1979; P. Olsen pers. comm.).

The high level of nest defence directed at other raptor species by brown falcons has been commented upon previously (Baker-Gabb 1982; Marchant and Higgins 1993), although this study extends the list of species repelled. Some pairs nested in relatively close proximity to other raptors, with a subsequent reduction in the area defended around nests, demonstrating that interspecific aggression did not limit nesting opportunities. Aside from corvids and some small passerines, black-shouldered kites were the only species routinely observed directing aggression towards brown falcons, with these small kites the only raptor recorded in the falcon's diet (M^cDonald *et al.* in press). One instance of kleptoparasitism was also recorded between a brown falcon and black-shouldered kite. Despite brown falcons being known pirates of many other species (Baker-Gabb 1984a), this is apparently the first reported instance of kleptoparasitism involving a black-shouldered kite.

Parental care and sex role partitioning

Yearly differences in the time devoted to nestling and post-fledging parental care might have been expected, according to the prevailing conditions and subsequent survival prospects of young (Korpimäki and Lagerström 1988; Hakkarainen and

Korpimäki 1994; Verhulst and Hut 1996). However, none of these relationships were apparent. The one significant relationship observed was a seasonal decline in the period of post-fledging parental care, a trait that has been described in other raptors previously (e.g. Bustamante and Hiraldo 1990).

Distinct sex role partitioning during parental care was also evident, with males supplying most of the food prior to eggs being laid until chicks were old enough to control their own body temperature. Females on the other hand undertook the bulk of incubation and brooding activities, feeding young and remaining close to the nest, presumably to protect offspring. This sex role differentiation has been noted in most other raptor species (Newton 1979; Marchant and Higgins 1993; Olsen 1995).

Prey deliveries to nests peaked in late afternoon and early in the morning, just after sunrise. This is in keeping with results previously reported for several pairs of brown falcons observed from hides (Baker-Gabb 1984*b*; Marchant and Higgins 1993). The comparatively low delivery rate observed by Bollen (1993) may be a consequence of most watches being undertaken in mid-afternoon, a period of infrequent prey delivery in this study. Female brown falcons frequently cached larger prey items if chicks could not consume them in one sitting. Caching behaviour has been noted previously in some brown falcons (Mooney 1982; Bollen 1993; Marchant and Higgins 1993); this study demonstrates that the practise is widespread and common throughout the entire breeding season. Caching has also been observed in many other falcons (Holthuijzen 1990; Cameron and Olsen 1993), where its main function is apparently to reduce hourly fluctuations in food availability. This is likely to apply to brown falcons, as cached prey was usually used to feed offspring immediately prior

to sunrise and after dark, periods when hunting was not likely to be successful. This strategy regularised food intake, particularly early after hatching when feeds were comparatively small and frequent, similar to the situation reported in peregrine falcons *F. peregrinus* (Cameron and Olsen 1993).

The feeding of fledged offspring from another brood, or brood parasitism/adoption, has not previously been reported in brown falcons, although the behaviour has been noted in many other bird species, including several raptors (Bustamante and Hiraldo 1989; Frumkin 1989). The high density of the population studied (M^cDonald *et al.* in press) may bring recently independent offspring into contact with other broods more often than usual. If adults could not recognise their own fledglings, this behaviour would increase the likelihood of brood parasitism occurring, although the ultimate factors driving this behaviour remain unclear (Bustamante and Hiraldo 1989).

Thus the breeding behaviour of brown falcons appears very similar in many respects to that of other members of the *Falco* genus, although vocalisations and territorial displays were given more frequently than is typical (cf. Marchant and Higgins 1993). While this may be an artefact of the dense population studied, other brown falcon populations, which are distributed more sparsely, also vocalise and display frequently (P. Olsen pers. comm.). As brown falcons occur at a high density throughout their range, particularly for a large falcon (Blakers *et al.* 1984), this behaviour may be a mechanism by which territory boundaries can be maintained and enforced with little risk of injury to combatants.

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**Chapter 5 – Territory fidelity, reproductive success and prey choice
in the brown falcon *Falco berigora*: a flexible bet-hedger?**



Plate 5.1. An unbanded adult male brown falcon from the focal population. Photo courtesy of Ian Montgomery.

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Abstract

The brown falcon *Falco berigora* is one of Australia's most common and widespread raptors, inhabiting a broad array of habitats and most climatic zones across Australia. We monitored a large, marked population (44 - 49 pairs) over three annual breeding seasons in southern Victoria. Reproductive parameters such as clutch size and the duration of parental care were constant across years. However, there were marked differences in brood size and the proportion of pairs breeding. Both sexes of falcons were found to have high territory and mate fidelity, with only 10% of members of each sex changing territories during the study. Falcons were flexible in their choice of nest sites, using a variety of tree species and even isolated nest trees. Nest sites and territories were regularly distributed throughout the study area, with the density of the population the highest on record for this species. The diet of the population as a whole was very broad, but each pair predominantly specialised on either lagomorphs, small ground prey, small birds, large birds or reptiles. Individuals that changed territory within the study area also switched their diet according to the predominant land-use within the new territory and thus prey availability. We argue that, at the population level, broad dietary breadth, flexibility in choice of nest site, and a conservative, static breeding strategy allows the species to persist in a broad range of environments, possibly through 'bet-hedging'. At the individual level, changeable dietary specialisation, high territory fidelity, strong year-round territorial defence, confining breeding to years when individual conditions were favourable and adjusting brood sizes when required appear to be the main strategies enabling brown falcons to thrive under a variety of conditions.

Introduction

The brown falcon *Falco berigora* is one of Australia's most common raptors, being the most widely reported species in a five-year survey of Australia's avifauna (Blakers *et al.* 1984). Moreover, throughout virtually all of its range, historical or contemporary breeding records exist (Blakers *et al.* 1984; Marchant and Higgins 1993). This large range, which includes a substantial breeding population in New Guinea, encompasses such diverse habitats as open woodland, alpine shrublands, deserts, swamp areas and coral cays, covering all altitudinal and rainfall zones throughout Australia (Marchant and Higgins 1993).

Despite this widespread distribution, which includes the environmentally unpredictable arid and semi-arid zones, the behaviour and life history of brown falcons appears to exhibit features often associated with k-selected species (Stearns 1992). For example, Australia-wide, it is generally sedentary (Marchant and Higgins 1993), lays a small relatively invariable clutch (Olsen and Marples 1993) and has a long life expectancy with delayed maturity (McDonald 2003). These characteristics are usually portrayed as an adaptation to an equable environment (e.g. Stearns 1992).

Bet-hedging has been suggested as an addition to the traditional r-k continuum (Slatkin 1974; Philippi and Seger 1989) and, as for r-selection, is predicted to be favoured in environments which vary from year to year in an unpredictable manner. Bet-hedgers have conservative life history characters similar to those of k-selected species, but for a different reason. Bet-hedgers are proposed to avoid risk by minimising variance in reproductive success at the expense of the mean, whereas k-selected species seek to maximise the value of the mean (Philippi and Seger 1989;

Stearns 1992). By minimising variation in production each year, bet-hedgers may sometimes raise fewer offspring in a good season than is possible. However, over the lifetime of an individual this conservative strategy is predicted to be a successful hedge against extreme losses (Slatkin 1974; Philippi and Seger 1989; Boyce *et al.* 2002), thereby maximising an individual's *lifetime* reproductive success and fitness.

Despite its widespread distribution, with the exception of studies by Baker-Gabb (1982, 1984*a,b*) and a review of the scattered, mainly anecdotal literature (Marchant and Higgins 1993), the reproductive and foraging ecology of the brown falcon has received little attention. Here we present the results of an intensive study of the reproductive success, pair and site fidelity, and diet selectivity of a large population of colour-marked brown falcons. Although a definitive test of the bet-hedging hypothesis is beyond the scope of the study, we use the results to argue that the brown falcon's conservative reproductive strategy is aimed at minimising variation in reproductive success. Coupled with plasticity in their use of resources, a risk-averse life history strategy allows the species to persist under an exceptionally wide range of climatic regimes showing marked variation in predictability.

Methods

Study area and general field methods

The study was conducted between July 1999 and June 2002, approximately 35 km southwest of Melbourne, at the Western Treatment Plant (WTP), Werribee (38°0'S 144°34'E), adjacent Avalon Airport (38°2'S 144°28'E) and small areas of surrounding private land. Details of the study site have been described elsewhere (Baker-Gabb 1982, 1984*a*). Four main habitat types defined by the principal land-

use exist in the study area: *Land filtration*, *Grass filtration*, *Untreated pasture* and *Lagoon* areas. All but Untreated pasture areas are confined to the WTP, with Land and Grass filtration areas regularly irrigated with wastewater. Land filtration areas are grazed by livestock, keeping grasses short and the habitat open, whereas Grass filtration areas are not, being dominated by thick fields of tall grass. Lagoon areas contain few trees and are dominated by reed beds and large water bodies that manage peak daily and inclement water flows in the WTP. Untreated pasture areas are routinely grazed, resembling Land filtration areas in habitat, but are not irrigated.

During the study, falcons were captured with bal-chatri and modified goshawk traps (Bloom 1987) and fitted with a unique combination of coloured bands and a metal service band, before being released at the point of capture. Nestlings raised in the study area were also colour-banded at an appropriate age (M^cDonald in press *a*). To identify territorial and pair relationships, banded birds were actively sought and their location plotted on 1:50 000 maps. Using these observations and behavioural interactions between birds, members of pairs and territory boundaries were established. Small numbers of unbanded birds were identified as remaining on the same territory from year to year based upon unique plumage characters.

Reproductive parameters

The following parameters of nest trees were recorded: tree species, tree height (m), relative nest height (nest height as a percentage of tree height), species that constructed chosen nests, nest aspect and whether chosen trees were the tallest within 100 m. Nest locations were plotted on 1:50 000 maps and the location of the nearest nest calculated at the end of each breeding season. Nest trees were climbed if

possible and the length and breadth of eggs measured to the nearest 0.01 cm with vernier callipers, at the longest and widest point, respectively. Nests were visited daily until clutches were complete. Egg volume was estimated using the formula: $0.51 \times \text{length} \times (\text{breadth})^2$ (Hoyt 1979). If not observed directly, laying date of the first egg for each nesting attempt was estimated in two ways. First, if eggs failed to hatch, the time since eggs were laid was estimated using a formula based on daily loss of egg weight during incubation (Olsen unpubl. data). If eggs hatched, laying date was estimated using an incubation period of 36 days (M^cDonald in press *b*) and estimating chick age if unknown using formulas in M^cDonald (in press *a*). Following hatching, nests were visited weekly to determine the number of birds that successfully fledged from each nest. A nesting attempt was classed as beginning following the laying of the first egg, and as successful if at least one nestling fledged.

Dietary diversity

The diet of pairs of brown falcons was assessed by collecting fresh pellets from under known roosts or nest sites, opportunistically recording direct hunting observations, collecting remains present in nests and identifying remains of prey present on captured falcons (e.g. feathers/fur stuck to talons). Pellets were assessed by hand and the minimum number of individual prey items present recorded.

During the breeding seasons of 2000 and 2001, more intensive diet assessments were made using nest surveillance cameras placed at nests for 48 h periods throughout the nestling phase. Small cameras with infrared lights (Model 43150674; Radio Parts Group, Melbourne) were connected to time-lapse video recorders (Hitachi VT1200E; Radio Parts Group, Melbourne) powered by deep cycle batteries (Besco N70T;

Battery World, Canberra). Recorders were run at 1/8 normal speed, which minimised visits to the nest tree to 24 h intervals to change batteries and tapes. The number and identity of all prey items brought to nests was subsequently identified from recorded footage.

Biomass of prey items was determined using average body weights for individuals of each species taken (Appendix 9.1). No wastage factors were incorporated as brown falcons routinely cache larger prey items (Mooney 1982; M^cDonald in press *b*); figures therefore represent captured biomass. Prey items were excluded from analyses if they were obscured from cameras or the observer (3.2% of observations) and could therefore not be satisfactorily identified. The remaining items were identified, if possible, to species or order level (invertebrates). Vertebrate prey not fully resolved (4.4%) were assigned the mean biomass of all prey items of that group, e.g. unidentified small passerines were estimated to weigh 40 g (Appendix 9.1). The size of items that obviously differed in length and weight, for example snakes, were estimated relative to falcon length and the biomass captured adjusted as indicated in Appendix 9.1.

Statistical analyses

Logistic regressions were used to determine the significance of yearly differences in the proportion of pairs occupying territories, attempting to breed or which were successful. One-way ANOVAs were used to assess yearly differences in continuous reproductive parameters such as nest site characteristics and clutch size. *Post hoc* analyses were subjected to a Bonferroni correction. The mean nest site aspect was calculated according to Zar (1996), with Rayleigh's *z* statistic used to determine the

statistical significance of this angle. The G -statistic of Brown (1975) and Brown and Rothery (1978) was used to assess the regularity of nest spacing. Contingency tables were used to identify differences in the proportion of prey items detected using different observation techniques, sexual differences in fidelity, as well as year and land-use effects upon dietary diversity. Levins' Index (Levins 1968) was used to calculate the breadth of the falcon's diet, $B = 1/\sum p_i^2$, where p_i equals the proportion of a particular prey group in the diet. Indices were standardised using the formula: $B_{STA} = (B_{obs} - B_{min})/(B_{max} - B_{min})$, where $B_{obs} = B$ as calculated above, $B_{min} = 1$ and B_{max} the maximum possible niche breadth (Colwell and Futuyma 1971). In addition, we determined the degree of dietary overlap between different pairs of falcons using Pianka's index ($O = \sum p_i q_i / (\sum p_i^2 / \sum q_i^2)^{-2}$; Pianka 1973). This index ranges from 0 (no overlap) through to 1 (complete dietary overlap). Finally, geometric mean prey weights were calculated following the methodology of Marti *et al.* (1993). All calculations were carried out using SPSS for Windows v 9.0 (SPSS Inc., Chicago). The study methodology was approved by the Australian National University Animal Experimentation Ethics Committee (Registration No. F.BTZ.02.99).

Results

Reproductive success across seasons

The proportion of territories occupied in each of the three breeding seasons was not significantly different (Wald statistic = 0.83, $df = 1$, $p = 0.36$; Table 5.1); however, only in 2001 were unpaired birds present on territories. Yearly differences were detected in the proportion of pairs which attempted to breed (Wald statistic = 10.98, $df = 1$, $p < 0.001$), with fewer pairs laying eggs each subsequent season studied

Table 5.1. Density, nearest nest distances, *G*-statistics, laying date, clutch characteristics and productivity of nesting attempts of a brown falcon population monitored over three seasons.

Mean \pm SE shown where appropriate, values within columns followed by different letters in superscript are significantly different ($p < 0.05$).

Year	No. pairs present	Area surveyed (km ²)	Density (km ² /pair)	No. breeding pairs	Nearest nest distance (m)	<i>G</i> -statistic	Lay date 1 st egg (Sept)	Clutch size	Clutch volume (cm ³)	No. pairs successful	Mean number of fledged young	
											Per breeding pair	Per successful pair
1999	45	143.9	3.2	40	1164.9 \pm 66.6	0.78	11 th \pm 2.5	2.5 \pm 0.1	-	29 ^a	1.8 \pm 0.2 ^a	2.5 \pm 0.1 ^a
2000	49	156.8	3.2	38	1274.3 \pm 73.9	0.78	15 th \pm 2.2	2.5 \pm 0.1	105.1 \pm 5.4	19 ^b	1 \pm 0.2 ^b	2 \pm 0.2 ^b
2001	44	156.8	3.56	26	1457.5 \pm 77.3	0.88	19 th \pm 2.2	2.5 \pm 0.1	105.8 \pm 5.8	13 ^b	1 \pm 0.2 ^b	1.9 \pm 0.2 ^b
All	-	-	-	-	-	-	15 th \pm 1.4	2.5 \pm 0.06	105.4 \pm 3.9	-	-	-

(Table 5.1). Similarly, pairs also tended to be more successful in the first year of the study (Wald statistic = 3.92, $df = 1$, $p = 0.048$; Table 5.1).

Mean lay dates were later with each season sampled, but again this trend was not significant ($F_{2,101} = 2.86$, $p = 0.06$; Table 5.1). Clutch size was unaffected by year ($F_{2,84} = 0.11$, $p = 0.90$; Table 5.1). All but two pairs laid a clutch of two or three eggs. Similarly, clutch volume did not differ between the 2000 and 2001 seasons ($F_{1,42} = 0.01$, $p = 0.93$; Table 5.1). The mean number of chicks fledged per nesting attempt was greater in 1999 than in later seasons ($F_{2,101} = 6.43$, $p = 0.002$; Table 5.1), as was the number of young fledged per successful nesting attempt ($F_{2,58} = 5.55$, $p = 0.006$; Table 5.1). Most chick mortality appeared to be due to either starvation, as chicks that perished gradually lost weight over a prolonged period before dying, and/or exposure during severe spring storms. Following several bouts of prolonged rain and cold windy weather many nests were abandoned in 2000 and 2001.

However, two clutches and one brood were also lost following the collapse of nests.

Nest site characteristics

Brown falcons do not construct their own nest; of the 104 nesting attempts observed most involved the appropriation of little raven *Corvus mellori* nests (92.3%). Smaller numbers of nests built by whistling kites *Haliastur sphenurus* (2.9%), Australian magpies (1.9%), wedge-tailed eagles *Aquila audax* (1%) and brown goshawks *Accipiter fasciatus* (1%) were used. One pair in 1999 laid eggs in a natural cup of cypress pine *Cupressus macrocarpa* foliage; this clutch was blown to the ground within a few days of laying. Pairs preferred to nest in the tallest tree available within their territory (77.9%). This preference was higher than that of the nest tree species

chosen, with similar numbers of pairs using sugar gums *Eucalyptus cladocalyx* (24%), cypress pines (22.1%), monterey pines *Pinus radiata* (20.2%), various exotic *Eucalyptus spp.* present on-site (14.4%) and a variety of other species (33.7%).

Mean nest tree height was $11.7 \text{ m} \pm 0.3\text{SE}$ ($n = 104$; range 6 – 20 m), nests used within chosen trees were usually the highest available, with relative nest height 83.7% (range 47 - 100%) across all years. Nest aspect relative to the trunk differed significantly from random (Rayleigh's $z = 5.01$; $z_{\text{crit},0.05,120} = 2.99$, $p < 0.01$), with a mean angle of 74° (c. ENE). However nests were found through all aspects ($10 - 350^\circ$) and those used within 45° of the mean angle were not more successful ($\chi^2 = 4.02$, $df = 3$, $p = 0.26$). The biological significance of this angle is thus questionable. Nests were occasionally re-used the following year (5.8%) and, in one case (1%), in all three years of the study, but were rarely intact for more than one season.

Nest spacing and nesting density

Mean distances between the nesting attempts of different pairs in the same year did not differ between 1999-2000 and 2000-01 ($F_{1,56} = 0.19$, $p = 0.67$), averaging $416 \text{ m} \pm 60\text{SE}$. Most pairs (60.3%) moved less than 300 m and 70.7% moved less than 500 m between subsequent nesting attempts in different years ($n = 58$). In every year of the study nests were spaced more regularly than expected by chance (G -statistic > 0.65 ; Table 5.1), although nearest nest distances increased as the study progressed, reflecting fewer nesting pairs each year. Densities of territory holding birds were very high, with one pair on average every 3.2 to 3.6 km^2 throughout the study period (Table 5.1).

Pair and site fidelity

Most birds were captured throughout the study, with 83 - 90% of female and 78 - 87% of male territory holders banded each season. Pairs occupied all-purpose territories throughout the entire year. Of the 45 pair bonds identified at the beginning of the study in 1999, 35.6% were observed for one season only (1999), 35.6% lasted two seasons (1999 and 2000), while 28.9% remained intact at the studies conclusion (at least three seasons). These figures should be treated as minima as some pairs may have been established for a considerable period before the study began. Between breeding seasons the majority of pairs stayed together (Table 5.2).

Territory fidelity for each sex was even higher, with no sexual differences evident ($\chi^2_4 = 1.04$, $p = 0.90$; Table 5.2). Few birds changed territory, thus the figures for birds remaining on the study site year after year were similar to those remaining in the same territory (Table 5.2), again without differences according to sex ($\chi^2_4 = 3.95$, $p = 0.41$).

Falcons rarely moved territory once recruited and pair bonds were usually only ruptured following the 'death' of a pair member. Mortality in this sense probably includes some undetected emigration. Only six males (10%) and six females (9.7%) were recorded changing territories, with five birds moving once and one bird twice for each sex. The high level of territory fidelity in this species is further demonstrated when the 1999 cohort alone is examined. Nearly half (44.4%) of males and 40% of females were still on the same territory after three seasons, whereas the figures for fidelity to the study site were 55.3% for males and 44.7% for females.

Table 5.2. The proportion of colour-banded brown falcon pairs remaining faithful, and individuals of both sexes remaining on the same territory or within the study site, from one breeding season to the next.

Breeding seasons	<i>n</i>	Prop. pairs faithful	Prop. birds on same territory		Prop. birds remaining on study site	
			Males	Females	Males	Females
1999-2000	45	0.64	0.78	0.76	0.80	0.80
2000-2001	49	0.41	0.53	0.57	0.61	0.63

Recruitment, philopatry and age at first breeding

Nine nestlings were observed returning to the study site as immatures, eight of which were successfully recruited into the breeding population. This gives a recruitment age of two years for females ($n = 4$) and $1.8 \text{ years} \pm 0.25\text{SE}$ for males ($n = 4$). None of these birds managed to breed in the year that they were recruited, a year when productivity was comparatively low for the study population. Interestingly, while none of the females recruited obtained territories close to where they were raised, one male took over a territory adjacent to, and another his actual natal territory. Further, two adult male falcons banded as nestlings prior to this study were on their natal territories at 16 and 18 years old.

Diet – all pairs

In all, 765 prey items were recorded over a total of 87 pair years using all collection methods, of which 740 items were identified (Appendix 9.1). A small number of observations were made outside of the breeding season. Exclusion of these samples did not change the results reported and they were retained in analyses. The method of data collection can influence the relative importance of prey items recorded in the diet of raptors (Collopy 1983; Marti 1987; Simmons *et al.* 1991; Redpath *et al.* 2001; Sharp *et al.* 2002), combining results from pellet analysis and remains collected at nests has been argued to alleviate this bias (Simmons *et al.* 1991). Thus, all data were retained to maximise sample sizes.

Forty-one different prey (mostly different species) were identified in the falcon's diet. Five species constituted 67.4% of the total prey items recorded: rabbits, house mice, European starlings, Richard's pipits and silver gulls (see Appendix 9.1 for

specific names). The importance of rabbits became more apparent when figures were converted to biomass, with rabbits alone accounting for 61.8% of the total biomass captured. Along with silver gulls (7.8%), blue-tongued lizards (5.1%), European starlings (4.9%) and eastern tiger snakes (3.4%), rabbits composed 82.9% of the total biomass captured. With the exception of unidentified prey and carrion (< 5% of 765 records), all prey items recorded belonged to one of five distinct dietary groups:

Lagomorphs, composed entirely of rabbit kittens, *Small ground prey*, mainly rodents, invertebrates and small skinks, *Small birds*, mainly passerines c. 40 g, *Large birds*, mainly non-passerines such as feral pigeons and silver gulls, and finally *Reptiles*, comprised mainly of blue-tongued lizards and eastern tiger snakes.

Each dietary group presents different problems for falcons in detection, capture and handling, reflected in the main methods used by falcons to catch each group. These were, based on observations of hunting birds and using the terminology of Fox (2001): Lagomorphs: short glide attacks or drops from low perches; Small ground prey: located by hovering in one location before a dive or drop was used to capture the prey; Small birds: long tail-chases, direct or indirect flying attacks, usually ending in a stoop or with falcons binding to the prey; Large birds: short, direct tail chasing and binding to prey or more rarely killing prey with a stoop; Reptiles: short glide and drop or stalked on foot.

Classifying prey into these functional dietary groups generated standardised dietary breadth figures of 0.721 based on abundance and 0.319 using biomass figures, with a geometric mean prey weight of 77.03 g. While the level of prey identification does affect dietary breadth calculations (Greene and Jaksić 1983), this is not a major

factor in this study, as different pairs did not take different species from within each dietary group.

Diet – comparisons between pairs

Each pair of brown falcons consistently took the bulk of prey items from one dietary group; pairs were therefore classified accordingly. For 71 pairs (82%), the proportion of prey items taken from the classified dietary group was at least 50% (mean 67.4%; range 50 - 100%); for the remaining 16 pairs this figure was 35.4% (range 23 - 46%). Yearly differences in the proportion of pairs taking large prey (Lagomorphs, Large birds or Reptiles) versus small prey (Small ground prey and Small birds) were not apparent ($\chi^2 = 0.22, p = 0.9$). Territories on either Land filtration or Untreated pasture areas tended to have a similar distribution of dietary groups within them (Fig. 5.1), and as such were combined to satisfy contingency table requirements. The dominant land-use regime of each territory significantly affected the dietary group taken by pairs of falcons ($\chi^2_8 = 25.68, p = 0.001$). Pairs preying upon Lagomorphs were more often found in Land filtration or Untreated pasture territories, whereas Small ground prey was most frequently taken in Grass filtration territories and Lagoon regions (Fig. 5.1). Large birds were mostly taken in Lagoon regions, while Small birds were preyed upon throughout. Reptiles were only taken in Land filtration or Untreated pasture territories (Fig. 5.1). This association between prey choice and land-use is further evident when the diets of the twelve birds which changed territories during the study is examined. All of these individuals were found to have the same diet as the territory's previous occupant, involving a switch from a different prey group in 10 cases (five of each sex).

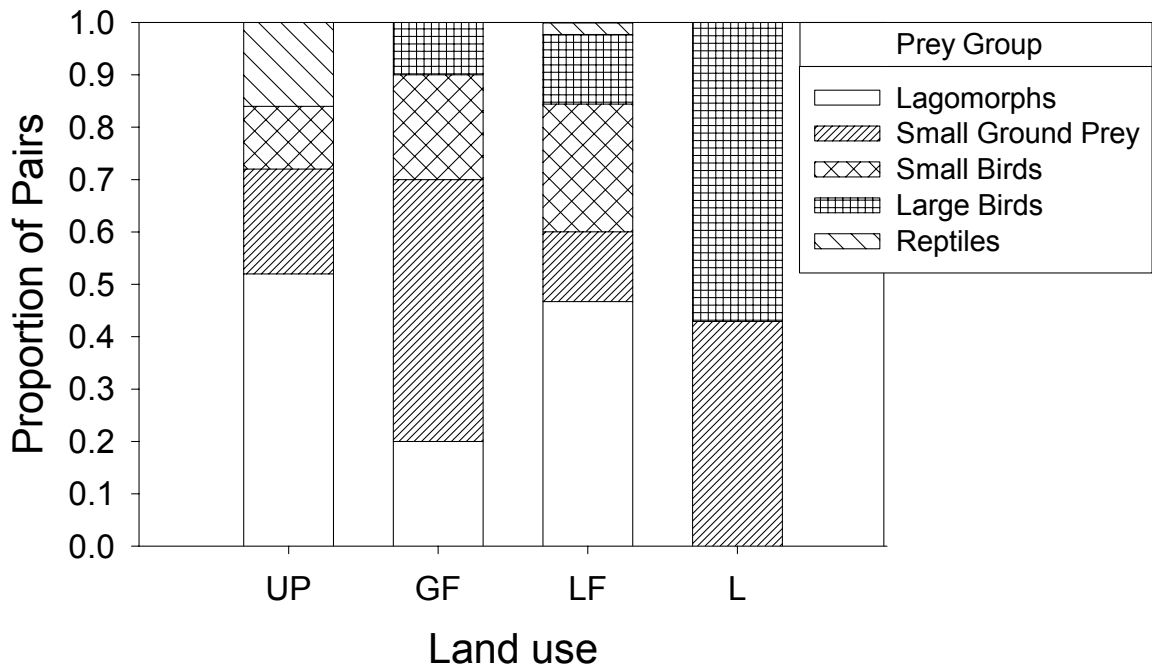


Figure 5.1. The proportion of brown falcon pairs taking one of five dietary groups within each of four different land-use regimes in the study area. Land-use key: UP: Untreated pasture ($n = 25$), GF: Grass filtration ($n = 10$), LF: Land filtration ($n = 45$) and L: Lagoon areas ($n = 7$). See methods for explanation of land-use regimes.

Dietary overlap in terms of abundance between pairs taking different dietary groups was minor (Table 5.3), with all but three comparisons having less than c. 50% overlap. Surprisingly, the diet of pairs mainly taking Lagomorphs overlapped the most with those pairs taking Small ground prey (58%) and Small birds (61%). Those taking Small birds and Large birds had the highest dietary overlap between all combinations (Table 5.3), although even this figure can be considered moderate. Overlap indices based on biomass figures were generally even lower than those of abundance, ranging from 15 - 44% for all but three comparisons (Table 5.3). The exceptions with a higher degree of overlap were those taking Lagomorphs and smaller prey items (Table 5.3). This affinity in biomass figures is due to the relative size differences between each prey item, as identified by the mean prey weights of each group (Table 5.4). Pairs taking smaller prey needed only a small number of rabbits in their diet to account for large proportions of total captured biomass (Fig. 5.2).

Discussion

Reproductive success

Over the three years of the study brown falcons had a small, rather invariable clutch, regardless of changing conditions. Moreover, mean laying dates were very similar from year to year, with the population breeding annually in mid-September. This contrasts with the r-strategy of some other raptors living in highly variable environments, which tend to vary their clutch and breeding season markedly according to seasonal and regional conditions, following fluctuations in their prey (e.g. Newton 1979; Korpimäki and Wiehn 1998).

Table 5.3. Proportion of dietary overlap based on abundance (% total prey taken) and biomass (% total weight captured) of pairs of brown falcons predominantly taking one of five different dietary groups.

Values close to 0 represent no overlap, values close to 1 indicate complete overlap.

Dietary groups		Biomass				
		Lagomorphs	Small ground prey	Small birds	Large birds	Reptiles
Abundance	Lagomorphs	-	0.98	0.91	0.26	0.38
	Small ground prey	0.58	-	0.92	0.33	0.44
	Small birds	0.61	0.42	-	0.29	0.42
	Large birds	0.48	0.50	0.74	-	0.15
	Reptiles	0.47	0.46	0.46	0.40	-

Table 5.4. The geometric mean prey weight and prey to predator weight ratios of different pairs of brown falcons classified as predominantly taking one of five dietary groups.

Dietary Group	No. pairs	Mean prey weight (g)	Prey/predator weight ratio (%)
Lagomorphs	36	170.5	29.21
Small ground prey	19	43.1	7.38
Small birds	16	74.6	12.78
Large birds	11	132.7	22.73
Reptiles	5	160.5	27.49

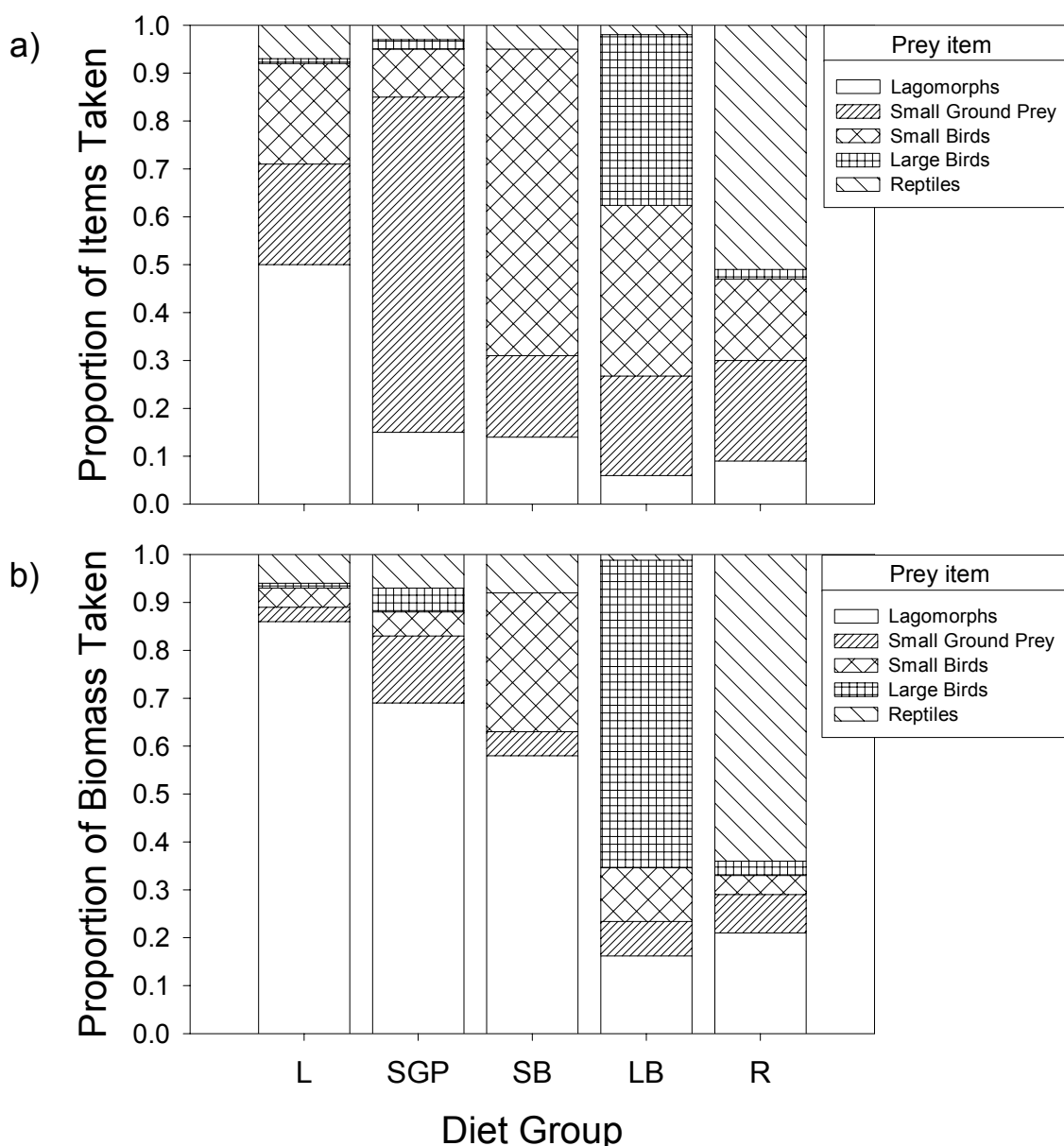


Figure 5.2. The proportion of prey items in the diet of different pairs of brown falcons according to: (a) abundance (% of total number of prey items taken) and (b) biomass (% total captured biomass). Pairs were classified as predominantly taking either Lagomorphs (L; 240 prey items, 69.4 kg biomass), Small ground prey (SGP; 184 prey items, 20.3 kg biomass), Small birds (SB; 129 prey items, 15.6 kg biomass), Large birds (LB; 126 prey items, 24.3 kg biomass) or Reptiles (R; 47 prey items, 9.7 kg biomass).

In areas where short-term conditions are unpredictable, an increased mean clutch size may allow more young to be raised in good years, however in poor years the effects could be detrimental. According to the theory of bet-hedging, a conservative mean clutch size may be the most productive over several seasons (Philippi and Seger 1989). It appears that at Werribee unpredictable spring storms were an important factor influencing reproductive failure during the study (Chapter 6), yet in all years clutch size was unaffected by conditions. When storms were severe (2000 and 2001), lower brood sizes were raised or breeding was abandoned altogether, while in 1999, the most successful year of the study, more pairs raised three chicks. Nevertheless, while a greater number of chicks were fledged per successful pair in 1999, this breeding strategy was in keeping with the predictions of the bet-hedging model, with a steady clutch size and a mean difference between the best and worst years of just 0.6 offspring fledged per successful pair. We will present evidence elsewhere that reductions in brood size were not a passive process due to low food availability, but rather involved the selective allocation of resources according to sex and hatch order amongst the brood (Chapter 8).

By contrast an r-strategist, the other commonly mooted strategy to cope with unpredictable environments, would be predicted to strive for the maximum clutch size possible under the circumstances (regardless of the risk) and would be expected to show a much greater variability than was observed, that is, large clutches in 1999 and small clutches in 2000 and 2001, and/or large losses in the latter two storm-plagued years.

Nest-site selectivity

Brown falcons preferred to use the nests of little ravens, a species abundant in the study area (Baker-Gabb 1984a). This preference did not limit breeding opportunities, as nests of other species were utilised if raven nests were unavailable. Falcons preferred nests in the tallest trees available, as do most tree-nesting raptors (Cade 1982; Marchant and Higgins 1993; Aumann 2001a; Sharp *et al.* 2001), however the species of tree chosen was subject to availability. The falcons readily used single, isolated nest trees, allowing them to breed in territories which contained just one large tree. This flexibility enabled them to breed in many areas of the study site that were not utilised by other raptors.

Pair and site fidelity

The brown falcon population had a high degree of mate and territory fidelity throughout all years of the study, perhaps as a consequence of the density of birds in the area. Densities and nearest nest distances were the highest, and smallest, respectively, reported to date for brown falcons (Baker-Gabb 1982, 1984a,b; Marchant and Higgins 1993; Aumann 2001a). This is likely due to the higher soil productivity of the study area, which in turn may influence food availability (Village 1982; Newton *et al.* 1986). Taken together with the large non-breeding population of falcons at Werribee (nearly one-third of falcons captured during this study were part of the floating population, M^cDonald unpubl. data), competition for breeding territories on the study site was likely to be intense. Indeed, agonistic interactions over territorial boundaries involving both sexes are frequently observed throughout the year (Baker-Gabb 1982; M^cDonald in press *b*). Given this, a dearth of gaps in the breeding population and a high probability of having their territory usurped may

have prevented birds from prospecting for better territories. The timing of most observed movement supports this hypothesis, as most (58%) occurred in 2001, the only year territories held by single birds were observed, indicating low numbers of birds in breeding condition at that time. This is consistent with a risk averse strategy, with falcons choosing to stay on their current territory, even following reproductive failure, rather than attempting to pair with a better mate and risk losing their current territory.

In contrast to many other raptors (Newton *et al.* 1983; Village 1985; Korpimäki 1988; Court *et al.* 1989), in which males are more site tenacious than females, sexual differences in brown falcon territory fidelity were not apparent. Most individuals of both sexes occupied the same territory year after year, even following breeding failure. In addition, high site philopatry was also observed, particularly amongst males, which often returned to or were adjacent to their natal territory. Higher male philopatry is common in birds (Greenwood 1980; Greenwood and Harvey 1982; Plissner and Gowaty 1996), however, the high return rate of female brown falcons to the study area is unusual in comparison with most raptors (Mearns and Newton 1984; Village 1985; Korpimäki 1988; Warkentin *et al.* 1991). As the sex which defends resources is likely to be more philopatric (Greenwood 1980), perhaps the high level of territorial defence provided by male and female brown falcons (M^cDonald in press *b*) favours high fidelity in both sexes, again with both sexes apparently hedging their bets, at least within this dense population. Rather than risk the all or nothing scenario of finding either no new partner or a better one, both sexes appear to be minimising annual variation in reproductive success by choosing to stay on the same territory with the same mate.

Dietary diversity

Most prey items were recorded during the breeding season, which may explain the comparatively high geometric prey weights of this study, as small invertebrate prey were more frequently recorded outside the breeding season in other studies (Baker-Gabb 1984*a,b*; Marchant and Higgins 1993; Aumann 2001*b*). No effort was made to separate prey captured by the different sexes. However, obvious sexual differences in the type of prey consumed were not apparent. Males routinely captured large rabbit kittens, the largest prey recorded. Many were too big for males to carry in flight; these were either eaten on the ground or butchered before being delivered to nests. Further, geometric mean weight of prey items delivered to nests did not steadily increase throughout the nestling period as females increased their hunting effort (M^cDonald *et al.* unpubl. data), a relationship expected if females routinely captured larger prey items than males.

Overall, the population had a very broad diet ($B_{STA} = 0.721$), with significant numbers of prey items taken from such diverse groups as mammals, reptiles, birds and invertebrates. By comparison, most falcons have a relatively narrow diet breadth (Marchant and Higgins 1993; Marti *et al.* 1993), with many concentrating on one size class of bird or mammal (Hector 1985; Steenhof and Kochert 1988; Sergio and Bogliani 1999; Aumann 2001*b*). Brown falcons did prey heavily upon rabbit kittens, and the importance of this introduced mammal in the diet of brown falcons (Baker-Gabb 1984*b*) and other Australian raptors (Marchant and Higgins 1993) has been noted previously. Indeed, the timing of brown falcon reproduction was closely tied to the availability of young rabbits; mean laying dates in this study coincided with the emergence of young rabbits from burrows, while nestling periods correlated with

peak numbers of kittens recorded during standardised road-counts (M^cDonald unpubl. data). Moreover, all commonly taken species recorded in the diet of this population were either introduced (rabbits, house mice, European starlings) or native species present in high densities due to the land-use regime (Richard's pipit, silver gulls). The implications of this for the management of this species are clear, particularly given recent reductions in numbers of breeding pairs following the introduction of rabbit calicivirus disease in some areas (RCD; Falkenberg *et al.* 2000).

Some authors have previously suggested that particular brown falcon pairs may specialise on small birds (Mooney 1989) or snakes (Sonter and Debus 1985; cf. Aumann 2001*b*), however this study is the first to quantify between pair differences in diet. The strong differences observed between pairs in such a relatively small area (c. 150km²) demonstrates the great dietary flexibility of the brown falcon, and cautions against generalisations derived from small diet samples of this and other species. In fact, overlap figures between pairs were, with the exception of one comparison, well below the 70% figure chosen by Marti and colleagues (1993) for grouping different *species* of raptors as predatory guilds. Further, overlap figures were also low in comparison with other interspecific dietary studies of predatory guilds (Clarke *et al* 1993; Aumann 2001*b*), further indicating the functional difference of pairs taking different prey items.

Between pair differences in dietary diversity are likely to be a response to differences in prey availability and/or vulnerability, as evident in the diets of raptor populations from different regions (Jaksić and Braker 1983; Collopy and Bildstein

1987; Arroyo 1997). Differences in prey taken in this study appear largely due to land-use type and not individual preference, as the falcons that moved territory also switched diet composition to that of the territory's previous occupant. This combination of extreme flexibility in diet and hunting technique, which would tend to stabilise fluctuations in prey availability for the population, with individual specialisation to suit the resources of each territory, also fits the predictions of the bet-hedging hypothesis in that both strategies minimise variability in prey availability. This variation however also leads to a reduction in the populations mean reproductive success as pairs which specialise upon Small ground prey and Small birds tend to have a lower reproductive success than those preying upon other prey items, particularly Lagomorphs. The affect of this reliance upon prey items of markedly different sizes will be examined elsewhere (Chapter 6).

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Chapter 6 – Weather dictates reproductive success and survival in the Australian brown falcon *Falco berigora*



Plate 6.1. A brood of three brown falcons approximately three and a half weeks old. Centre nestling is female, outer two male. Youngest brood member on far left, eldest far right.

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Abstract

We examined the influence of parental age, pair-bond duration, prey size and weather conditions on various measures of reproductive success and survival of a sedentary brown falcon *Falco berigora* population that was virtually free from predation and human persecution. Pairs on territories that enabled them to capture large prey items were more likely to initiate breeding. Females taking larger prey items experienced higher mortality rates when they bred late in the season, whereas those taking smaller prey had a greater probability of survival when laying later in the season - relationships likely linked to opposing seasonal differences in prey availability. Interannual differences were by far the most influential variable assessed, affecting almost every reproductive success parameter and female survival. Pairs on-site in the first year of the study were more successful breeders and had greater survival prospects than those present in the latter two seasons. This pattern corresponds strongly to the observed frequency of heavy rain downpours and implicates these events as the main cause of reproductive failure and mortality amongst adult females. These detrimental effects were likely due to an increased chance of chilling, exposure and starvation for chicks and parents alike. The importance of unpredictable climatic variables in shaping the reproductive success and survival of brown falcons and raptors from other regions indicates that, in the absence of significant nest predation, weather, in this case in the form of heavy rain, may well be the most important factor influencing long-term reproductive success in this group.

Introduction

Food has long been thought to be one of the main factors influencing the reproductive success of birds (Lack 1954; Perrins 1970; Daan *et al.* 1986). This relationship has been well demonstrated for raptors (Newton 1986; Korpimäki and Norrdahl 1991; Simmons 2000), and is supported by experimental evidence (Newton and Marquiss 1981; Meijer *et al.* 1989; Wiehn and Korpimäki 1997).

More recently, the influence and importance of other factors has attracted research attention. For example, in many birds older breeders are more successful than younger ones, although this pattern is sometimes followed by a period of senescence before death in older individuals (see Clutton-Brock 1988; Sæther 1990; Martin 1995 for reviews). Avian pairs re-forming or maintaining past pair-bonds have also been observed to have greater reproductive success in comparison with newly formed pairs (Fowler 1995), perhaps due to increased coordination of parental care activities within the pair (Yamamoto *et al.* 1989). While this phenomenon often operates in conjunction with increasing parental age, pair-bond duration has been shown to have a greater (positive) effect on the likelihood of breeding success than age alone in some species (Bradley *et al.* 1995).

Abiotic factors also play a significant role in shaping the reproductive ecology of many avian species, including raptors. Significant impacts of inclement weather on the breeding of a variety of birds of prey have been observed (e.g. Olsen and Olsen 1988, 1989*a,b*; Potapov 1997; Steenhof *et al.* 1997, Steenhof *et al.* 1999; Dawson and Bortolotti 2000), prompting some authors to suggest that weather may be the

most important factor influencing reproduction in this group (Kostrzeaw and Kostrzeaw 1990; Krüger 2002).

Most of these studies have focused on the influence of a small number of variables in isolation and few have examined potential interactions. Moreover, most studies on raptors have examined species which are either migratory (e.g. Newton 1986; Dawson and Bortolotti 2000) or have a very narrow diet breadth (e.g. Korpimäki and Hakkarainen 1991; Krüger 2002; Laaksonen *et al.* 2002). Austral raptors tend to be more sedentary than their northern hemisphere counterparts and their populations generally suffer little predation (Marchant and Higgins 1993). Thus, they might be expected to differ from better-known northern species in the relative importance of various determinants of reproductive success.

We examined several factors likely to influence the reproductive success of the Australian brown falcon *Falco berigora*, a medium sized falcon (males: 486 g \pm 5SE, $n = 69$; females: 658 g \pm 7SE, $n = 91$) which maintains all-purpose territory boundaries and pair-bonds year-round (M^cDonald in press *a*; M^cDonald *et al.* in press). The population studied has a very catholic diet, due to differences in prey availability mediated through changes in the principal land-use regime of each territory. Thus, within the study site neighbouring pairs take the majority of prey items from distinctly different prey-size groups (M^cDonald *et al.* in press). Average geometric mean prey weight of items captured ranges from 155 g for pairs taking larger prey (e.g. rabbits *Oryctolagus cuniculus*) to just 59 g for pairs taking smaller prey (e.g. passerines and house mice *Mus musculus*). Smaller prey is not delivered to nests at a significantly different rate to large prey (M^cDonald in press *a*), resulting in

fewer resources available for reproduction and subsistence among pairs taking small prey. Hence, the opportunity existed to compare the survival and reproductive success of pairs with access to widely different resource levels. Previous raptor studies have shown that within species, pairs with predominantly large prey in their diet performed better in various measures of reproductive success than those taking mainly smaller prey (Holthuijzen 1990; Slowtow and Perrin 1992; Olsen *et al.* 1993; Swann and Etheridge 1995).

This chapter aims to investigate the impact of prey size, pair-bond duration, parental age and weather on various measures of reproductive success of the brown falcon. Lastly, evidence suggests that lifespan is one of the most important influences upon lifetime reproductive success in several bird species (Thomson *et al.* 1996), including raptors (Newton 1989; Krüger 2002). Thus, the relationship between the above factors on year to year survival of both sexes was also modelled.

Methods

Study area and general field methods

The study was conducted between July 1999 and June 2002, approximately 35 km southwest of Melbourne in southeast Australia, at the Western Treatment Plant, Werribee (38°0'S 144°34'E), adjacent Avalon Airport (38°2'S 144°28'E) and small areas of surrounding private land. Details are given elsewhere of the c.150 km² study site (Baker-Gabb 1984) and study population (M^cDonald 2003; in press *a,b*; M^cDonald *et al.* in press).

Reproductive parameters

Each breeding season all nests within the study area were found and their contents determined by climbing to the nest or through the use of a mirror pole. Eggs were measured to the nearest 0.01 cm with vernier callipers at the longest and widest point, and volume estimated using the formula: $0.51 \times \text{length} \times (\text{breadth})^2$ (Hoyt 1979). Once clutches were complete, *Mean egg volume* was determined for each clutch. If not observed directly, laying date of the first egg for each clutch, hereafter *Lay date*, was estimated using formulas to estimate the time-lapsed since laying or the age of hatched nestlings (see M^cDonald in press *b* for details). When clutches were close to hatching, nests were visited regularly to determine *Brood size*, the number of eggs that hatched successfully. Following hatching, nests were visited weekly to determine the number of birds which survived to fledge; nesting attempts were deemed to be a *Success* if at least one offspring fledged. To correctly assign sex to each nestling, a small blood sample (c. 10 - 20 μL) was collected from each nestling's alar vein and a Polymerase chain reaction (PCR)/*HaeIII* digest reaction used (Griffiths *et al.* 1998). Sex ratios of broods were determined at both hatching and fledging. Chicks were colour banded when approximately 28 days old, allowing the subsequent identification of each chick successfully fledged.

Pair characteristics

The size of prey taken by each pair was determined using the methods of M^cDonald *et al.* (in press). Briefly, data collected from nest surveillance cameras, prey remains, direct hunting observations and pellets showed that each pair within the study area predominantly took either *Large prey* (e.g. lagomorphs, gulls, elapid snakes) or *Small prey* (e.g. rodents, small passerines and invertebrates).

Falcons were captured with bal-chatri and modified goshawk traps (Bloom 1987) and fitted with a unique combination of colour bands and a metal service band before release at the point of capture. From plumage characteristics the age of each member of the pair was determined (Weatherly *et al.* 1985; M^cDonald 2003) and they were classified as possessing either adult (not acquired until at least 4 years old) or immature plumage (birds range from 2 - 4 years old).

By identifying banded territory holders the number of years pair-bonds were maintained was also determined, hereafter referred to as *Experience*. By definition experience was unknown in the first year of the study, restricting examination of this variable to data from 2000 and 2001. *Survival* of male and female territory holders was also determined by monitoring the presence of banded individuals within the study area each breeding season. This estimate of survival probably does not account for a small degree of emigration, however brown falcons within the study area display very high site fidelity (M^cDonald *et al.* in press).

Weather

Weather data were obtained from a permanent weather station located c. 10 km northeast of the study site (Laverton Royal Australian Airforce Base, 37°51'S 144°44'E). To obtain a daily index of conditions we subjected mean daily maximum and minimum temperatures (°C), wind speed (m sec⁻¹) and total precipitation (mm) details from this station to a principal components analysis, extracting two components. In this analysis we used weather data around the clock for each 24 h period, because brown falcons use stick nests (M^cDonald *et al.* in press) and are constantly exposed to the prevailing conditions. The first component (hereafter

Temperature) explained 42.7% of variation in the dataset. High values are indicative of days with a high maximum and minimum daily temperature, whereas lower values indicate cooler weather. The second component (hereafter *Rain/wind*) explained 31.5% of variation in the dataset, with low values representing calm, dry periods and high values days with strong winds and high rainfall. In addition we recorded the number of *rain days* - characterised as receiving at least 4 mm of precipitation. In all, 10.6% of the 1230 days assessed in the study were scored as rain days, with each rain day receiving on average $10.7 \text{ mm} \pm 10.3 \text{ SD}$ of precipitation.

Statistical analyses

General linear regressions and generalised linear models with a binomial error distribution (Genstat Committee 1993) were used to assess relationships between reproductive success and the various pair- and weather-related parameters described above. All main effects and biologically meaningful two-way interactions were initially entered into models before terms were dropped sequentially. The significance of terms was then assessed using the change in deviance statistic derived when each term was dropped. If this value was significant, terms were retained until a final parsimonious model was obtained. All calculations were carried out using Genstat 5 Release 4.21 (Genstat Committee 1993). For simplicity only significant interactions are presented in tables. The study methods were approved by the Australian National University Animal Experimentation Ethics Committee (F.BTZ.02.99).

Results

Analyses were constrained in two ways. First, temperature estimates were positively correlated with Julian lay date during the breeding season ($F_{1,101} = 121.8$; $p < 0.001$; $R^2 = 90.7$). Given this, where appropriate, we have used lay date in models in place of temperature. Second, interannual differences in weather conditions were modelled using the term *Year*, as weather conditions were similar in the last two seasons sampled. Little difference existed in mean temperature scores over the three seasons, however, in the first year of the study conditions were clearly much drier than the others, experiencing far fewer rain days (Fig. 6.1). Interannual differences were therefore highly correlated with these changes in the number of rain days recorded.

Further, because immatures had a lower reproductive success and survival than adults in most aspects assessed in this study (Table 6.1), it was necessary to control for age separately. Due to low sample sizes of breeding pairs containing at least one immature bird, analyses reported here are restricted to those assessing pairs comprised of adults only.

Interannual differences in reproductive success and survival

The breeding activities of 100 adult-adult pair years were assessed, with clutches initiated by 93 pairs. Significant interannual differences were apparent in most aspects examined: pairs breeding in 1999 were more likely to fledge at least one nestling, lay earlier and had a greater probability of hatching their clutch or fledging nestlings in comparison with subsequent breeding seasons (Fig. 6.2a-d; Table 6.2). Indeed, interannual differences were apparent in every facet of reproductive success examined except clutch size and the probability that breeding was initiated (Table

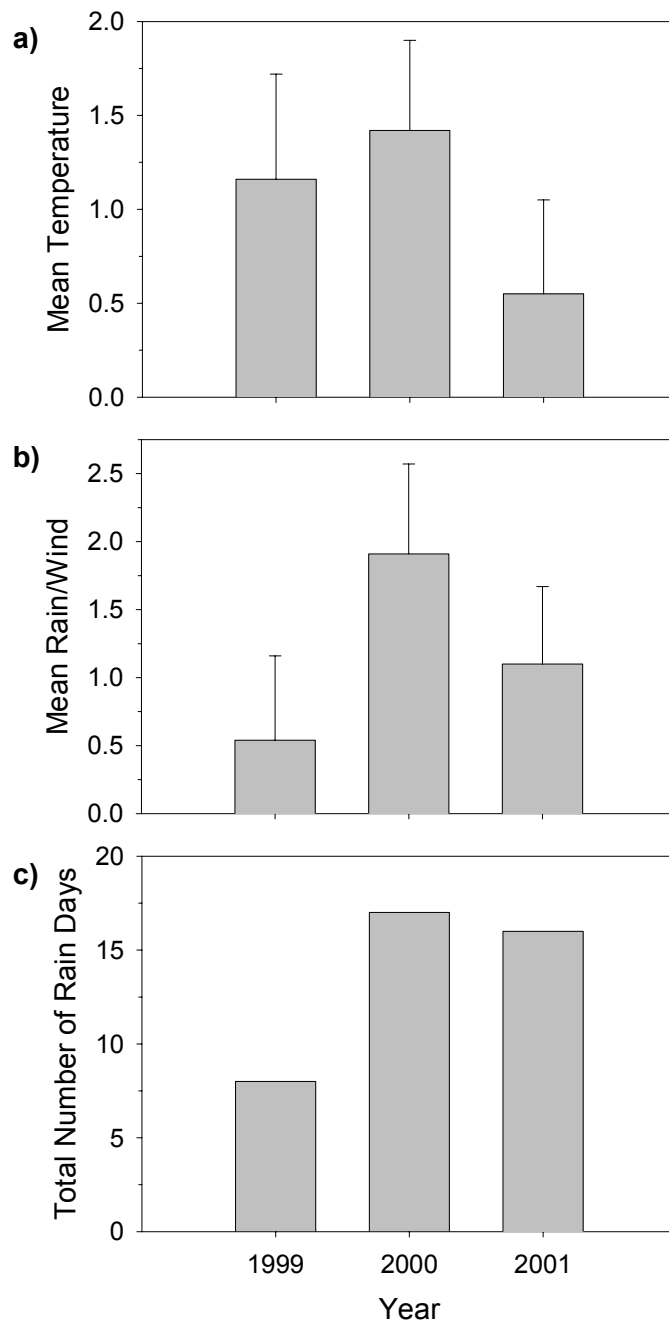


Figure 6.1. Mean daily prevailing weather conditions during the three breeding seasons (1 September – 30 November; $n = 91$ days per year) sampled in this study. Temperature and rain/wind scores are derived from a principal components analysis, larger values indicate warmer (temperature) and wetter and windier conditions (rain/wind), respectively. Rain days were defined as a 24 h period receiving at least 4 mm of rainfall. Error bars indicate \pm one standard error.

Table 6.1. The influence of age on reproductive success and survival of the brown falcon. Statistics indicate significance of contingency table or general linear model analyses.

Variable	Immature	Adult	Significance of age difference	
Partner age	Mainly immature	Both ages	$\chi^2_1 = 34.0$ $p < 0.001$	
Prey size	Mainly small prey	Large and small prey	Males: $\chi^2_1 = 12.5$; $p < 0.001$	Females: $\chi^2_1 = 10.1$; $p = 0.001$
Probability of breeding	Low	High, usually initiate a clutch	Males: $\chi^2_1 = 51.9$; $p < 0.0001$	Females: $\chi^2_1 = 43.4$; $p < 0.0001$
Lay date	Late	Full range	$F_{1,103} = 5.48$; $p = 0.02$	
Survival to next season (territory holders only)	Low	Full range	Males: $\chi^2_1 = 7.5$ $p = 0.01$	Females: $\chi^2_1 = 1.8$ $p = 0.19$

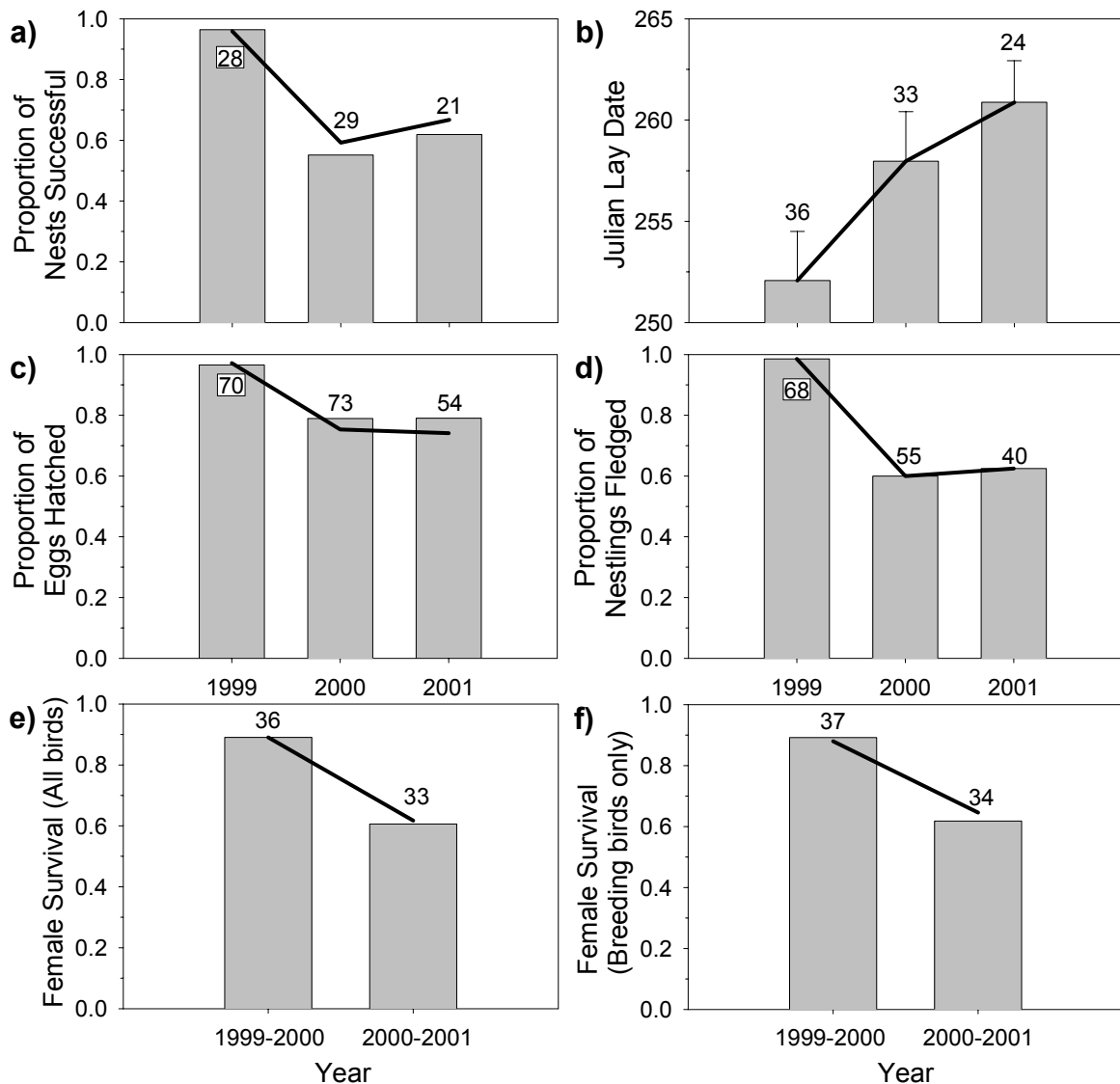


Figure 6.2. The influence of year upon the reproductive parameters: (a) success (fledging at least one nestling); (b) Julian lay date; (c) the probability of a given egg hatching; (d) the probability of a given nestling fledging; and the survival of (e) all female falcons on-site and (f) those that bred. Lines indicate model predictions (Tables 6.2, 6.3), whereas columns and numbers indicate means (\pm one standard error in b) and sample sizes of actual data.

Table 6.2. Summary of factors influencing adult brown falcon pairs: (a) probability of attempting to breed; (b) Julian lay date; (c) clutch size; (d) probability of any given egg hatching; (e) probability of any given nestling fledging and (f) probability of successfully fledging at least one nestling. Data modelled using generalised linear models with binomial error distributions (*a, d-f*) or general linear models (*b,c*); figures indicate the change of deviance statistic associated with each term; significant terms emboldened.

Term of interest	df	Change in deviance	<i>p</i> value
<i>a) Attempt to breed</i>			
Model: Probability of attempting to breed = -1.66 (if small prey) + 3.45			
Prey size	1	4.16	0.041
Year	2	3.80	0.15
Experience	1	1.46	0.23
<i>b) Lay date</i>			
Model: Lay date = 2.91 (in 2001) – 5.89 (in 1999) + 257.97			
Year	2,92	3.46	0.036
Prey size	1,90	3.87	0.052
Experience	1,89	2.04	0.16
<i>c) Clutch size</i>			
Lay date	1,77	3.19	0.078
Hatching sex ratio	1,24	1.05	0.32
Year	2,76	0.76	0.47
Mean egg volume	1,25	0.22	0.64
Experience	1,73	0.02	0.89
Prey size	1,72	0.02	0.89
<i>d) Probability of a given egg hatching</i>			
Model: Prob. of hatching = 2.02 (if 1999) + 0.01 (if 2001) - 0.04 (Julian lay date) + 12.47			
Year	2,76	10.8	0.005
Lay date	1,75	8.35	0.005
Clutch size	1,74	2.27	0.14
Mean egg volume	1,36	1.75	0.19
Experience	1,72	1.63	0.21
Hatching sex ratio	1,60	1.56	0.22
Prey size	1,73	1.17	0.28
<i>e) Probability of a given nestling fledging</i>			
Model: Probability of a given nestling fledging = -3.8 (if 2000) – 3.69 (if 2001) + 4.2			
Year	2,68	19.82	<0.0001
Hatching sex ratio	1,62	3.94	0.052
Brood size	1,66	3.71	0.058
Lay date	1,65	2.37	0.13
Experience	1,63	0.43	0.51
Prey size	1,64	0.25	0.62
<i>f) Probability of successfully fledging at least one nestling</i>			
Model: Probability of success = 0.81 (Brood size) – 2.77 (if 2000) – 2.45 (if 2001) + 1.45			
Brood size	1,75	8.78	0.0004
Year	2,76	5.50	0.006
Hatching sex ratio	1,60	2.07	0.16
Lay date	1,74	0.67	0.42
Prey size	1,73	0.08	0.78
Experience	1,74	0	1

6.2). Moreover, female survival was greater from 1999-2000 breeding seasons than 2000-01, both for all territory holders and when only breeding females were considered (Fig. 6.2*e,f*; Table 6.3*a,b*). This pattern of greater reproductive success and survival in the first year of the study, and low success/survival in latter two years of the study negatively correlated with the distribution of rain days each breeding season (Figs. 6.1, 6.2).

Brood-specific determinants of reproductive success

Beyond these interannual differences, pairs capturing large prey more often initiated breeding attempts than those taking small prey (Fig. 6.3*a*; Table 6.2*a*). Moreover, a seasonal decline in the probability of eggs hatching was also apparent (Fig. 6.3*b*; Table 6.2*d*). After eggs hatched, the probability of successfully fledging at least one nestling increased with brood size (Fig. 6.3*c*; Table 6.2*f*). Although a large number of possible influences upon clutch size were examined, none explained a significant degree of variation in clutch size (Table 6.2*c*).

The influence of factors other than year upon survival

In addition to interannual effects, breeding females taking larger prey items experienced a reduction in survival probability the later their clutches were initiated, whereas females taking small prey experienced an increase in survival probabilities if they laid later in the season (Fig. 6.4; Table 6.3*b*). Survival rates of males, both all territory holders and breeding birds alone, were independent of all variables assessed in this study (Table 6.3*c,d*).

Table 6.3. Summary of factors influencing the probability of different sexes of adult brown falcons surviving to the next breeding season: (a) all females; (b)

only females which bred; (c) all males; and (d) only males which bred. Data

modelled using generalised linear models with binomial error distributions; details as per

Table 6.2.

Term of interest	df	Change in deviance	p value
a) Female survival: All birds			
Model: Probability of female survival = -1.63 (if 2000-01) + 2.11			
Year	1	7.58	0.008
Experience	1	2.43	0.12
Attempted to breed	1	1.08	0.3
Male survival	1	0.51	0.48
Prey size	1	0.42	0.52
b) Female survival: Breeding birds			
Model: 0.12 x Lay date (if Small prey) – 30.3 (if Small prey) – 0.06 (Lay date) – 1.41 (if 2000-01) + 16.82			
Year	1	4.56	0.03
Lay date x Prey size	1	5.87	0.02
Prey size	1	0.57	0.45
Lay date	1	0.13	0.72
Success of breeding attempt	1	1.7	0.19
Hatching sex ratio	1	0.65	0.42
Male survival	1	0.37	0.54
<i>Within successful pairs only:</i> Number of young fledged	1	0.55	0.46
<i>Within successful pairs only:</i> Fledgling sex ratio	1	0	1
c) Male survival: All birds			
Experience	1	2.24	0.13
Prey size	1	1.55	0.21
Year	1	1.48	0.22
Female survival	1	1.09	0.3
Attempted to breed	1	0.89	0.35
d) Male survival: Breeding birds			
Success of breeding attempt	1	2.76	0.1
Prey size	1	2.12	0.15
Lay date	1	2.03	0.15
Year	1	1.52	0.22
Hatching sex ratio	1	0.2	0.65
Female survival	1	0.07	0.79
<i>Within successful pairs only:</i> Number of young fledged	1	2.71	0.1
<i>Within successful pairs only:</i> Fledgling sex ratio	1	0.21	0.65

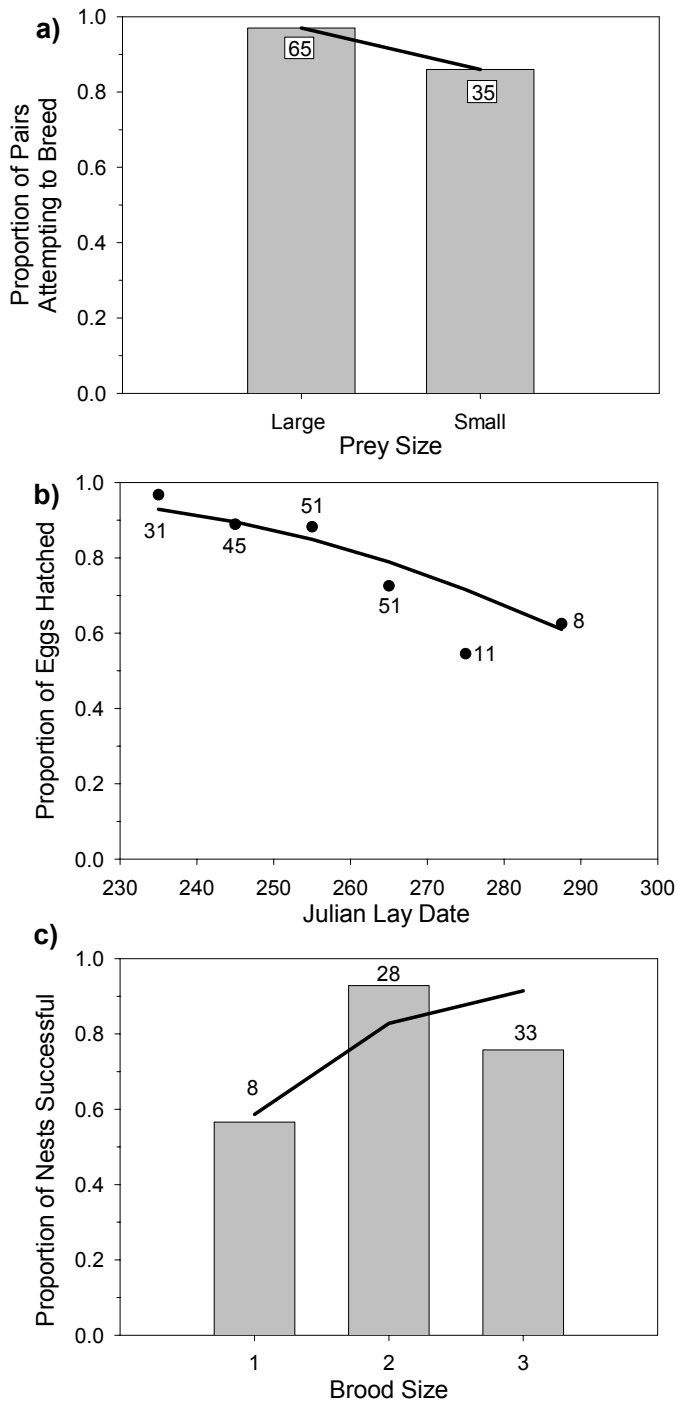


Figure 6.3. The influence of parameters other than year on: (a) the proportion of pairs initiating a breeding attempt; (b) the proportion of eggs hatched; and (c) the outright success of breeding attempts. Lines indicate model predictions for a mean year (Table 6.1), whereas columns/dots and numbers indicate means and sample sizes of actual data.

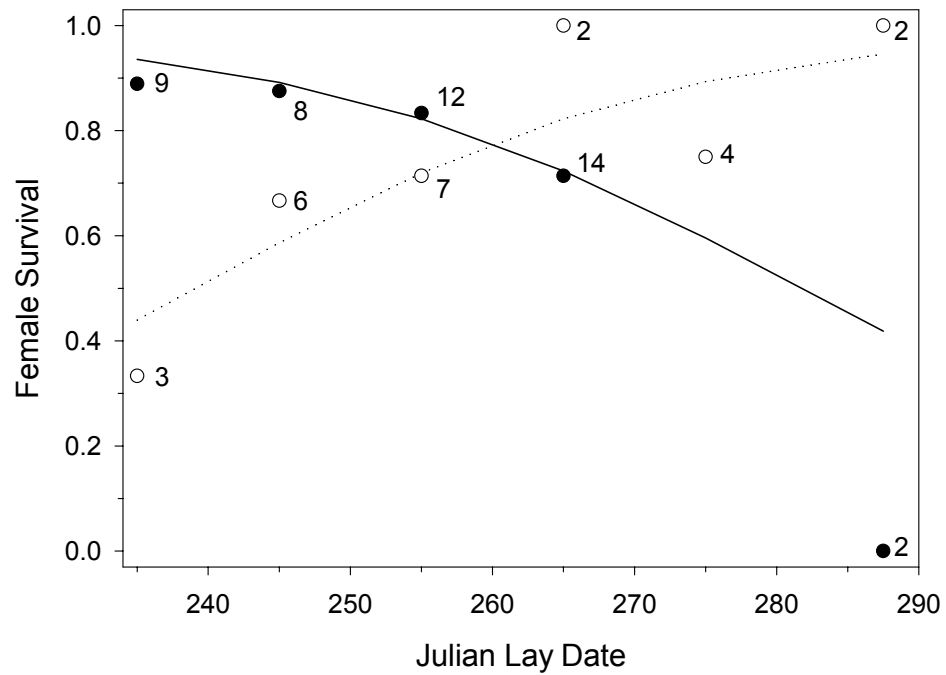


Figure 6.4. The probability that a breeding female will survive until the next breeding season according to prey size and Julian lay date of the breeding attempt for a mean year. Lines indicate model predictions (Table 6.3) and dots proportions of actual data. Females taking large prey are depicted by unbroken lines and solid circles, those capturing small prey dashed lines and open circles. Numbers indicate sample sizes.

Discussion

Adult brown falcons of both sexes had greater reproductive success and survival probabilities than their immature counterparts in the study population. When the breeding activities of pairs containing adults only were examined, pairs which were able to capture larger prey items were more likely to initiate breeding. Beyond these age and prey size effects, a seasonal decline in the probability of eggs hatching was also observed, in common with the seasonal productivity declines well known in other raptors (e.g. Daan *et al.* 1986; Korpimäki and Wiehn 1998). However, interannual differences were by far the most pervasive influence upon pair reproductive success and female survival. Pairs breeding in the 1999 season fared better than those in the two subsequent seasons, which both experienced relatively poor levels of breeding success and survival. On examination of yearly climatic variables, 1999 was clearly a relatively dry year with few storms in comparison with the other two seasons. Thus it appears that weather, primarily heavy rain, was the most important determinant of reproductive success and female survival in the study population. Density dependent effects were not assessed in this study, however, these influences are unlikely to have affected the fecundity or survivorship of the population. In 1999, when the study population was at its densest, breeding was most productive and survival rates were high.

The influence of interannual differences upon reproductive success and survival

The number of rain days experienced explained a significant amount of variation in nearly every facet and stage of the breeding attempt as well as female survival probabilities. Negative impacts from heavy downpours are likely to affect raptors in two ways. First, indirect effects arise due to a probable decrease in hunting ability

during heavy rainfall (Newton 1978; Hiraldo *et al.* 1990; Dawson and Bortolotti 2000), thereby increasing the likelihood of starvation or a loss of condition for both nestlings and territory holders. This is a likely consequence of inclement weather in the study population as prey deliveries during rain were generally rare (M^cDonald in press *a*). Second, direct effects upon condition and survival are due to the increased levels of exposure and chilling associated with heavy rain which, when combined with indirect effects, place further stress upon offspring and parents alike. Even in the comparatively mild conditions of southern Australia, an increased number of heavy downpours is likely to have led to later lay dates, a reduced probability of clutches hatching, nestlings fledging and the breeding attempt being successful, as well as reduced survival prospects for female territory holders. The deleterious effects of heavy rain upon raptor nestlings of other species has been described elsewhere (Newton 1986; Mearns and Newton 1988; Kostrzeaw 1989; Olsen and Olsen 1989*b*; Kostrzeaw and Kostrzeaw 1990; Village 1990; Potapov 1997; Dawson and Bortolotti 2000, 2002). Taken together with previous studies in other regions, this suggests that for raptors, a group for which nest predation levels are generally negligible, heavy, unpredictable rainfall is perhaps the most influential factor on survival and fitness.

The influence of parental age and experience upon reproductive success and survival

The greater productivity of adult birds in comparison to immatures reported in this study has been observed in other bird species including raptors (Sæther 1990; Martin 1995) and may be indicative of adult birds providing more effective parental care, perhaps operating in conjunction with greater energy reserves, experience and/or

effort devoted to the breeding attempt (Forslund and Pärt 1995). For example, adult female peregrine falcons (*F. peregrinus*; Mearns and Newton 1988) and Eurasian sparrowhawks (*Accipiter nisus*; Newton and Rothery 1998) both fledge more nestlings than younger members of the same population. Lower survival prospects of younger birds have also been recorded in raptors (Newton *et al.* 1983; Picozzi 1984) and again are likely to indicate a lack of skill on behalf of younger birds, perhaps in their hunting ability (Wunderle 1991). Poorer access to prey or an inferior hunting ability may reduce food intake over critical months and thus increase immature falcon mortality when conditions are less than ideal. For example, immature male Tengmalm's owls have lower prey caches than their adult counterparts during periods of low prey availability (Laaksonen *et al.* 2002).

The complete lack of influence of the duration of pair-bonds (*experience*) and egg size upon reproductive success in this study was unexpected given the marked interannual differences observed. The poor conditions experienced in the last two years of the study would likely have highlighted any significant advantage associated with either egg size (see Martin 1987 for review) or pair-bond duration (see Wooller *et al.* 1992; Bradley *et al.* 2000 for reviews). Egg size may not have been important as most chick mortality occurred after hatching, hence small differences in initial chick size due to increased egg size may not confer a significant advantage in the face of heavy rainfall.

Recently, amongst two migratory raptors pair-bond duration has also been demonstrated to have little effect on reproductive success (Warkentin *et al.* 1991; Newton and Rothery 1998). Moreover, amongst different seabird species the

improvements associated with a longer pair-bond plateau off after several seasons, implying the coordination of a pair's activities can be accomplished at different speeds amongst different species (Wooller *et al.* 1992). Brown falcons maintain year round territory boundaries, with most turnover occurring well before the onset of breeding (M^cDonald in press *b*; M^cDonald *et al.* in press). Thus, even newly formed pairs had several months to cement pair-bonds before initiating a breeding attempt, potentially reducing the importance of past experience on current reproductive success.

The influence of prey size upon reproductive success and survival

In contrast to most other aspects of reproductive success examined, the probability of a pair attempting to breed was not related to any of the interannual differences examined, instead pairs taking larger prey items were more likely to breed. Thus access to greater resources appears to have enabled these females to reach the required threshold in body condition necessary for clutch initiation earlier in the season (as, for example, in kestrels; Meijer *et al.* 1988). Moreover, cached prey is important during periods of inclement weather for maintaining a high level of food intake (Masman 1986), and brown falcons are more likely to cache larger prey items than smaller ones (M^cDonald in press *a*). Thus pairs taking larger prey may have also had a larger 'buffer' against prey shortages. Together, these differences confer a significant advantage to pairs taking large prey, however, the effect was quantitative (in the sense of Slotow and Perrin 1992): if enough energy was available to initiate breeding, reproductive success was not further influenced by prey size. This is in contrast to the qualitative effect of large prey size upon productivity observed in

some other raptors (Holthuijzen 1990; Olsen *et al.* 1993; Swann and Etheridge 1995).

Prey size was also influential in determining the survival of breeding females, with females taking larger prey having higher survival probabilities if they laid earlier in the breeding season, whereas females taking smaller prey exhibited higher survival probabilities the *later* they laid in the breeding season. This interaction is perhaps indicative of seasonal differences in prey availability. For example, the availability of small passerines and thus smaller prey items increased with the appearance of recently fledged young towards the end of the falcons breeding season. Thus females taking smaller prey may benefit by timing breeding later in the season when conditions are more favourable. Conversely, larger prey items such as young rabbits are available relatively early in the breeding season (M^cDonald unpubl. data) and females utilising this prey source may thus benefit from an earlier lay date, perhaps giving them a longer period to prepare for winter after their young reach independence.

Parameters not exhibiting interannual differences

The influence of interannual differences was so marked on virtually all aspects of reproductive success and survival that areas not exhibiting these effects are worthy of further examination. Clutch size was not related to any factor examined in this study, and the probability of a pair attempting to breed was also unrelated to interannual differences, and thus presumably the presence of heavy rainfall. One likely explanation is that this lack of seasonal differences is a consequence of the apparent bet-hedging reproductive strategy of the brown falcon (M^cDonald *et al.* in

press). The species appears to lay a constant, moderate clutch size each season regardless of prevailing conditions, adjusting brood size downwards through selective parental allocation later in the season if necessary. The subsequently low, inflexible clutch size resulting from this behaviour is thus not likely to be further influenced by climatic conditions at the time of clutch formation. The probability of clutch initiation is largely determined by a female's access to food (Meijer *et al.* 1988) and thus prey size is more likely to be influential than relative short bouts of inclement weather early in the breeding season as discussed above.

Male survival, in contrast to female survival, was also unrelated to interannual differences, both for breeding and non-breeding birds. One explanation for this is the distinct sex role differentiation evident in most raptors (Newton 1979; Marchant and Higgins 1993) and indeed this species (McDonald *in press a*). Female raptors contribute the vast bulk of incubation and brooding activities, thus for brown falcons using stick nests, exposed females may be more susceptible to a loss of condition and/or death during inclement weather. Males on the other hand are free to utilise the best available shelter on their territory, thereby increasing their survival probability and reducing the impact of storms.

There was little influence of past-breeding history on the survival of either sex, in contrast to some other avian studies (Erikstad *et al.* 1998; Green 2001); perhaps the apparent bet-hedging reproductive strategy of brown falcons (McDonald *et al.* *in press*) maintains the cost of reproductive attempts below the threshold which impairs survival to the benefit of longevity. Longevity is likely to be of critical importance in determining fitness in this species as in other raptors (Newton 1989; Krüger 2002),

particularly given the heavy influence of unpredictable storms upon reproductive success in any given year.

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Chapter 7 – Selection on body size in a raptor with pronounced reversed sexual size dimorphism: is bigger better?



Plate 7.1. Vernier callipers are used to take the culmen measurement of an adult male brown falcon from the focal population in 2001. Photo courtesy of Doris Graham.

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Abstract

An overabundance of hypotheses have been proposed to account for reversed sexual size dimorphism (RSD; females the larger sex) in raptors. Previous research principally focused upon examining interspecific patterns of RSD, rarely testing predictions of various hypotheses within populations. To redress this, we utilised data from both sexes of a large brown falcon *Falco berigora* population to evaluate the importance of size and body condition indices upon the hunting prowess of males and the reproductive success, recruitment and survival probabilities of both sexes. Female-female competition for territorial vacancies was likely to be intense as the floating population was female-biased and intrasexual agonistic interactions were frequently observed. In this competitive population larger adult females were more likely to be recruited, indicating directional selection favouring increased female body size. Further, after recruitment larger females were more likely to successfully fledge offspring, providing a mechanism by which RSD is maintained in the population. In contrast, male recruitment was unrelated to either body size or condition indices. Smaller immature males more often held their territories over two breeding seasons than their larger counterparts, however they also took small prey more frequently, a diet related to poor reproductive success. We argue that, together, these results are indicative of selection favouring an increase in female body size and a reduction or maintenance in male body size. Of all the hypotheses proposed to account for the maintenance and evolution of RSD in raptors, this scenario is consistent only with the predictions of the intrasexual competition hypothesis.

Introduction

The evolution and maintenance of sexual size dimorphism in birds has long fascinated biologists, with Darwin (1871) himself writing on the subject in his pivotal treatise. In cases of non-reversed sexual size dimorphism (NRSD), where the male is the larger sex, dimorphism has been attributed to sexual selection for larger male size and the competitive advantages this confers during competition for females (see Andersson 1994 for review). Despite this, a consensus concerning the evolution and maintenance of *reversed* sexual size dimorphism (RSD), where females are the larger sex, has yet to be reached. Indeed for the typically RSD raptors, comprised of the Falconiformes and Strigiformes, well over 20 hypotheses have been proposed (see Amadon 1959, 1975; Earhart and Johnson 1970; Snyder and Wiley 1976; Newton 1979; Andersson and Norberg 1981; Mueller and Meyer 1985; Jehl and Murray 1986; Lundberg 1986; Mueller 1986, 1990; Andersson 1994; Simmons 2000 for reviews).

Despite this, predictions arising from hypotheses have rarely been rigorously tested, particularly in intraspecific studies. Most hypotheses proposed have been based on generalisations from secondary data sources using comparative analyses. In these analyses simple single measures of body size have usually been used, with samples often separated both temporally and spatially within/between species assessed in comparisons. Unless these single structures are important in maintaining RSD, they provide limited predictive power (McGillivray 1985). A better approach may be to use principal component analyses (PCA) to generate overall estimates of size spread across several measures, keeping body mass separate to avoid biasing the PCA (Rising and Somers 1989; Alisauskas and Ankey 1990; Freeman and Jackson 1990).

Moreover, hypotheses proposed to account for RSD should have general application (Jehl and Murray 1986) and be able to explain both the direction and degree of the dimorphism (Olsen and Cockburn 1993), preferably in more than one group, a feature lacking in many hypotheses proposed to account for RSD in raptors.

In a bid to address the general lack of, and many cases limitations of, existing data in this field, we investigated the direction of selection upon body size in both sexes of a large population of colour-banded Australian brown falcons *Falco berigora*. In turn this information was then used to assess the relevance and broad applicability of the various hypotheses proposed to account for RSD in raptors.

Methods

Study area and general field methods

The brown falcon is a moderately dimorphic raptor in which adult males are typically c. 75% of female body mass, with linear measures such as wing length c. 90% those of females (M^cDonald unpubl. data). The study was conducted between July 1999 and June 2002, approximately 35 km southwest of Melbourne in south-eastern Australia, at the Western Treatment Plant, Werribee (38°0'S 144°34'E), adjacent Avalon Airport (38°2'S 144°28'E) and small areas of surrounding private land. Details of the study site have been described elsewhere (Baker-Gabb 1984), as has the study population (M^cDonald 2003, in press *a,b*; M^cDonald *et al.* in press).

Body size indices

Falcons were captured with bal-chatri and modified goshawk traps (Bloom 1987) and fitted with a unique combination of colour bands and a metal service band, before being released at the point of capture. Before their release flattened wing chord, tail length, exposed culmen, head to bill length and body mass measures were taken of all birds captured.

The diet of each pair and thus falcon was determined using the methods of M^cDonald *et al.* (in press). Briefly, each pair within the study area was found to predominantly take one of two distinct prey sizes, according to the prevailing land-use regime of each territory. Large prey items were mainly juvenile rabbits *Oryctolagus cuniculus*, with a mean geometric prey mass of 155 g, whereas small prey items weighed on average 59 g and were usually rodents, invertebrates or small passerines (M^cDonald *et al.* in press).

Captured falcons were classified as possessing either adult (not acquired until at least 4 years old) or immature plumage (birds range from 2 - 4 years old) based on banding records or plumage characteristics (Weatherly *et al.* 1985; M^cDonald 2003). Juveniles less than 2 years of age were excluded from analyses. The bare parts and front plumage of falcons were also scored for relative brightness according to M^cDonald (2003).

To obtain individual body size indices the four measurements taken at capture (excluding body mass) were analysed using a principal component analysis (PCA) for each sex. For 91 females captured (48 adults and 43 immatures), the first

component explained 44.2% of total variance and was heavily influenced by wing and tail length, hereafter *feather*. The second component explained an additional 28.2% of variance and was closely related with head to bill and exposed culmen length, hereafter *structure*. A total of 69 males were sampled during the study (41 adults and 28 immatures). A separate PCA of male size parameters yielded a first component explaining 39.9% of total variation, which was closely related to exposed culmen and head to bill size (i.e. *structure*). Wing and tail length were closely correlated with the second component, *feather*, which explained an additional 34.5% of variation. For both sexes, an index of body condition was obtained by using model II regression and extracting the residuals of a linear regression between *structure* and body mass (Green 2001), after first controlling for date of capture, thereby removing seasonal influences. For both sexes greater *feather*, *structure* and condition indices indicate larger/heavier birds.

Recruitment

The identity of all banded falcons holding territories was established each year of the study, allowing survival to be assessed and each individual to be scored as either obtaining a territory in the year of capture or remaining part of the unsuccessful floating population. Individuals no longer on the study site were presumed to have died, although a small degree of emigration is likely (McDonald *et al.* in press). The length of time individuals remained on the study site (tenure) was also determined from these data.

Reproductive parameters

During each breeding season all nests within the study area were found and their contents determined by visiting the nest or using a mirror pole. Length and breadth of eggs were measured to the nearest 0.01 cm with vernier callipers at the longest and widest point, respectively. Egg volume was estimated using the formula: $0.51 \times \text{length} \times (\text{breadth})^2$ (Hoyt 1979); once clutches were complete mean egg volume was determined for each clutch. If not observed directly, laying date of the first egg for each clutch, hereafter lay date, was estimated using the methods outlined in M^cDonald *et al.* (in press). When clutches were close to hatching nests were visited regularly to determine the number of eggs successfully hatched, that is brood size. Following hatching, nests were visited weekly to determine the number of offspring fledged and thus if the breeding attempt was successful (fledged at least one offspring). To correctly assign sex to each nestling molecular methods were used (Polymerase chain reaction/*HaeIII* digest; Griffiths *et al.* 1998). Chicks were marked at hatching and banded at approximately 28 days of age. Sex ratios of broods were determined at both hatching and fledging.

Nest defence

The responses of each pair to nest visits were recorded during the 2000 and 2001 breeding seasons. As the population is largely free of nest predators, human persecution is likely to be the only significant form of predation (M^cDonald *et al.* in press). During each nest visit PM scored the parents response as either: 0: Female flushed from nest and silently flew from view, 1: Female called briefly after being flushed, before flying from view, 2: When flushed female stayed within 50 m and within view of the nest site, 3: Both sexes attended nest area, female making

numerous swoops within 3 m of climber, 4: Both sexes swooping within 3 m of climber and 5: Physical contact made with climber by defending female.

Male quality

During the breeding seasons of 2000 and 2001 intensive assessments of prey deliveries by known (banded) males to nests were conducted using surveillance cameras (Model 43150674; Radio Parts Group, Melbourne) placed at nests for 48 h periods throughout the nestling phase. Cameras were powered by deep cycle batteries (Besco N70T; Battery World, Canberra) and connected to time-lapse video recorders (Hitachi VT1200E; Radio Parts Group, Melbourne) run at 1/8 normal speed. This setup reduced visits to the nest area to 24 h intervals to change batteries and tapes. As females began to hunt by the time the eldest chick was 3 - 4 weeks old (M^cDonald in press *b*), analyses of prey delivery were confined to the early (eldest chick 0 - 14) and mid-nestling phases (eldest chick 14 - 28 days old) when males provided the bulk of prey items. The number of and identity of prey delivered by males to each nest was subsequently identified from video footage. Each item was then assigned a mean weight from M^cDonald *et al.* (in press) and the total biomass delivered by each male per 48 h calculated.

Statistical analyses

Generalised linear models with binomial error distributions (Genstat Committee 1993) were used to assess relationships between size variables (structure, feather and condition) and binomial estimates of fitness in the year of capture, such as the probability of a bird attempting to breed and being successful once breeding was initiated, and the probability of a female successfully hatching a given egg or

fledging a nestling. Generalised linear models were used to assess the impacts of size upon tenure and continuous measures of reproductive success such as lay date and mean egg volume. As mean egg volume was not measured in all years of the study, the first clutch measured from a given female was compared to structure scores only (fixed in immature and adult birds), regardless of the year of capture. Previous research has determined that both the mortality and reproductive success of this species is influenced by factors other than body size, in particular climatic conditions and age (Chapter 6). To account for this, year of capture was included as a variable in models and both ages of each sex were analysed separately. Year was not a significant factor in any analysis reported and thus for simplicity statistics for this variable are not presented.

We utilised restricted maximum likelihood (REML) procedures to account for size influences upon nest defence and male prey delivery rates. When analysing nest defence scores we included a random model with female and nest number, with the main model including Julian nest visit date, the number of previous nest visits, nest stage (incubation, early, mid or late nestling phase) and whether either sex had experienced human interference in previous years.

A total of 387 prey deliveries by males were recorded, accounting for 57.7 kg of prey mass. A minority (4.9%) of prey items were obscured from the camera preventing identification, linear regressions predicting prey mass from the number of mouthfuls given to chicks at each age (early or mid-nestling phase) were constructed to generate mass estimates of these items. Regressions explained 42.3% (early; $F_{1,200} = 146.7, p < 0.05$, Biomass [g] = 15.5[feed duration, min] + 9.7) and 52.9% (mid-

nestling phase; $F_{1,162} = 182.0, p < 0.05$, Biomass [g] = $20.8[\text{feed duration, min}] + 26.9$) of variation in prey weight. The total biomass delivered by males per 48 h was then calculated and normalised with a square root transformation ($X' = [X + 0.5]^{1/2}$; Zar 1996) before being subjected to a REML analysis. The random model used included the variables pair, male number (randomly assigned) and the number of times focal males had been observed in each breeding season. In addition to size variables of both sexes, the main model included the terms brood reduction (death of at least one nestling), year, chick age (early or mid-nestling phase), brood size, lay date, prey size, brood sex ratio at hatching and experience (number of years pair known to have bred together).

For all analyses initial models fitted included all explanatory terms and biologically meaningful two-way interactions. Interactions and terms were then dropped in a step-wise fashion by examining the change in deviance between the full model and the sub-model fitted. The procedure was repeated until a final parsimonious model was obtained. For simplicity, interaction terms are not presented unless significant. Calculations were carried out using either SPSS for Windows v 8.0 (SPSS Inc., Chicago; PCA analyses) or Genstat 5 Release 4.21 (Genstat Committee 1993; remainder). Study methods were approved by the Australian National University Animal Experimentation Ethics Committee (F.BTZ.02.99).

Results

Recruitment, tenure and survival

Adult females with a larger structure score were more likely to hold a territory in the year of capture (Fig. 7.1*a*; Table 7.1). However, as some individuals sampled may

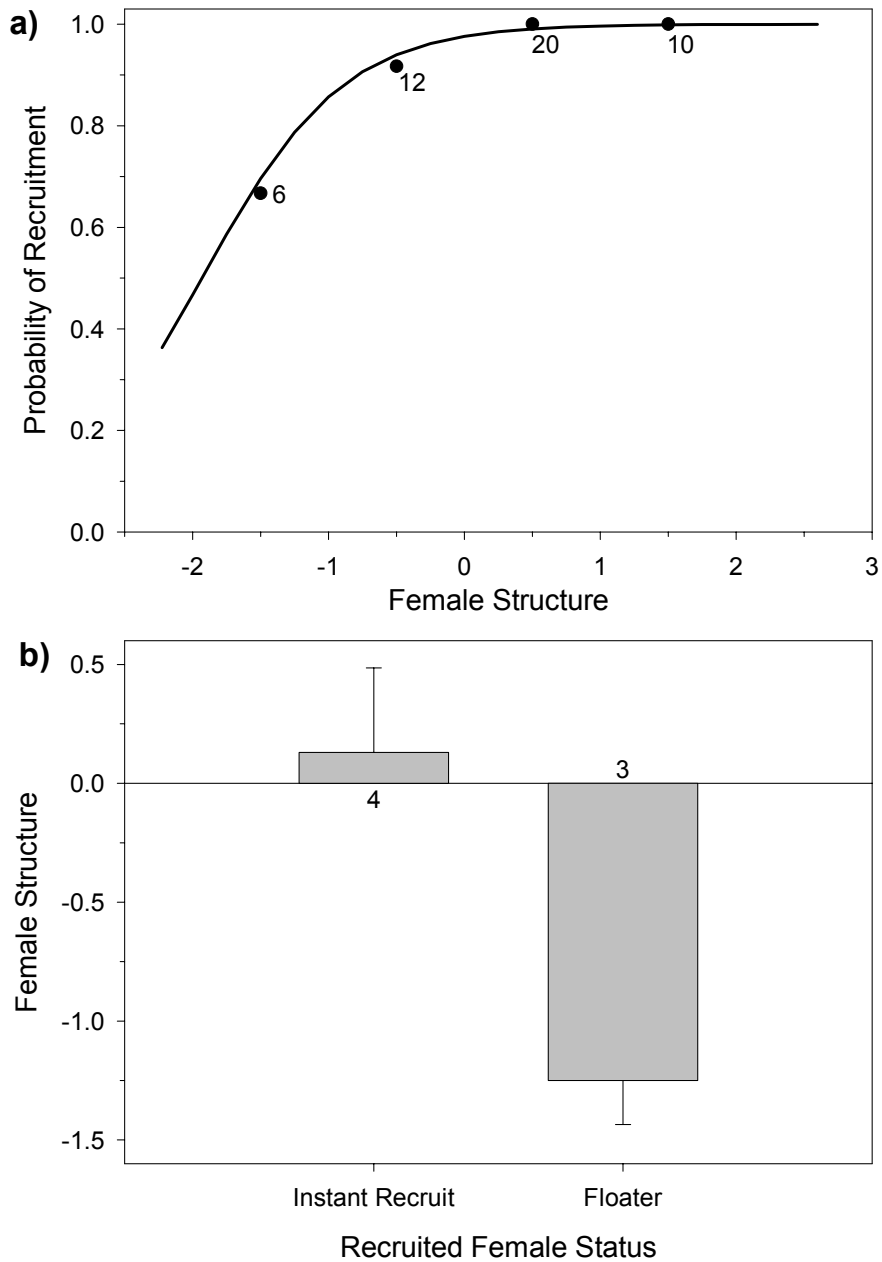


Figure 7.1. Adult female brown falcon body size (structure) and (a) the probability of recruitment into the breeding population in the year of capture and (b) the relationship between female structure and the method of recruitment. Line plot indicates model predictions (Table 7.1), points and bars indicate means of data (\pm one standard error in b), numbers show sample sizes, respectively.

Table 7.1. Summary of factors influencing the probability of recruitment, tenure, survival and the probability of attempting to breed amongst brown falcons of different sex and age groups. Data modelled using general linear models with binomial distributions, except in the case of tenure, where a general linear model was used. Figures indicate change of deviance statistics associated with structure (S), feather (F) and body condition indices (C) and approximate a chi-squared distribution with one degree of freedom unless noted otherwise. * = $p < 0.05$, ** =

$p < 0.01$.

Parameter Examined	Adult Females			Adult Males			Immature Females			Immature Males		
	S	F	C	S	F	C	S	F	C	S	F	C
Prob. of Recruitment	7.3**	2.9	0.1	-	-	-	1.0	0.2	1.0	0.34	3.5	1.9
Tenure	F _{1,42} = 0.01	F _{1,41} = 0.5	F _{1,40} = 1.4	F _{1,37} = 0.4	F _{1,36} = 1.14	F _{1,35} = 1.2	F _{1,17} = 0.02	F _{1,16} = 0.4	F _{1,15} = 0.7	F _{1,21} = 0.7	F _{1,20} = 0.8	F _{1,19} = 0.06
Prob. of Survival	0.5	1.0	0.4	0.5	0.2	3.1	0.2	1.7	2.9	4.7*	1.2	1.6
Prob. Adult partner	0.3	0.2	0.2	1.9	0.1	0.02	0.01	0.9	0.1	0.3	0.02	0.01
Prob. of taking large prey	0.01	1.2	0	0.3	0.2	1.0	0.6	0.9	1.1	8.3**	0.2	1.2
Attempt to Breed	3.2	0.01	0.4	0	0.6	0.2	0.03	0.08	2.2	0.4	0.01	0.2

have inherited uncontested territories, we also compared the structure size of falcons gaining immediate recruitment into the breeding population: ‘instant recruits’, against those females that spent time as part of the floating population. Adult female instant recruits again had larger structure scores (Fig. 7.1*b*) than other recruited females ($R^2 = 0.5$, $F_{1,6} = 9.5$, $p = 0.02$). Recruitment of immature females and both age groups of males was not influenced by size or body condition indices (Table 7.1).

The length of tenure was not influenced by structure, feather or body condition scores amongst any sex or age group (Table 7.1). The same was true for the probability of survival to the next breeding season, with the exception of immature males (Table 7.1). Immature males with a larger structure score had a reduced probability of survival to the next breeding season (Fig. 7.2*a*; Table 7.1).

Mate/territory quality and the likelihood of breeding

Body size or condition indices were not related to the probability of either age or sex group obtaining an adult partner or initiating a breeding attempt (Table 7.1).

Immature males with larger structure scores however were more likely to take large prey (Fig. 7.2*b*; Table 7.1), however for adult males and both ages of females no relationships between body size or condition indices were apparent (Table 7.1).

Breeding success

Low sample sizes of successful birds prevented an analysis of the effect of body size upon the productivity of breeding attempts by immature falcons. Adult females with a larger feather score were more likely to be successful (Fig. 7.3*a*) and had a greater

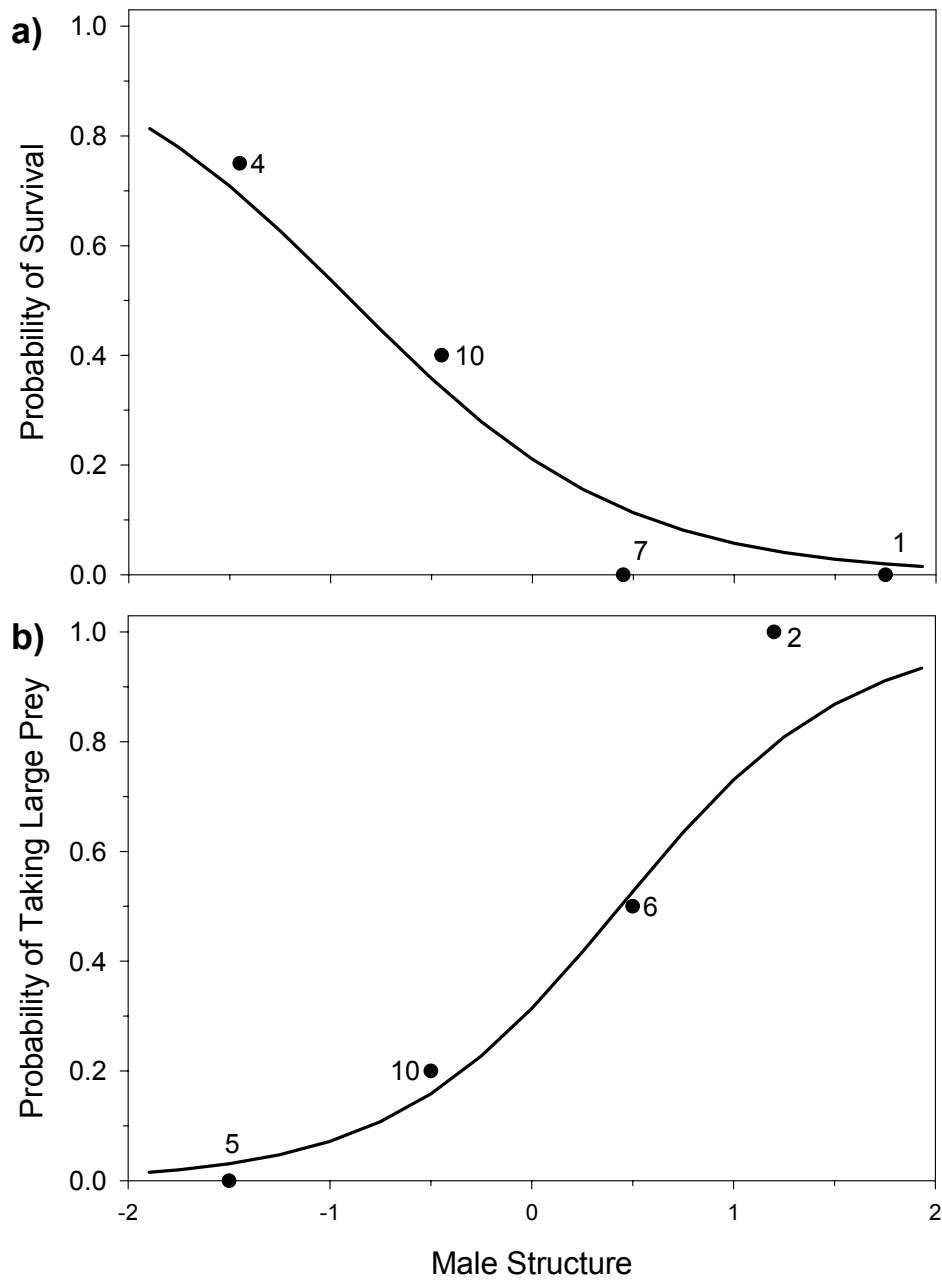


Figure 7.2. The probability of an immature male brown falcon (*a*) surviving to the following breeding season and (*b*) taking large prey in the year of capture, according to body size (structure). Lines indicate model predictions (Table 7.1), whereas points and numbers show data means and sample sizes, respectively.

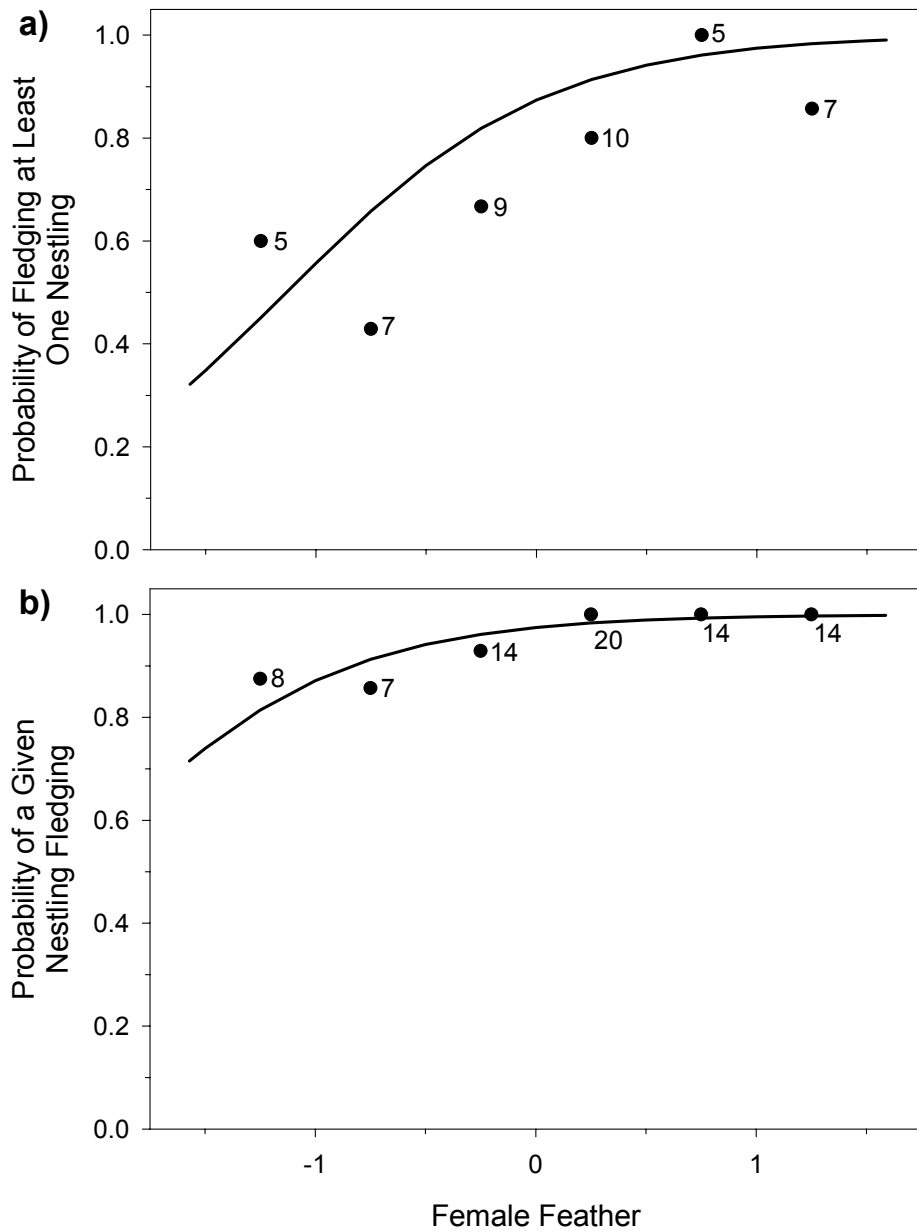


Figure 7.3. The probability of (a) a nest successfully fledging at least one nestling and (b) any given nestling surviving to fledge according to adult female falcon body size (feather). Lines indicate model predictions (Table 7.2), whereas points and numbers show data means and sample sizes, respectively.

probability of fledging a given nestling within their brood (Fig. 7.3*b*; Table 7.2).

Adult male body condition indices were more important than body size *per se*, with males in better condition paired with females that laid earlier in the season (Fig.

7.4*a*) and having a greater chance of fledging their nestlings (Fig. 7.4*b*; Table 7.2).

Clutch size and sex ratio at hatching were unrelated to body size or condition indices of either adult sex; adult female body size was also unrelated to mean egg volume and the probability of an egg in her brood hatching (Table 7.2).

Nest defence intensity

The intensity of a pair's nest defence to a human 'predator' increased with the number of visits to the nest and brood size (Table 7.3). Neither male nor female size or condition indices were important variables in the model (Table 7.3).

Male hunting prowess

The amount of prey delivered to nests by males was not related to their own body size or condition index, or to that of their partner (Table 7.4). Instead, males with brighter, completely yellow bare parts delivered significantly more prey ($1.8 \text{ kg} \pm 0.2\text{SE}$; $n = 17$) in 48 h than those with only partially yellow bare parts ($1.2 \text{ kg} \pm 0.2\text{SE}$, $n = 20$; Table 7.4). More importantly, males taking larger prey items delivered $1.8 \text{ kg} (\pm 0.2\text{SE}, n = 22)$ of prey to their nests per 48 h, almost twice that supplied by males taking small prey ($1 \text{ kg} \pm 0.1\text{SE}, n = 19$; Table 7.4).

Discussion

Adult females in the study population with larger structure (skeletal) measures had a higher probability of obtaining a territory in the study site than their smaller

Table 7.2. Summary of factors influencing various parameters of reproductive success amongst brown falcons of different sex and age groups. Data modelled using general linear models with binomial distributions (breeding success and the proportion of eggs hatched or nestlings fledged), or general linear models (remainder). Figures indicate change of deviance statistics associated with structure, feather and body condition indices and approximate a chi-squared distribution with one degree of freedom unless noted otherwise. * = $p < 0.05$, ** = $p < 0.01$.

Parameter Examined	Adult Females			Adult Males		
	Structure	Feather	Condition	Structure	Feather	Condition
Breeding success	1.0	7.7**	1.32	3.5	0.4	2.5
Lay date	$F_{1,37} = 0.3$	$F_{1,36} = 0.01$	$F_{1,35} = 0.2$	$F_{1,30} = 1.5$	$F_{1,31} = 0.01$	$F_{1,32} = 10.1**$
Clutch size	$F_{1,32} = 0.3$	$F_{1,31} = 0.4$	$F_{1,30} = 1.6$	$F_{1,25} = 0.1$	$F_{1,26} = 0.9$	$F_{1,27} = 0.04$
Mean egg volume	$F_{1,31} = 0.03$	-	-	-	-	-
Prop. of eggs hatched	0.3	0.2	0.9	-	-	-
Hatching sex ratio	$F_{1,29} = 0.1$	$F_{1,28} = 0.01$	$F_{1,27} = 0.05$	$F_{1,23} = 0.9$	$F_{1,24} = 0.4$	$F_{1,25} = 0.7$
Prop. of nestlings fledged	3.2	4.3*	0.4	3.0	0.3	9.8**

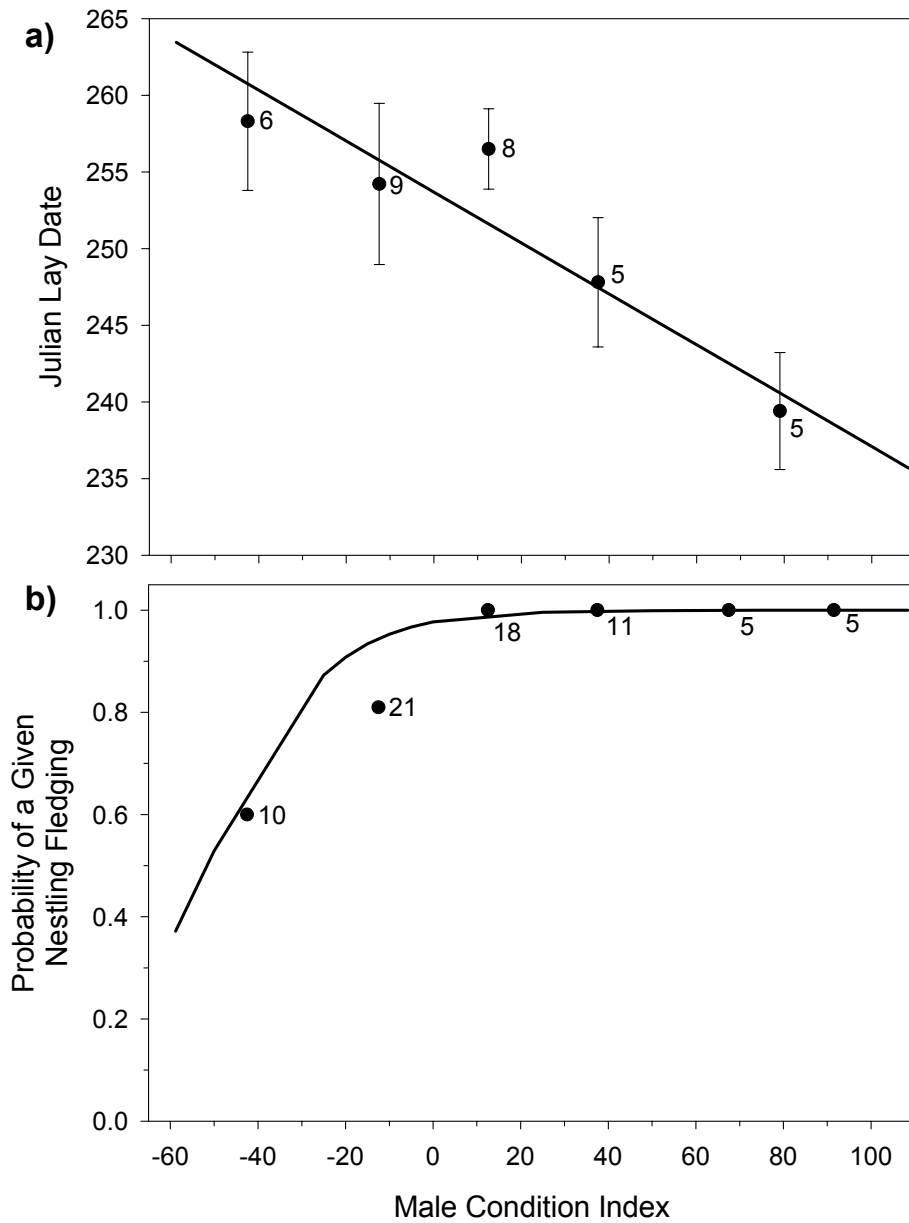


Figure 7.4. The relationship between adult male falcon body condition index and (a) Julian lay date of nesting attempts and (b) the probability of a given nestling fledging. Lines indicate model predictions (Table 7.2), whereas points and numbers show data means (\pm one standard error in *a*) and sample sizes, respectively.

Table 7.3. Summary of analyses of the intensity of nest defence during 87 visits to the nests of 22 brown falcon pairs using restricted maximum likelihood modelling. Random model included female and nest number. Change in deviance statistics for each term initially included in the model are presented, emboldened values indicate $p < 0.05$.

Term of interest	df	Change in deviance	<i>p</i> value
Number of previous visits to nest	1	20.64	<0.0001
Brood size	1	10.21	0.001
Male feather	1	1.50	0.22
Date of visit	1	1.31	0.25
Nest stage	1	1.21	0.3
Female feather	1	0.52	0.47
Sex ratio at hatching	1	0.24	0.63
Female condition index	1	0.07	0.79
Male new to human interference	1	0.02	0.89
Male structure	1	0.01	0.91
Female structure	1	0.01	0.92
Female new to human interference	1	0.01	0.94
Male condition index	1	0	0.99
Female Age	1	0	1

Table 7.4. Summary of analyses of factors influencing the biomass of prey delivered to brown falcon nests by males in 48 h periods using restricted maximum likelihood modelling. Random model included pair, observation and male number. Change in deviance statistics for each term initially included in the model are presented, bold values indicate $p < 0.05$.

Term of interest	df	Change in deviance	<i>p</i> value
Prey size	1	22.6	<0.0001
Male bare part colour	1	8.6	0.003
Nestling age	1	2.44	0.12
Female bare part colour	1	1.33	0.25
Male structure	1	1.34	0.25
Male age	1	1.35	0.25
Lay date	1	1.07	0.3
Brood reduction	1	0.76	0.38
Male condition index	1	0.51	0.47
Sex ratio at hatching	1	0.45	0.5
Year of observation	1	0.47	0.5
Female age	1	0.4	0.53
Female structure	1	0.33	0.57
Female condition index	1	0.26	0.61
Female feather	1	0.08	0.77
Male front plumage colour	1	0.08	0.77
Brood size	1	0.08	0.78
Female front plumage colour	1	0.03	0.85
Male feather	1	0.03	0.87
Experience	1	0.01	0.94
Success	1	0	1

counterparts. Moreover, once recruited, adult females with larger feather scores (wing/tail lengths) were more often successful in their breeding attempt and had a greater probability of fledging a given nestling within their brood. In contrast, adult male recruitment was unrelated to body size or condition indices. However, fatter males were more productive, having a greater chance of fledging their nestlings and pairing with partners that initiated clutches earlier in the season. Immature male falcons with smaller structure scores were more likely to survive to the next breeding season. Thus directional selection on body size appears to be favouring large size amongst adult females and a reduction or stabilisation of male size in the brown falcon population studied.

These results strongly support larger female structure being a factor in gaining successful recruitment into the breeding population, given this relationship was evident amongst all birds captured and also within the sub-group bypassing the floating population. Further, the greater breeding success of individuals with large feather scores provides a mechanism by which RSD could be maintained in the population. Females were more prevalent in the floating population than males (M^cDonald unpubl. data) and this, along with frequent female-female agonistic interactions (M^cDonald in press *b*), indicates strong female competition for access to vacancies in the breeding population. Strong female intrasexual competition has been noted in other raptor species (Newton 1986, 1988; Temeles 1986; Simmons 2000) with larger individuals usually prevailing during intraspecific disputes (Hansen 1986; Knight and Skagen 1988). Moreover, sex-biased provisioning of last-hatched brown falcon nestlings, a hatch order synonymous with small final body size, results in sex-biased differential mortality in the study population (Chapter 8).

Mothers fed and raised their last-hatched sons, but rarely fed last-hatched daughters, leading to the death of all the last-hatched female nestlings monitored (Chapter 8).

This result provides further evidence for selection favouring large body size in female falcons.

Despite their apparent competitive superiority, larger females did not choose higher quality mates or territories. While it is possible females were competing over a factor not sampled in this study, high population density appears a more likely explanation for this apparent lack of mate choice. The population studied is the densest recorded for this species (M^cDonald *et al.* in press). Given territory fidelity is high and both sexes defend territories from intruders of either sex (M^cDonald in press *b*), a large degree of female mate choice may be prevented due to a high probability of being usurped. Moreover, despite male condition being an important indicator of quality, no evidence of competition between females for fatter males was found (M^cDonald unpubl. data), providing further evidence that mate choice was not a viable strategy in the population studied.

In contrast to females, male body size was not an important determinant of recruitment among either age group or the productivity of adult falcons. Instead, adult males with higher indices of body condition bred earlier and, perhaps as a consequence, had a greater probability of fledging nestlings within their brood. Nevertheless, at least within those males sampled, fatter falcons were not supplying their brood and partner with a greater biomass of prey. Instead, bare part colouration and prey size were important indicators of prey delivery rates, both factors that females could potentially assess directly if the opportunity for mate choice arose.

Survival patterns indicated directional selection favouring small immature males, which, paradoxically, were more likely to capture small prey, a diet leading to poor reproductive success (Chapter 6). Superficially these results appear to support the idea of intrasexual niche differentiation RSD hypotheses that predict a reduction in male size and thus prey taken by male raptors (e.g. Storer 1966). However, body size was not an important determinant of prey choice amongst adult males or females of any age. Moreover, both sexes of brown falcons within pairs take similar prey items, with the largest and smallest birds alike (either within or between sexes) being able to capture both the smallest and largest prey items recorded (M^cDonald *et al.* in press).

A possible explanation of these effects is intrasexual competition, as larger immature male falcons were occupying territories conducive to the capture of preferred large prey they may have been more likely to be replaced by competitively superior males (e.g. adults), leading to greater ‘mortality’ rates. Alternatively, large prey such as eastern tiger snakes *Notechis scutatus* and rabbits are more dangerous and difficult to capture than smaller prey items, particularly for relatively inexperienced immatures. Hunting accidents or starvation may also have increased mortality amongst larger immature males taking large prey. Unfortunately measures of mortality excluding emigration were not possible to ascertain in this study.

Implications for hypotheses proposed to account for RSD

i) Behavioural hypotheses argue that larger female raptors are better able to prevent male infanticide or to force smaller males into pairing, provisioning them or their offspring (Amadon 1975; Cade 1982; Smith 1982; Mueller and Myer 1985; Mueller

1986, 1990). These hypotheses lack universal application and cannot predict the direction of dimorphism. More critically, behavioural hypotheses are severely compromised by the existence of NRSD species with similar life history strategies and weaponry to Falconiformes exhibiting RSD (e.g. some *Ninox* owls; Schodde and Mason 1980; Olsen and Olsen 1987; Olsen and Cockburn 1993; Higgins 1999). Moreover, in the current study brown falcon pairs with larger females did not begin laying earlier and male infanticide was not recorded in the population, despite some males visiting nests and even feeding nestlings in the absence of females (McDonald *in press b*). Clearly these hypotheses cannot explain the prevalence of RSD within the study population or amongst raptors as a whole.

ii) Ecological hypotheses suggest that RSD has evolved to reduce intersexual and/or intrapair competition for food (e.g. Selander 1966; Storer 1966; Snyder and Wiley 1976). These hypotheses have drawn many criticisms (see Olsen and Cockburn 1993 for review), chief among which is the failure to explain the presence of RSD in species where the sexes spend little time together (Newton 1979; Myers 1981) and the scant evidence of significant sexual resource partitioning (Mueller 1990). Resource partitioning was also not evident in the study population (McDonald *et al.* *in press*). A much stronger relationship exists between the agility of prey and the degree of RSD (Newton 1979; Temeles 1985; Simmons 2000); this is usually argued, but not yet demonstrated, to have occurred through a reduction in male size favouring the capture of more agile prey (e.g. Newton 1979; Temeles 1985). Body size influences on prey taken by immature male brown falcons at first glance appear to support this hypothesis. However, on closer inspection most small prey items such as insects and house mice *Mus musculus* are not more agile than large prey such as

rabbit kittens, silver gulls *Larus novaehollandiae* and feral pigeons *Columba livia* (McDonald *et al.* in press). Indeed, the mean structure score of all males taking passerine birds ($-0.2 \pm 0.3\text{SE}$; $n = 16$) is not significantly smaller than that of falcons taking other prey items ($0.08 \pm 0.2\text{SE}$; $n = 45$; $F_{1,59} = 1$, $p = 0.3$). Thus sexual resource partitioning is unlikely to be a primary factor in the maintenance and evolution of RSD within raptors.

iii) Sex role differentiation hypotheses focus on the distinct parental roles evident for most male and female raptors, as females provide most of the incubating/brooding effort while males supply their offspring and female partner with food over the bulk of the breeding season (e.g. Newton 1979; Marchant and Higgins 1993). Given this, sex role partitioning hypotheses argue that smaller males have been favoured for their greater foraging efficiency or superior territorial defence, while larger female size allows more effective incubation, larger egg/clutch sizes and/or better nest defence (Reynolds 1972; Selander 1972; Balgooyen 1976; Lundberg 1986; Hakkarainen and Korpimäki 1991, 1995; Hakkarainen *et al.* 1996). Clearly the intensity of nest defence by brown falcons was unrelated to body size in either sex, and this, along with the fact that small males are the main defender of nest sites in many other raptors exhibiting marked RSD (Wiklund and Stigh 1983; Andersson and Wiklund 1987; Simmons 2000), indicates nest defence is unlikely to influence the maintenance or evolution of RSD in raptor populations. Prey delivery rates by male brown falcons were also unrelated to body size, indicating smaller males were not more effective hunters. Further, larger female brown falcons did not hatch a greater proportion of their eggs or lay larger eggs or clutches.

Despite this, female brown falcons with larger feather scores were more likely to fledge nestlings within their brood and had a greater chance of reproductive success, providing some support for the hypothesis that larger female size has evolved to improve a female's brooding ability (e.g. Snyder and Wiley 1976). However, this hypothesis is not likely to provide a general explanation for the existence of RSD in raptors as it cannot explain the degree of dimorphism evident between raptor species, the existence of both RSD and NRSD in species such as the *Ninox* owl genus and the lack of RSD in many other bird groups. A possible role of larger feathers in facilitating more successful brooding of young by female brown falcons during inclement weather is more likely to be a consequence of recruitment favouring increasing female structure size, and thus RSD, than the principal factor responsible for the evolution of RSD.

iv) Hypotheses centred around the effects of sexual selection can be divided into two types, those that suggest RSD is maintained by: (1) intersexual selection: females select smaller, more agile males which are capable of performing more attractive display flights and are better hunters (Safina 1984; Widén 1984; Jehl and Murray 1986; Hakkarainen and Korpimäki 1991, 1995; Hakkarainen *et al.* 1996; Simmons 2000) and (2) intrasexual selection favours an increase in size of females which compete for a scarce resource, a male holding a territory that is ready to breed (Olsen and Olsen 1984, 1987). This hypothesis posits that male size is driven by natural selection.

The results from this study have demonstrated that smaller (adult) male brown falcons were not more successful hunters, a relationship consistent to the best of our

knowledge with data from other species. One example often cited to the contrary is that of the Tengmalm's owl *Aegolius funereus*, in which males that were large (during food-rich years) or small (during food-poor years) enjoyed greater reproductive success, apparently through an increase in the number of prey items supplied to their nest (Hakkarainen and Korpimäki 1991, 1995). However, if these relationships are re-assessed using the total biomass delivered, the only statistically significant relationship remaining is that large, not small, males provided more food in years of high prey abundance (Hakkarainen and Korpimäki 1995).

Moreover, neither size nor condition-mediated assortative mating with larger females favouring smaller males was apparent within the population studied (McDonald unpubl. data), indicating mate choice was not a primary factor in determining settlement patterns and thus RSD. Other raptor studies have also failed to find a female preference for small males in several field-based mate choice studies (Bowman 1987; Marti 1990; Palokangas *et al.* 1992; Warkentin *et al.* 1992), although laboratory tests of mate choice in common kestrels *F. tinnunculus* found a preference for smaller males, but only when differences were marked (Hakkarainen *et al.* 1996). The relevance of this finding to pairs in the field is unknown. Together these results suggest that the intersexual selection hypothesis does not appear likely to be a significant factor in maintaining RSD patterns.

In contrast, the results gathered in this study provide clear support for the intrasexual competition hypothesis (Olsen and Olsen 1984, 1987), as larger females were more effective competitors for access to breeding territories and thus operational males; increased mortality of larger immature males and greater breeding success of larger

females would maintain this level of RSD. Some (e.g. Andersson 1994) have refuted the intrasexual competition hypothesis, citing the results of Wiklund and Village (1992). However this study, which examined sexual differences in the intensity of responses to simulated territorial intrusions, failed to account for the relative body size of territory owners compared to intruders, a critical component of the intrasexual competition hypothesis. Massemin *et al.* (2000) examined selection pressure in common kestrels, failing to find strong directional selection in any sex (as expected in this species with limited dimorphism), including no indication that larger females were favoured. However, their study failed to assess recruitment patterns, the period when larger female size is likely to be of most benefit. Searching for benefits of increased female size in reproductive success alone cannot be considered a conclusive test of the intrasexual selection hypothesis.

In contrast to many other proposed RSD hypotheses, the intrasexual competition hypothesis also has application to other bird species, including raptors with NRSD (e.g. *Ninox* owls; Olsen 1991). It also accords well with current understanding of sexual selection, which is largely based on sex differences in ‘parental investment’ that result in one sex becoming limited and the other competitive (Kokko and Monaghan 2001; Kokko and Johnstone 2002). In addition, this hypothesis can predict the degree of RSD in a species: dimorphism increases as the importance of securing a high quality male becomes more critical, for example in species taking prey difficult to capture, accounting for the strong relationship between prey agility and RSD in many raptors (Olsen and Olsen 1987). Conversely, for species capturing non-agile prey, intrasexual competition is not expected to be as important and RSD minimal, as found in a recent study of American kestrels *F. sparverius* (Bortolotti

and Iko 1992). Moreover, intraspecific comparisons of the allometric relationship between body size and egg size in females and testis size in males, after controlling for the effects of phylogeny, suggest that it is indeed females which have diverged in size (become larger) in RSD species (Pleasants and Pleasants 1988; Olsen 1991; Olsen and Cockburn 1993).

Conclusion

The results gathered in this study, based upon intensive sampling of large numbers of both sexes of the population, clearly support selection favouring an increase in female size and thus the predictions of the intrasexual competition hypothesis. While intrasexual selection has been accepted as the best explanation for dimorphism in many other vertebrates (e.g. Lindenfors *et al.* 2002), including birds (e.g. Payne 1984; see Andersson 1994 for review), it is puzzling that this hypothesis has been largely ignored within the raptor literature until comparatively recently. This is particularly true as the intrasexual hypotheses has the added advantage of being able to account for both the degree and direction of dimorphism in raptors, including troublesome species exhibiting NRSD. Outside of raptors, fitness advantages of larger females in other predatory birds such as skuas and jaegers may also match the predictions of this hypothesis (Catry *et al.* 1999). Given the promising results reported here, we urge further research in this area; experimental tests of the intrasexual competition hypothesis are now required.

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Chapter 8 – Sex allocation and nestling survival in a dimorphic raptor: does size matter?



Plate 8.1. Close-up of a 26 day old nestling brown falcon. Photo courtesy of Ian Montgomery.

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Abstract

Fisher's theory predicts equal sex ratios at the end of parental care if the costs associated with raising each sex of offspring are equal. However, in raptors, which display various degrees of reversed sexual size dimorphism (RSD; females the larger sex), sex ratios biased in favour of smaller males are not often reported. This suggests that offspring of each sex may confer different fitness advantages to parents. We examined the relative potential costs and benefits associated with raising each sex of offspring of the brown falcon *Falco berigora*, a medium-sized falcon exhibiting RSD (males c. 75% of female body mass) and subsequent sex ratios. Female nestlings did not require more food, nor did they hatch from larger eggs or remain dependent upon parents for longer periods than male offspring. Together with previous studies this result indicates that even in markedly dimorphic species the relative costs of raising the larger sex are likely to be less than that predicted by body size differences alone. Moreover, focal mothers fed their last-hatched sons but not daughters, resulting in the complete mortality of all last-hatched female nestlings. Last-hatched nestlings suffer a reduced growth rate, resulting in smaller final body size. As males of any size but only larger females are likely to be recruited, the biased food allocation and consequent post-hatch sex ratio manipulation of last-hatched offspring is likely to reflect the differing benefits of investing in smaller members of each sex, consistent with broad-scale Trivers-Willard effects.

Introduction

Sex allocation theory has been one of the most successful areas of evolutionary ecology, predicting the level of parental investment and associated sex ratio skews observed in many invertebrates with considerable accuracy, (e.g. haplo-diploid parasitoid wasps: Charnov 1982; King 1987). However, amongst mammals (see Clutton-Brock and Iason 1986 for review) and, in particular, birds (see Clutton-Brock 1986; Gowaty 1993; Sheldon 1998 for reviews), results have been less compelling. While apparent manipulation independent of differential mortality has recently been reported (e.g. Komdeur *et al.* 1997; Appleby *et al.* 1997; Heinsohn *et al.* 1997), biases are usually slight and often inconsistent between or even temporally within populations, reflecting the numerous and complex selective pressures likely to be influencing sex allocation in higher vertebrates (Charnov 1982; Frank 1990; Cockburn *et al.* 2002).

Sex allocation patterns among raptor populations have attracted considerable research attention (see Newton 1979; Olsen and Cockburn 1991; Krackow 1993 for reviews), because most raptorial birds exhibit reversed sexual size dimorphism (RSD; females the larger sex). This dimorphism suggests that larger daughters may be more costly than sons. Fisher's (1930) hypothesis consequently predicts biased population sex ratios at the end of parental care in favour of males, the cheaper sex (Charnov 1982; Frank 1990). However, male-biased sex ratios have rarely been observed in raptors (e.g. Rosenfield *et al.* 1996; Brommer *et al.* 2003), with sex ratios at parity (e.g. Negro and Hiraldo 1992), or even biased towards females (e.g. Tella *et al.* 1996; Appleby *et al.* 1997) not uncommon. One explanation for this discrepancy is that body size may be a poor indicator of potential parental costs, as

increased food requirements of the larger sex have been observed in some raptors (Anderson *et al.* 1993a; Krijgsveld *et al.* 1998; Riedstra *et al.* 1998), but not others (Newton 1978; Collopy 1986; Newgrain *et al.* 1993; Boulet *et al.* 2001; Brommer *et al.* 2003).

Alternatively, at the family level there may be potential benefits associated with raising one sex over the other (Charnov 1982; Frank 1990). Apparently adaptive allocation bias has been reported for several raptor species, with the most common pattern involving sex-biased hatch or laying order sequences with either female (Bortolotti 1986; Godfray and Harvey 1986; Olsen and Cockburn 1991; Leroux and Bretagnolle 1996) or male chicks being more likely to hatch first (Bednarz and Hayden 1991). The prevailing sex may change according to lay date within seasons (Dijkstra *et al.* 1990; Olsen and Cockburn 1991; Zijlstra *et al.* 1992; Daan *et al.* 1996; Smallwood and Smallwood 1998) or territory productivity (Dzus *et al.* 1996), and it has been suggested that the sex most likely to breed at one year of age is overproduced in early broods (Dijkstra *et al.* 1990). Finally, some raptors produce more of the smaller sex (males) when parents are in poor condition or prey supplies are low (Wiebe and Bortolotti 1992; Aparicio and Cordero 2001).

In an attempt to bring some focus to such disparate research findings, Cockburn *et al.* (2002) recently proposed five, potentially non-exclusive, classes of adaptive sex allocation hypotheses. The brown falcon *Falco berigora* is a medium-sized falcon exhibiting RSD (Males: 486 g \pm 5SE, $n = 69$; Females: 658 g \pm 7SE, $n = 91$; M^cDonald unpubl. data). It is not siblicidal and has a socially monogamous breeding system with individual pairs maintaining exclusive all-purpose territories throughout

the year (M^cDonald in press *a*; M^cDonald *et al.* in press). Previous research has demonstrated that brood sex ratios do not influence survival or future fecundity of either brown falcon parent, even in years of poor breeding success (Chapter 6). As such, two of the five classes proposed by Cockburn *et al.* (2002) are potentially relevant to brown falcons:

i) Sex allocation reflects the frequency-dependent advantage enjoyed by the rare sex. Fisher's (1930) hypothesis is the most oft-cited hypothesis in this category, predicting equal investment among the sexes and thus population sex ratios proportional to the relative costs on future reproductive potential of raising each sex.

ii) Parents in good condition invest most in the sex deriving the greatest increase in reproductive value from a given level of investment. Trivers-Willard (1973) effects in the narrowest sense predict mothers in good condition will invest in the sex most likely to benefit from an increased level of investment. More broadly, Trivers-Willard effects predict greater investment in the sex that will benefit most, regardless of maternal condition.

We therefore examined sex allocation patterns in the brown falcon in light of the predictions raised by these two classes of hypotheses.

Methods

Study area and general field methods

The study was conducted between July 1999 and June 2002, approximately 35 km southwest of Melbourne in southeast Australia, at the Western Treatment Plant,

Werribee (38°0'S 144°34'E), adjacent Avalon Airport (38°2'S 144°28'E) and small areas of surrounding private land. Details of the c. 150 km² study site (Baker-Gabb 1984) and study population have been provided elsewhere (McDonald 2003; in press *a,b*; McDonald *et al.* in press).

Egg volume, hatch order and food allocation according to sex

During each breeding season all nests within the study area were found and their contents determined by climbing to the nest or through the use of a mirror pole. Eggs were marked to facilitate individual recognition and measured to the nearest 0.01 cm with vernier callipers at the longest and widest point, with volume estimated using the formula: $0.51 \times \text{length} \times (\text{breadth})^2$ (Hoyt 1979). For several days prior to hatching nests were visited daily and when possible nestlings matched to the eggs from which they hatched. During these visits hatch order was also ascertained either directly or from the methods outlined in McDonald (in press *b*). Once emerged from eggs, nestlings were marked with a small piece of Micropore tape (3M; Pymble, New South Wales) loosely folded around either the left or right humerus until they reached an appropriate age for banding. This tape was replaced with each visit to allow for growth, and did not leave behind adhesive residue or interfere with growing humerals or remiges. Once hatched, a small blood sample (c. 10 - 20 μL) was collected from each nestling's alar vein and a Polymerase chain reaction (PCR)/*HaeIII* digest reaction used to assign sex to each nestling (Griffiths *et al.* 1998). Chicks were fitted with colour band combinations prior to fledging at approximately 28 days of age.

To determine the amount of prey required to raise each nestling sex small cameras with infrared lights (Model 43150674; Radio Parts Group, Melbourne) were placed at the nests of broods in the 2000 and 2001 breeding seasons. Cameras were placed at nests for 48 h periods during the early (eldest nestling 0 - 14), mid (eldest nestling 15 - 27) and late-nestling phase (eldest nestling greater than 27 days old). They were powered by deep cycle batteries (Besco N70T; Battery World, Canberra) and connected to time-lapse video recorders run at 1/8 normal speed (Hitachi VT1200E; Radio Parts Group, Melbourne); this minimised visits to the nest tree to 24 h intervals to change batteries and tapes. Micropore tape used to mark nestlings (see above) was also used to identify individual offspring on subsequent viewing of video footage. During each feeding event (prey brought to the nest cup and distributed amongst offspring by, in all but one event, the female parent) the position of each chick relative to the prey being offered was noted at the beginning of the feed. Chicks were then assigned within broods as being either 'closest' or 'furthest' from prey. For each feeding event the number of mouthfuls of prey provided to each nestling was recorded, with the chick receiving the first mouthful during each feeding event recorded as being 'fed first'.

Recruitment of offspring into the breeding population

To determine possible benefits associated with raising one sex over the other, recruitment rates of banded offspring of a known sex, age and cohort into the study population were monitored throughout the study period.

Growth and survival to independence

To determine the biological significance of detected biases in resource allocation amongst broods monitored with surveillance cameras, wing length, head to bill length and body mass were measured weekly as per the methods outlined in M^cDonald (in press *b*). Survival to fledging and independence for each nestling was also monitored during weekly visits to the nest site or bi-weekly visits to the natal territory post-fledging.

Statistical analyses

Sex ratio data were assessed for deviances from parity using a G test for goodness of fit with a Yates correction for continuity (Zar 1996). Generalised linear models were used to assess differences in egg volume between male and female eggs after controlling for hatch order. The probability of a given nestling fledging according to sex and hatch order was assessed using a generalised linear model with a binomial error distribution (Genstat Committee 1993). Contingency tables were used to assess biases in the distribution of chicks relative to prey items offered during feeding events according to sex and hatch order. Restricted maximum likelihood (REML) procedures were applied to account for various influences upon the number of mouthfuls of food chicks received during feeding events and nestling size (i.e. growth rates) during the nestling phase.

When analysing food supplied to offspring a random model including pair number, the number of times the brood had previously been observed, the number of the feeding event being recorded and a unique number for each chick was used. The number of mouthfuls supplied to each chick during a feeding event was log

transformed using the formula $X' = \ln(X+1)$, in order to account for zeros (Zar 1996). The main model fitted included terms for brood age (early, mid or late in the nestling phase), year of measure, Julian hatch date of the eldest nestling and observation date for each brood, as well as nestling sex, hatch order and whether or not the nestling survived to fledging.

Assessments of nestling growth rates were made using male chicks only, as complete female mortality in the third-hatched position prevented a thorough assessment of hatch order implications upon growth rates in this sex. Measurements assessed were confined to linear phases of growth when chicks were 7 - 20 and greater than 20 days old (McDonald in press *b*). We utilised a random model incorporating pair number, the hatch order of each chick and year, with the main models used incorporating hatch order, nestling age and brood size.

For all analyses initial models fitted included all explanatory terms and biologically meaningful two-way interactions. Interactions and terms were then dropped in a step-wise fashion by examining the change in deviance between the full model and the sub-model fitted. The procedure was repeated until only significant terms remained in the model. For simplicity, interaction terms are presented only when significant. All calculations were carried out using Genstat 5 Release 4.21 (Genstat Committee 1993). Study methods were approved by the Australian National University Animal Experimentation Ethics Committee (F.BTZ.02.99).

Results

Sex ratios

Sex ratios did not differ between years across the study population, or within hatch order. Although more male nestlings were observed in focal broods monitored by surveillance cameras at hatching, fledging and independence, this bias was not significantly different from parity at any stage (Table 8.1). Likewise, amongst first and second-hatched chicks sex ratios did not differ from parity (Table 8.1), although a trend existed for first-hatched eggs to be male. However, among third (last-) hatched nestlings, while sex ratios did not differ from parity following hatching, by fledging only male offspring remained, a significant deviation from equal sex ratios (Table 8.1). This pattern continued at the population level amongst all broods assessed during the study, with 12 of 17 (71%) last-hatched male nestlings fledging, compared to just 6 of 12 females (50%) in this hatch position.

Costs of raising larger female chicks relative to males: egg volume

Female chicks did not hatch from eggs of a larger volume than their male counterparts ($F_{1,20} = 1, p = 0.3$). Egg volume was unaffected by hatch order ($F_{2,20} = 0.6, p = 0.5$) or the interaction between hatch order and sex ($F_{2,20} = 0.5, p = 0.6$; mean volume = $42.4 \text{ cm}^3 \pm 0.8\text{SE}, n = 26$).

Costs of raising larger female chicks relative to males: food allocation

A total of 1208 nestling feeding events were recorded during video surveillance of 27 broods (17 in 2000 and 10 in 2001), involving 567 prey items. The survival rate of 64 chicks monitored by surveillance cameras (77%) was equal to that of 94

Table 8.1. Sex ratio data for the study population as a whole and within each hatch order. Sex ratios which deviate from parity ($p < 0.05$) using a G test for goodness of fit with a Yates correction for continuity are emboldened. Sex ratios presented as the proportion of offspring which are male.

Parameter	<i>n</i>	Sex ratio	G _c , df = 1
<i>All offspring</i>			
Hatching sex ratio	64	0.58	1.27
Fledgling sex ratio	49	0.61	2.05
Sex ratio at independence	38	0.63	2.15
<i>First-hatched offspring</i>			
Hatching sex ratio	27	0.67	2.40
Fledgling sex ratio	24	0.67	2.07
Sex ratio at independence	17	0.71	2.16
<i>Second-hatched offspring</i>			
Hatching sex ratio	24	0.42	0.38
Fledgling sex ratio	20	0.45	0.05
Sex ratio at independence	17	0.53	0
<i>Third-hatched offspring</i>			
Hatching sex ratio	13	0.69	1.25
Fledgling sex ratio	5	1	5.29
Sex ratio at independence	4	1	3.92

nestlings not subject to surveillance measured in other years of the study. The number of mouthfuls supplied to chicks within a brood was influenced by several factors: a negative effect of brood size indicated chicks in smaller broods were fed more per capita than those in larger broods (Fig. 8.1*a*; Table 8.2). Moreover, the nestling that received the first mouthful during a feeding event received more food than its brood mates; this disparity increased with nestling age (Fig. 8.1*b*; Table 8.2). Similarly, nestlings that were closest to prey at the beginning of the feed received more mouthfuls of food than other chicks, with those furthest away obtaining the least amount of food (Fig. 8.1*c,d*; Table 8.2).

Finally, a sex by hatch order interaction existed (Fig. 8.1*e*; Table 8.2). Males and females hatching either first or second received similar amounts of food, averaging 8.55 and 8.53 mouthfuls per feed, respectively (Fig. 8.1*e*). Amongst males, hatch order did not determine the quantity of food received. However, third (last-) hatched female nestlings received much less food than their earlier hatched counterparts (Fig. 8.1*e*).

Consequences of differential food allocation for nestlings

The above results indicate that sex and hatch order were of critical importance in determining allocation patterns in brown falcon nests. Thus the frequency of nestlings being recorded as ‘closest’, ‘furthest’ or ‘fed first’ was assessed relative to these variables during each feeding event (Table 8.3). Sex biases were not evident for any variable, however, biases attributable to hatch order were apparent amongst the distribution of closest and fed first scores (Table 8.3). *Post-hoc* analyses comparing one hatch order against the other two indicated these biases were driven

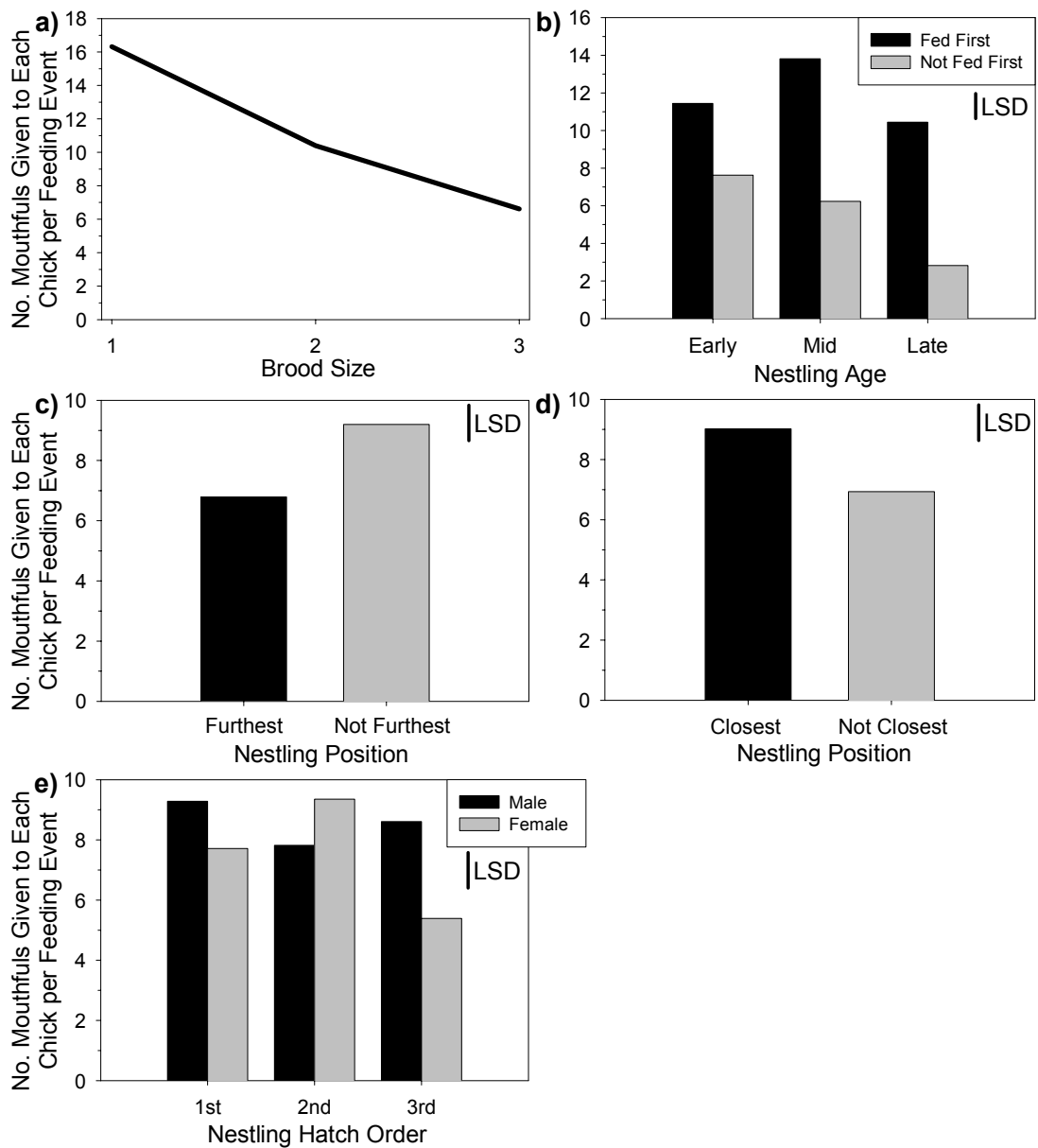


Figure 8.1. The number of mouthfuls of food supplied per brown falcon nestling per feeding event according to: (a) brood size; (b) nestling age and whether they were fed first; whether nestlings were either (c) furthest away; or (d) closest to prey during feeding events; and (e) sex by hatch order. Bars and line in (a) indicate REML model predictions (Table 8.2) and LSD lines least significance differences ($p < 0.05$).

Table 8.2. Summary of analyses of factors influencing the number of mouthfuls supplied to nestlings within brown falcon broods assessed using restricted maximum likelihood modelling. Random model utilised included pair, observation, feeding event and nestling number. Change in deviance statistics for each term initially included in the model are presented, significant terms emboldened ($p < 0.05$).

Term of interest	df	Change in deviance	<i>p</i> value
Brood size	1	12.2	<0.001
Nestling age x Fed first mouthful	2	26.4	<0.001
Furthest away from food	1	10.5	0.001
Sex x Hatch order	2	10.9	0.004
Closest to food	1	6.7	0.01
Fed first mouthful	1	78.9	<0.001
Nestling age	2	11.8	0.003
Hatch order	2	3.3	0.2
Sex	1	0.8	0.4
Year	1	0.6	0.4
Nestling survived	1	0.05	0.8
Hatch date	1	0.01	0.9

Table 8.3. Results of contingency table analyses assessing the distribution of nestlings that were closest or furthest from prey or supplied with the first mouthful of food during feeding events, according to sex and hatch order.

Significant terms ($p < 0.05$) emboldened.

Term of interest	Sex			Hatch order		
	χ^2	df	<i>p</i> value	χ^2	df	<i>p</i> value
Closest	0.9	1	0.4	9.3	2	0.01
Furthest	0.01	1	0.9	0.3	2	0.9
Fed first	1.6	1	0.2	29.5	2	<0.0005

by last- (third) hatched nestlings rarely being closest to prey items ($\chi^2_1 = 9.3, p = 0.01$), being unlikely to receive the first mouthful of food ($\chi^2_1 = 24.2, p < 0.0005$), which more often than expected went to first-hatched chicks ($\chi^2_1 = 15.1, p < 0.0005$; Fig. 8.2). This relationship between the likelihood of being fed first and hatch order persisted within each age group separately.

Overall, nestling mortality rates of each sex did not differ ($\chi^2_1 = 1.9; p = 0.2$).

Similarly yearly differences in mortality rates were not apparent ($\chi^2_1 = 1.8; p = 0.18$). A tendency for last-hatched chicks to be in less competitive positions during feeding events and for last-hatched female chicks at least to receive less food was of biological significance. Last-hatched nestlings of both sexes experienced lower survival probabilities than their earlier-hatched counterparts ($\chi^2_2 = 10; p = 0.007$; Fig. 8.3). The interaction between sex and hatch order did not significantly influence mortality rates ($\chi^2_2 = 2.6; p = 0.3$; Fig. 8.3), however none of the third (last-) hatched female nestlings sampled by nest surveillance cameras survived to fledge (Fig. 8.3).

Given this sex-biased mortality the assessment of growth rates during the early and late-nestling phase was restricted to male nestlings. Last-hatched males experienced a reduced growth rate when aged between 7 and 20 days in body mass (Fig. 8.4a) and had smaller head to bill lengths when 21 days or older in comparison with their earlier-hatched brood mates (Fig. 8.4b; Table 8.4).

Benefits associated with raising each sex of offspring: recruitment

During the study a total of 8 offspring, 4 birds of each sex, were recruited into the breeding population. All 4 males, 3 first-hatched and 1 third-hatched bird, obtained a

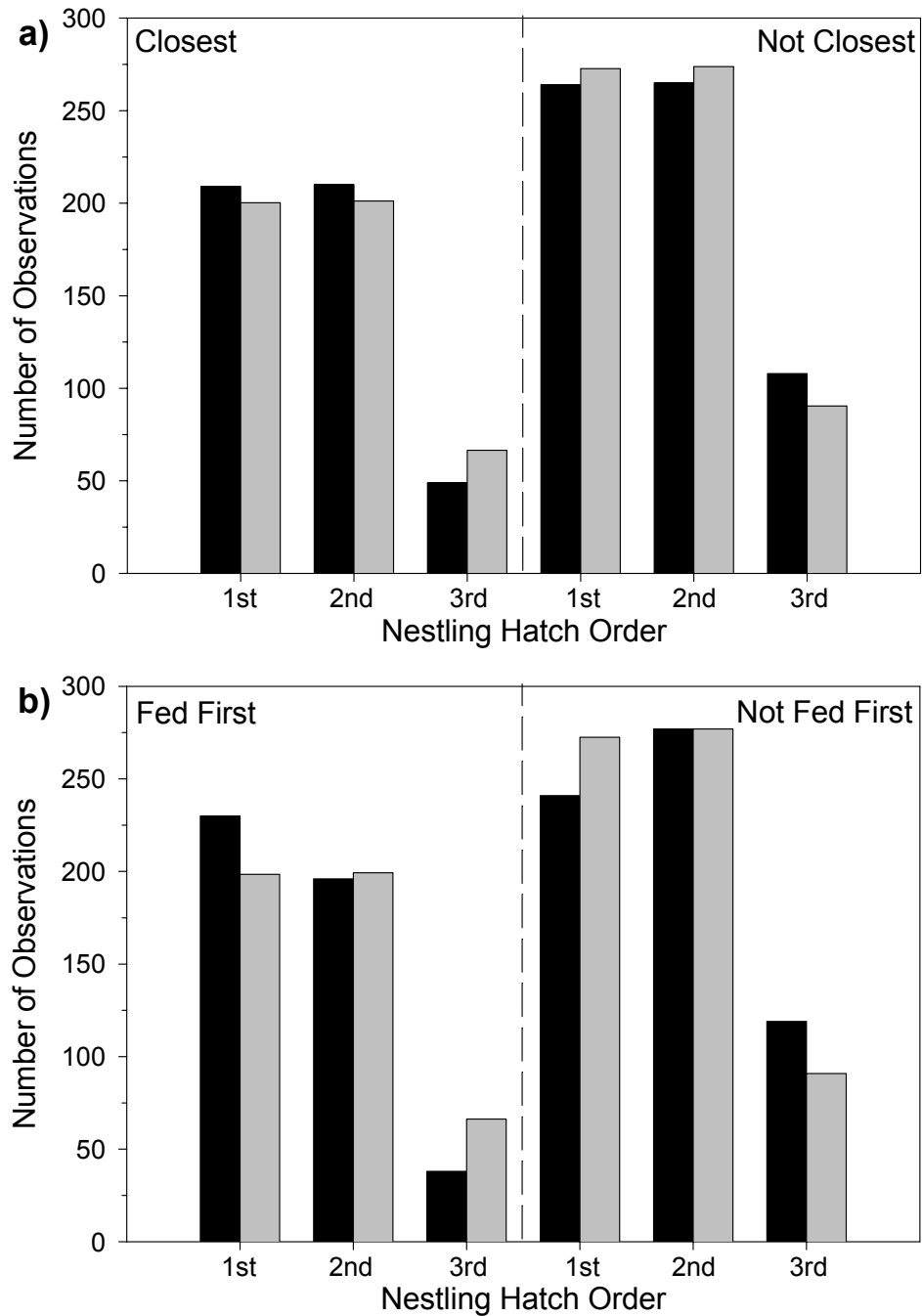


Figure 8.2. Observed (solid bars) and expected (shaded bars) distribution of brown falcon nestlings of different hatch orders according to whether or not they were (a) closest; or (b) furthest away from prey during feeding events. Both graphs depict significant differences ($p < 0.05$).

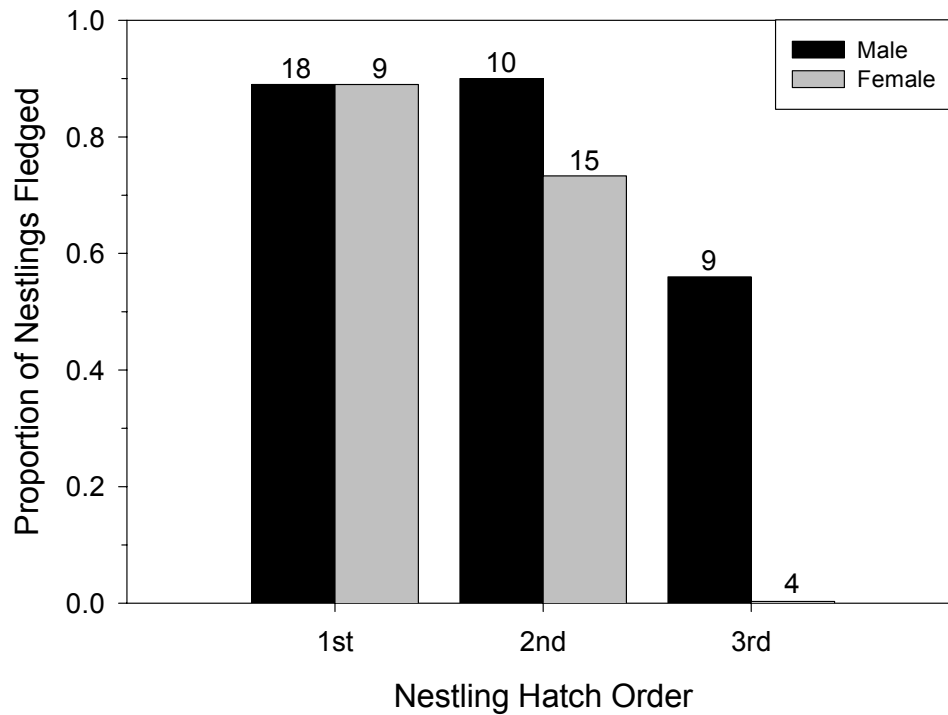


Figure 8.3. The proportion of brown falcon males (solid bars) and females (shaded bars) that survived to fledge in nests monitored with surveillance cameras according to nestling hatch order. Numbers above bars indicate sample sizes.

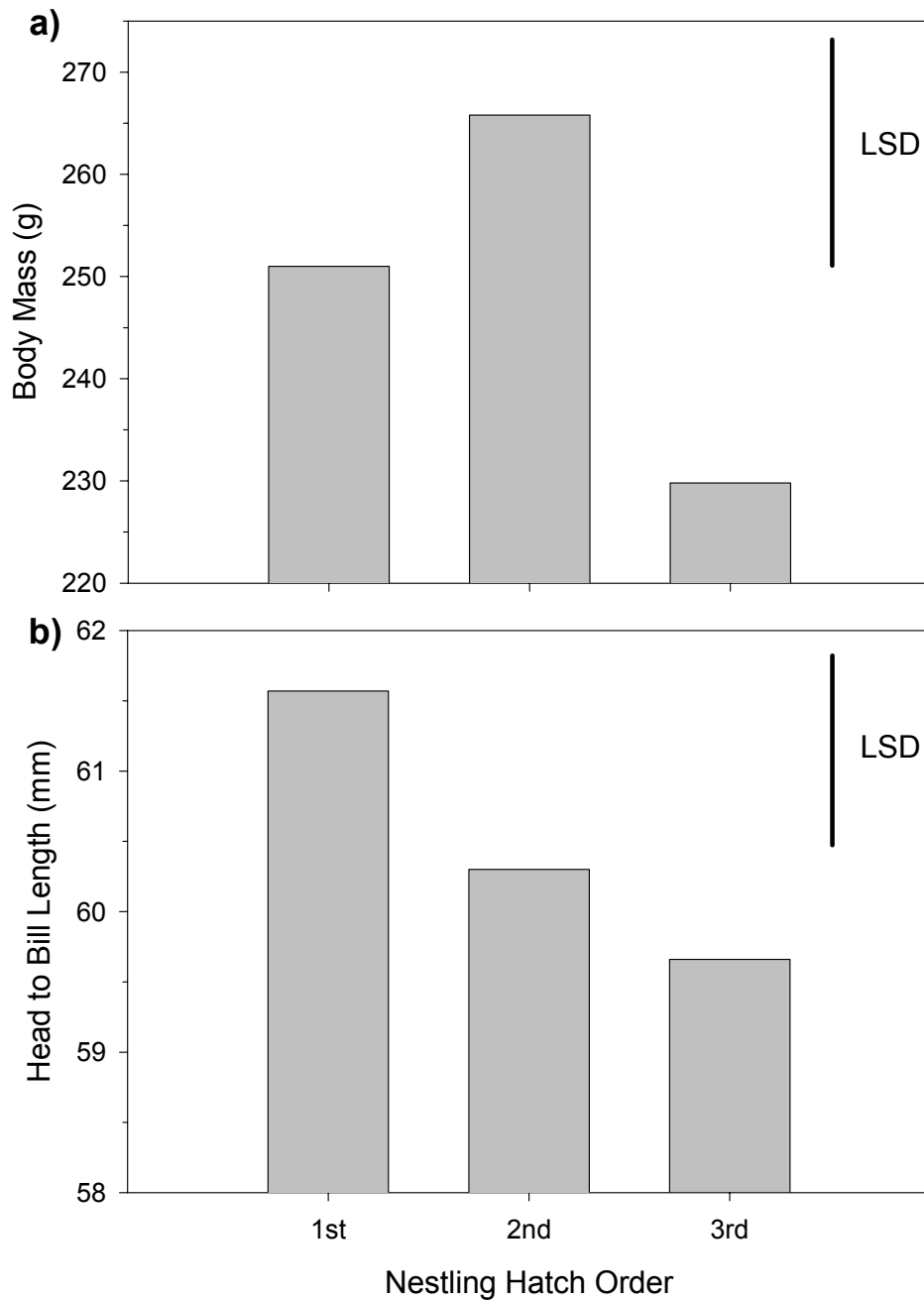


Figure 8.4. Body size of male nestling brown falcons according to hatch order for (a) body mass early; and (b) head to bill length late in the nestling phase. Bars indicate REML model predictions (Table 8.4) and lines least significant differences ($p < 0.05$).

Table 8.4. Summary of analyses of factors influencing the growth of wing length, head to bill length and body mass in male brown falcon nestlings aged 7-20 (a-c) or greater than 20 days old (d-f) using restricted maximum likelihood modelling. Random model utilised included pair, hatching order and year of measurement. Change in deviance statistics for each term initially included in the model are presented, significant terms emboldened ($p < 0.05$).

Term of interest	df	Change in deviance	<i>p</i> value
<i>Nestlings aged 7-20 days old</i>			
<i>a) Wing length</i>			
Age	1	1247.8	<0.001
Hatch order	2	4.8	0.09
Brood size	1	3.13	0.08
<i>b) Head to bill length</i>			
Age	1	337.7	<0.001
Hatch order	2	2.64	0.3
Brood size	1	5.63	0.02
<i>c) Body mass</i>			
Age	1	439.3	<0.001
Hatch order	2	8.36	0.02
Brood size	1	4.21	0.04
<i>Nestlings older than 20 days</i>			
<i>d) Wing length</i>			
Age	1	1528.5	<0.001
Hatch order	2	2.17	0.3
Brood size	1	1.7	0.2
<i>e) Head to bill length</i>			
Age	1	41.9	<0.001
Hatch order	2	8.8	0.01
Brood size	1	0.4	0.6
<i>f) Body mass</i>			
Age	1	39.1	<0.001
Hatch order	2	4.02	0.1
Brood size	1	1.3	0.3

territory the year they returned. Three females, 1 first and 2 second-hatched birds, were successfully recruited immediately upon returning to the study site. The fourth bird, a third (last-) hatched female, remained in the floating population for over 12 months before gaining a territory.

Discussion

Despite distinct RSD, male and female brown falcon offspring hatching either first or second were given equal amounts of food during the nestling period without a reduction in the probability of either sex fledging. Both sexes in these hatch orders were then recruited into the study population at the same age, indicating benefits to parents of raising each sex were similar. However, for third-hatched chicks, mothers tended to ignore daughters, feeding their last-hatched sons similar amounts to earlier-hatched nestlings, but supplying last-hatched daughters with much less prey. This reduction in food supply resulted in the death of all last-hatched female offspring for which food consumption was monitored, implying differences in the value of sexes raised in this hatch position.

Differential costs in raising sons and daughters in raptors with RSD

Considering only first and second-hatched offspring, no sex differences in egg volume or feeding rate (this study), incubation, nestling or post-fledgling parental care periods (McDonald in press *a*) were observed, indicating potential costs to parents in raising each sex were not different. Moreover, the sex ratio of a brood raised the previous year did not impose any costs upon parental survival or breeding in subsequent seasons (Chapter 6). While it is possible that the contents of eggs differed according to sex, based on current knowledge this seems unlikely as each

sex hatched at a similar size (McDonald in press *b*). Similarly, while larger female offspring were not given more mouthfuls of food, they may have been fed mouthfuls containing a different energy or nutritional content. This possibility was examined during viewing of videotapes and no evidence of sex-biased allocation of different prey species and/or tissues was observed (McDonald in press *a*).

Together, these data imply that females, despite being larger in this species, did not impose greater costs upon parents to raise to independence than their smaller male siblings. A lack of sex differences in food requirements in other dimorphic raptors has been described previously (Newton 1978; Collopy 1986; Newgrain *et al.* 1993; Brommer *et al.* 2003) and may reflect differential growth, behaviour and/or metabolism (e.g. Stamps 1990; Torres and Drummond 1999). Whatever the cause, it is now clear that sexual differences in food requirements in dimorphic birds are not as great as those predicted based upon body size differences alone (Newgrain *et al.* 1993; Krijgsveld *et al.* 1998; Torres and Drummond 1999), indicating that sex-specific costs should not necessarily be assumed *a priori* in dimorphic birds. As Fisher (1930) notes, it is the cost upon future reproductive value or success of parents that is the key factor in determining sex allocation, biased sex ratios are predicted only if sex differences in food requirements are sufficient to detract from future reproductive success of parents. For the brown falcon, this was not apparently the case.

Fisherian versus Trivers-Willard effects upon sex allocation patterns

A persistent hatch order effect on position during feeding events and subsequent growth and mortality rates is common in most asynchronously hatching altricial

birds (see Krebs 1999 for review). However, biased sex allocation by brown falcon mothers raising their last-hatched sons but not daughters cannot be explained by this phenomenon. The reduction in food supplied to daughters was sufficiently severe to result in the complete mortality of all last-hatched females monitored by surveillance cameras. These deaths cannot simply be explained by the larger sex being more prone to starvation (e.g. Teather and Weatherhead 1988; Slagsvold 1990). In any case, for this semi-altricial species, the greater reach or possible competitive ability during feeding events of larger female nestlings may well have been expected to lead to male-biased mortality patterns amongst last-hatched nestlings (Teather 1992; Anderson *et al.* 1993b, 1997). Moreover, as only female brown falcons fed offspring, differences in parental feeding strategies (e.g. Kilner 2002) are irrelevant. It is possible that nests monitored by surveillance cameras with a last-hatched female were all under food stress and thus would have suffered brood reduction regardless of offspring sex. Experimental evidence is required to discount this hypothesis completely, however, it appears unlikely as the lay date of each nest from which a last-hatched female perished was earlier than average for the respective year. As common to many other species, brown falcon nests laid earlier in the season have greater reproductive success (Chapter 6) and, by extension, are therefore less likely to be suffer food stress.

Two of the five classes of hypotheses accounting for adaptive sex allocation patterns (Cockburn *et al.* 2002) have relevance to brown falcons, Fisherian and Trivers-Willard effects. As fitness returns from last-hatched sons are likely to outweigh those of daughters in the same hatch position, the assumptions of Fisher's theory (1930) are not met, indicating Fisherian effects are also not influencing allocation patterns

amongst broods. However, the allocation of a greater amount of resources to last-hatched males compared to females matches the broad-scale predictions of the Trivers-Willard (1973) hypothesis, in that males in this position, due to sex-specific influences of body size upon intrasexual competition, exhibit a greater chance of providing fitness returns to parents with continued investment.

Last-hatched chicks were smaller than their earlier-hatched counterparts. Most critically, last-hatched falcons had smaller skeletal measurements (head to bill length) late in the nestling period, just prior to fledging. Growth is determinate in birds and, in skeletal terms at least, in falcons is all but completed at fledging (McDonald in press *b*). Disadvantages associated with poor nestling conditions prevail in later life in other birds (Thomas *et al.* 1999), including raptors (Appleby *et al.* 1997; Arroyo 2002), and two lines of evidence suggest that the small size of last-hatched brown falcon nestlings also persists into adulthood. Firstly, mortality of recently fledged raptors is characteristically high, with young birds generally possessing poor hunting skills and/or diets. In most species starvation is the main mortality factor in this period (see Newton 1979; Olsen 1995 for reviews). Given this, obtaining extra resources following fledging to complete compensatory growth appears unlikely in many bird species (Sedinger *et al.* 1995). Further, last-hatched brown falcon offspring recaptured in this study at 2 years of age (fully grown) were still relatively small, with a male ranked 46th ($n = 69$) and a female 79th ($n = 90$) largest in terms of skeletal size.

Previous research has demonstrated that in this species, initial male recruitment is independent of body size, although small immature males are more likely to retain

their territories in the year following recruitment. Thereafter body size did not influence reproductive success. However, amongst female falcons, those with larger skeletal measures are more likely to prevail in intrasexual competition and be recruited (Chapter 7). Thus small third-hatched offspring are not disadvantaged if they are male, but have little prospect of recruitment if they are female. Recruitment for the sample of offspring assessed in this study followed these patterns, with males from all hatch orders obtaining territories in the season they returned to the study site, yet only first and second-hatched females were able to do likewise. The only last-hatched female returning to the study site remained in the floating population for over 12 months before finally obtaining a territory in 2002, the worst breeding season recorded in the study. Drought conditions had prevailed in the study site for three consecutive years and many territories were vacant, indicating competition for territories was likely to be relaxed.

Successful recruitment of some small females may occasionally occur, thus if the rearing of these individuals does not impose a cost upon their earlier-hatched brood mates parents may occasionally gain some fitness from fledging these individuals. Consistent with the Trivers–Willard hypothesis, this is most likely to occur in good seasons, and indeed 5 last-hatched females fledged in 1999 in good conditions compared to just one during three subsequent breeding seasons of low reproductive success (Chapter 6). Similarly, parents of higher quality may be able to provide sufficient resources to overcome this last-hatched chick disadvantage for their female offspring more often and subsequently raise more last-hatched females without impacting upon their own fitness.

Acknowledgments

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Appendix 9.1.

The number taken and mean biomass of different prey items recorded in the diet of brown falcons *Falco berigora* sampled at the study site

Prey marked with an asterisk (*) have not previously been recorded in the diet of brown falcons.

Item	Age/size	Specific name	No. taken	Biomass per item (g)	Diet group [†]	Source of biomass [§]
<i>Mammals</i>						
House mouse		<i>Mus musculus</i>	159	17	2	5
Black rat	Adult	<i>Rattus rattus</i>	16	280	2	5
	Juvenile		1	100	2	5
Rabbit	Juvenile	<i>Oryctolagus cuniculus</i>	177	500	1	2
<i>Birds</i>						
Cattle egret		<i>Ardea ibis</i>	1	332	4	1
Black-shouldered kite		<i>Elanus axillaris</i>	1	290	4	1
Australian spotted crake		<i>Porzana fluminea</i>	3	67	3	1
*Baillon's crake		<i>Porzana pusilla</i>	1	18.5	3	1
Unidentified crake/rail			2	52	3	1
*Purple swamphen	Chick	<i>Porphyrio porphyrio</i>	1	50	3	9
Eurasian coot		<i>Fulica atra</i>	3	429	4	1
*Black-tailed native-hen		<i>Gallinula ventralis</i>	1	410	4	1
Unidentified Charadriidae			3	50	3	1
*Black-winged stilt		<i>Himantopus himantopus</i>	1	151.5	3	1
Silver gull		<i>Larus novaehollandiae</i>	34	328.1	4	1
*Spotted turtle-dove		<i>Streptopelia chinensis</i>	2	157.7	3	1
Feral pigeon		<i>Columba livia</i>	4	465	4	2
Crested pigeon		<i>Ocyphaps lophotes</i>	2	206.9	3	1
*Yellow-rumped thornbill		<i>Acanthiza chrysorrhoa</i>	1	9.34	3	1
Willie wagtail		<i>Rhipidura leucophrys</i>	1	20	3	1
Australian magpie		<i>Gymnorhina tibicen</i>	8	317.2	4	1
Richard's pipit		<i>Anthus novaeseelandiae</i>	56	27	3	2
Common skylark		<i>Alauda arvensis</i>	4	39	3	2
Unidentified pipit/skylark			3	33	3	2
House sparrow		<i>Passer domesticus</i>	6	26.81	3	1
*Welcome swallow		<i>Hirundo neoxena</i>	1	14.68	3	1
*Fairy martin		<i>Hirundo ariel</i>	1	11.49	3	1
European starling		<i>Sturnus vulgaris</i>	90	77.76	3	1

Appendix 9.1. (cont)

Item	Age/Size	Specific Name	No. taken	Biomass (g)	Diet group [†]	Source of biomass [§]
Unidentified small passerine			28	40	3	9
<i>Amphibians</i>						
*Eastern banjo frog		<i>Limnodynastes dumerilii</i>	5	25	2	4
Southern bell frog		<i>Litoria raniformis</i>	1	30	2	2
Unidentified frog	Large		2	27.5	2	2
	Small		2	10	2	4
<i>Reptiles</i>						
*Swamp skink		<i>Egernia coventryi</i>	3	20	2	3
*Blue-tongued lizard	Adult	<i>Tiliqua scincoides</i>	24	300	5	8
	<30 cm		1	60	5	8
Unidentified skink	>20 cm		1	30	2	3
	10-20 cm		1	20	2	3
	0-10 cm		21	10	2	3
Eastern tiger snake	> 1 m	<i>Notechis scutatus</i>	15	300	5	7
	15-75 cm		1	75	5	7
	c.15 cm		8	30	5	7
Unidentified large reptile			5	300	5	9
<i>Invertebrates</i>						
Coleoptera			6	2	2	2
Orthoptera			1	2	2	2
Unidentified invertebrate			19	2	2	9
<i>Carrion</i>						
Chicken leg		<i>Gallus gallus</i>	3	100	6	6
Sheep		<i>Ovis aries</i>	10	100	6	6
Unidentified			25		6	

[†]1: Lagomorphs, 2: Small ground prey, 3: Small birds, 4: Large birds, 5: Reptiles, 6: Miscellaneous. See Chapter 5 for details.

§Source of estimates

1. Baker, G. B., Dettmann, E. B., Scotney, B. T., Hardy, L. J. & Drynan, D. A. D. (1997). *Report on the Australian Bird and Bat Banding Scheme, 1995-96*. Environment Australia: Canberra.
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9. Estimated from mean weights of possible species recorded in the diet of falcons sampled in this study.

Appendix 9.2 – Brown falcon *Falco berigora* pair successfully raise

Australian hobby *F. longipennis* nestlings

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Summary

During a long-term study of the behaviour and ecology of the brown falcon *Falco berigora* in southern Victoria, a pair was observed successfully raising Australian hobby *F. longipennis* nestlings. This unusual observation is most likely a consequence of only a single nest site being available within the territory of both pairs.

Introduction

Although the brown falcon *Falco berigora* is one of Australia's most common and widespread raptors (Blakers *et al.* 1984; Baker-Gabb and Steele 1999), research into its ecology and behaviour has been relatively limited. In an attempt to rectify this deficiency, a long-term study of a large population in and around the Western Treatment Plant (38°0'S 144°34'E), approximately 35 km southwest of Melbourne, was initiated in 1999 and remains ongoing (M^cDonald 2003; in press *a, b*; M^cDonald

et al. in press). During this project an observation of brown falcons raising Australian hobby *F. longipennis* chicks was recorded and is reported here.

Observations

On 23 October 2002 a brown falcon nest was located by PM on the western edge of the study site. The nest appropriated was that of a little raven *Corvus mellori*, situated 17 m up a 22 m tall sugar gum *Eucalyptus cladocalyx* (Plate 1a). This nest site and height was typical for the focal pair (both sexes of which have been colour-banded since 1999), but is relatively high for the population as a whole (M^cDonald *et al.* in press). Owing to its precarious location, it was not possible to reach the nest safely. Given that no whitewash was evident below the nest and the incubating/brooding female quickly returned to the nest once flushed, the nest was considered likely to be in the incubation stage.

The nest site was next visited by PM on 15 November 2002. At this stage one nestling was clearly visible from the ground, while at least one other was partially obscured within the nest. Surprisingly, the visible nestling was an Australian hobby, readily identified by its distinct facial markings. From the amount of down still present upon its body, the nestling was estimated to be approximately 3 - 4 weeks old. The same pair of brown falcons observed in October was again present 50 m from, and within view of, the nest during this visit. No hobbies were observed in the nest area, despite a search of the entire nest-tree grove.

A further visit to the nest area was conducted at 1645 h on the afternoon 22 November 2002, by which time two nestlings were clearly visible from the ground.

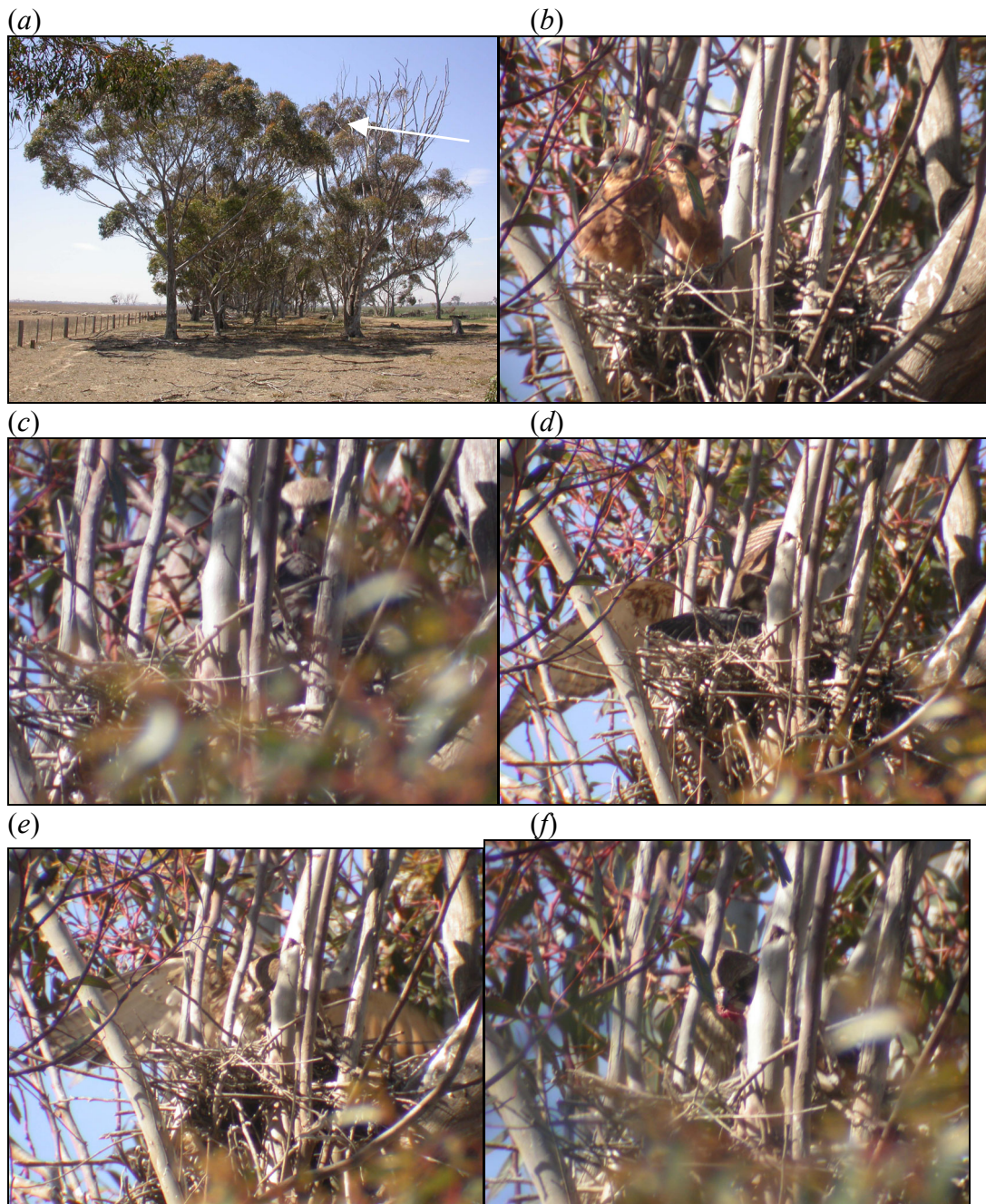


Plate 9.1. (a) The brown falcon *F. berigora* nest 17 m up a 22 m sugar gum *E. cladocalyx* (note arrow). (b) Two Australian hobby *F. longipennis* nestlings at the edge of the nest cup on 23 November 2002. (c-f) Female brown falcon feeding hobby nestlings later the same day with an unidentified prey item. Images © Nick P. Williams 2003 - FalconImages.com.

At this age the identity of both nestlings could clearly be confirmed as Australian hobbies when viewed through 10x magnification binoculars and a Nikon ED Fieldscope fitted with a 20x - 60x magnification eyepiece (Plate 1*b*). One chick appeared to have no down remaining on its body, while the other had just a few small tufts on its crown. Again, both sexes of brown falcon were in the general vicinity of the nest, with no sign of any other Australian hobbies present. When flushed from a perch on an emergent dead branch, offering a commanding view of the nest area, the adult female brown falcon flew over the nest tree, eliciting harsh begging calls from the nestlings, before returning to the same perch. On each of our visits to the nest site the female occupied this particular perch. The use of a favourite 'lookout' perch is typical behaviour of breeding female brown falcons with large nestlings (M^cDonald in press *b*). After confirming the identity and number of chicks, we left the area at 1730 h.

To determine which species was feeding the nestlings, NPW returned to the area at 1915 h that day and observed the nest area from approximately 600 m away until darkness fell at c. 2130 h. During this period the female brown falcon remained upon her favoured lookout perch for long periods, but at one stage drove off a passing whistling kite *Haliastur sphenurus* from the area. Throughout the observation no Australian hobbies were observed in the vicinity.

On 23 November 2002 NPW observed the nest area from the same location between 0830 and 1200 h. Between noon and 1745 h NPW moved to a new position 50 m from, and in sight of, the nest itself. Throughout most of this period the female brown falcon remained on her lookout perch within sight of the nest area. The

nestlings were active during much of the afternoon, preening, wing-stretching and emitting bouts of food-begging calls. They were not fed until 1628 h when the female brown falcon landed on the rim of the nest with a welcome swallow *Hirundo neoxena*, which was given whole to one of the nestlings. At 1701 h the female brown falcon again brought food to the nest, this time a small mammal, most likely a house mouse *Mus musculus*, which was again given whole to the well-grown nestlings. A third and final feeding event was witnessed at 1720 h. The female brown falcon received an unidentified prey item in an aerial food-pass from her male partner c.100 m east of the nest site. This larger prey item was then fed piecemeal to the young hobbies by the female brown falcon for 9 minutes (Plates 1c-f). A further visit to the nest area to observe post-fledging behaviour was not possible. However, both nestlings were likely to have successfully fledged within 2 - 3 days given their advanced stage of development.

Discussion

Intraspecific adoption or fostering of recently fledged individuals is common in many bird species, including several raptors (e.g. black *Milvus migrans* and red kites *M. milvus*: Bustamante and Hiraldo 1989; Northern hobby *F. subbuteo*: Dronneau and Wassmer 1989). Fostering of unrelated nestlings is sometimes observed within species following mate-replacement during a breeding attempt. This situation frequently arises during the incubation phase, where new female falcons may continue incubating the replaced bird's clutch (e.g. Ratcliffe 1993; Olsen and Stevenson 1996). Indeed, feeding of recently independent fledglings from other broods has been recorded in the focal brown falcon population (M^cDonald in press b).

However, interspecific adoption of nestlings is more rare, although several other natural and perhaps contrived cases have been reported overseas (e.g. Ratcliffe 1963, 1993; Baumgart 1971; Tlusty and Hamerstrom 1992; Watson *et al.* 1993; Watson and Cunningham 1996). Only two other Australian examples exist to the best of our knowledge. One is that of a black-breasted buzzard *Hamirostra melanosternon* pair raising a brood of nankeen kestrels *F. cenchroides* (Cupper and Cupper 1981). However in this situation the buzzards did not usurp the kestrel nest, rather the young kestrels were apparently taken from the natal nest as prey items. Once dropped within the buzzard nest the begging calls of the kestrel chicks may have elicited a maternal as opposed to a predatory response from the female buzzard (Cupper and Cupper 1981). The other report is of an Australian kestrel feeding recently fledged black falcon *F. subniger* nestlings in an apparently isolated incident (Cupper and Cupper 1981).

Given that Australian hobby eggs take 28 - 35 days to hatch, with a subsequent nestling period of 34 - 38 days (Marchant and Higgins 1993), the willingness of falcons to incubate eggs other than their own may provide an explanation for the behaviour reported here. With these incubation/nestling periods and the behaviour of the incubating brown falcon when first observed, it is likely that the hobby nest was taken over by the brown falcons before the eggs hatched. Since the study began in 1999, the territory of the focal brown falcon pair has also included a breeding pair of Australian hobbies. Thus the most likely scenario is that the resident pair of hobbies initiated a breeding attempt that was either aborted or usurped before the eggs hatched. Given the focal nest was the only suitable breeding site in both pairs' territories, competition for it was likely to have been intense. Post-fledging

observations could not be undertaken to determine if the brown falcon parents continued to feed their adopted brood once fledged.

These observations strongly suggest that brown falcons had successfully fostered an Australian hobby clutch and were intent on rearing the subsequent nestlings to fledgling. Although impossible to ascertain from current data, the behaviour of these hobby chicks at a breeding age would be of interest to determine whether they attempted to pair with other brown falcons or their own species.

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