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

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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, the brown falcon 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 (M^{c}Donald 2003*a*). 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 that vary from year to year in an unpredictable manner. Bet-hedgers have

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conservative life-history characters similar to those of *k*-selected species, but for a different reason. Bet-hedgers are believed 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, the reproductive and foraging ecology of the brown falcon has received little attention, with the exception of studies by Baker-Gabb (1982, 1984*a*, 1984*b*) and a review of the scattered, mainly anecdotal literature (Marchant and Higgins 1993). 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.

Materials and Methods

Study area and general field methods

The study was conducted between July 1999 and June 2002, approximately 35 km south-west 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*). The four main habitat types, defined by the principal land-uses, in the study area are *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 and resemble 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^{c}Donald 2003*b*). 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. On the basis of their unique plumage characters, small numbers of unbanded birds were identified as remaining on the same territory from year to year.

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 (Hoyt 1979):

$$0.51 \times \text{length} \times (\text{breadth})^2.$$

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, unpublished data). If eggs hatched, laying date was estimated using an incubation period of 36 days (M^{c}Donald 2004) and estimating chick age if unknown using formulae in M^{c}Donald (2003*b*). After hatching, nests were visited weekly to determine the number of birds that successfully fledged from each nest. A nesting attempt was classed as beginning when the first egg was laid, 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 were recorded.

During the breeding seasons of 2000 and 2001, more intensive diet assessments were made using 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 one-eighth 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 (see Appendix). No wastage factors were incorporated as brown falcons routinely cache larger prey items (Mooney 1982; M^{c}Donald 2004); 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). 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 the Appendix.

Statistical analyses

Logistic regressions were used to determine the significance of yearly differences in the proportion of pairs that occupied territories, that attempted to breed or that 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),

$$B = 1/\Sigma \mathrm{p}_1^{\,2},$$

where p_1 equals the proportion of a particular prey group in the diet, was used to calculate the breadth of the falcon's diet. Indices were standardised using the formula:

$$B_{\mathrm{STA}} = (B_{\mathrm{obs}} - B_{\mathrm{min}}) / (B_{\mathrm{max}} - B_{\mathrm{min}}),$$

where $B_{\mathrm{obs}} = B$ as calculated above, $B_{\mathrm{mi}n} = 1$ 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 (Pianka 1973),

$$\mathrm{O} = \Sigma \mathrm{p_i q_i} / (\Sigma \mathrm{p_i}^2/\Sigma \mathrm{q_i}^2)^{-2}.$$

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 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, d.f. = 1, $P = 0.36$) (Table 1); however, only in 2001 were unpaired birds present on territories. Yearly differences were detected in the proportion of pairs that attempted to breed (Wald statistic = 10.98, d.f. = 1, $P < 0.001$), with fewer pairs laying eggs each subsequent season studied (Table 1). Similarly, pairs also tended to be more successful in the first year of the study (Wald statistic = 3.92, d.f. = 1, $P = 0.048$) (Table 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 1). Clutch size was unaffected by year ($F_{2,84} = 0.11$, $P = 0.90$) (Table 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 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 1), as was the number of young fledged per successful nesting attempt ($F_{2,58} = 5.55$, $P = 0.006$) (Table 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%),

Table 1. Demographic and reproductive parameters of a brown falcon population monitored over three seasons

Mean ± s.e. are shown where appropriate. Values within rows followed by different superscript letters are significantly different ($P < 0.05$)

	1999	2000	2001	All
No. of pairs present	45	49	44	–
Area surveyed (km^2)	143.9	156.8	156.8	–
Density (km^2/pair)	3.2	3.2	3.56	–
No. of breeding pairs	40	38	26	–
Nearest nest distance (m)	1164.9 ± 66.6	1274.3 ± 73.9	1457.5 ± 77.3	–
G statistic	0.78	0.78	0.88	–
Laying date of 1st egg (September)	11th ± 2.5	15th ± 2.2	19th ± 2.2	t 15th ± 1.4
Clutch size	2.5 ± 0.1	2.5 ± 0.1	2.5 ± 0.1	2.5 ± 0.06
Clutch volume (cm^3)	–	105.1 ± 5.4	105.8 ± 5.8	105.4 ± 3.9
No. of successful pairs	29^a	19^b	13^b	–
Mean no. of fledged young				
Per breeding pair	1.8 ± 0.2^a	1.0 ± 0.2^b	1.0 ± 0.2^b	–
Per successful pair	2.5 ± 0.1^a	2.0 ± 0.2^b	1.9 ± 0.2^b	–

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 ± 3.2 (s.d.) m ($n = 104$; 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 $z = 5.01$; $z_{\mathrm{crit},0.05,120} = 2.99$, $P < 0.01$), with a mean angle of 74° (~ENE). However, nests were found through all aspects (10–350°) and those used within 45° of the mean angle were not more successful ($\chi^2 = 4.02$, d.f. = 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 ± 60 (s.e.) m. 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 ($G > 0.65$) (Table 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 3.2–3.6 km^2 throughout the study period (Table 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), and 28.9% remained intact at the conclusion of the study (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 most pairs stayed together (Table 2).

Territory fidelity for each sex was even higher, with no sexual differences evident ($\chi^2_4 = 1.04$, $P = 0.90$) (Table 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 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 ruptured only after 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%) the males and 40% of the 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 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

		1999–2000	2000–01
No. of pairs		45	49
Proportion of pairs faithful		0.64	0.41
Proportion of birds on same territory	Males	0.78	0.53
	Females	0.76	0.57
Proportion of birds remaining on study site	Males	0.8	0.61
	Females	0.8	0.63

Recruitment, philopatry and age at first breeding

Nine nestlings were observed returning to the study site as immatures; eight of these were successfully recruited into the breeding population. This gives a recruitment age of 2 years for females ($n = 4$) and 1.8 ± 0.25 (s.e.) years 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 recruited females obtained territories close to where they were raised, one male took over a territory adjacent to his natal territory, 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 these, 740 items were identified (Appendix). 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.

In total, 41 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 for specific names). The importance of rabbits was even 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 comprised 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 ~40 g; *large birds*, mainly non-passerines such as feral pigeons and silver gulls; and finally *reptiles*, comprising mainly blue-tongued lizards and eastern tiger snakes.

Each dietary group presents different problems for falcons with respect to their 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

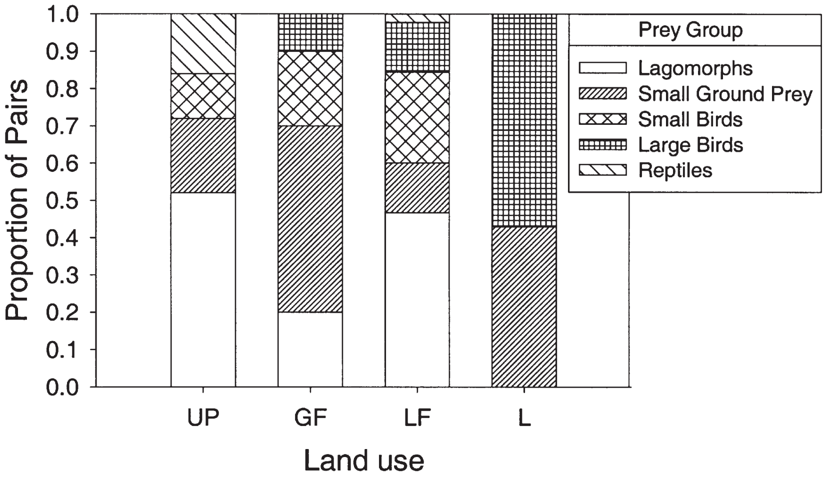

Fig. 1. The proportion of brown falcon pairs taking one of five dietary groups within each of four different land-use regimes in the study area. Land-use key: UP: untreated pasture; GF: grass filtration; LF: land filtration; L: lagoon areas. See Methods for explanation of land-use regimes.

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; and 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 calculations of dietary breadth (Greene and Jaksić 1983), this is not a major factor in this study because different pairs did not take different species from within each dietary group.

Diet – comparisons between pairs

Each pair of brown falcons consistently took most 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. 1), and therefore 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. 1). Large birds were mostly taken in lagoon regions, while small birds were preyed upon throughout. reptiles were taken only in Land filtration or Untreated pasture territories (Fig. 1). This association between prey choice and land-use is further evident when the diets of the twelve birds that changed territories during the study are examined. All of these individuals were found to have the same diet as the territory's

Table 3. Proportion of dietary overlap based on abundance (percentage of total prey taken) and biomass (percentage of total weight captured) of pairs of brown falcons predominantly taking one of five different dietary groups

Values vary between 0 and 1; the higher the value the greater the overlap. Values below the diagonal relate to abundance data; those above the diagonal relate to biomass data

Dietary group	Lagomorphs	Small ground prey	Small birds	Large birds	Reptiles
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 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. of 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

previous occupant, involving a switch from a different prey group in 10 cases (5 of each sex).

Dietary overlap in terms of abundance between pairs taking different dietary groups was minor (Table 3), with all but three comparisons having less than ~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 3), although even this figure can be considered moderate. Overlap indices based on biomass figures were generally even lower than those of abundance, being 15–44% for all but three comparisons (Table 3). The exceptions with a higher degree of overlap were those taking lagomorphs and smaller prey items (Table 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 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. 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).

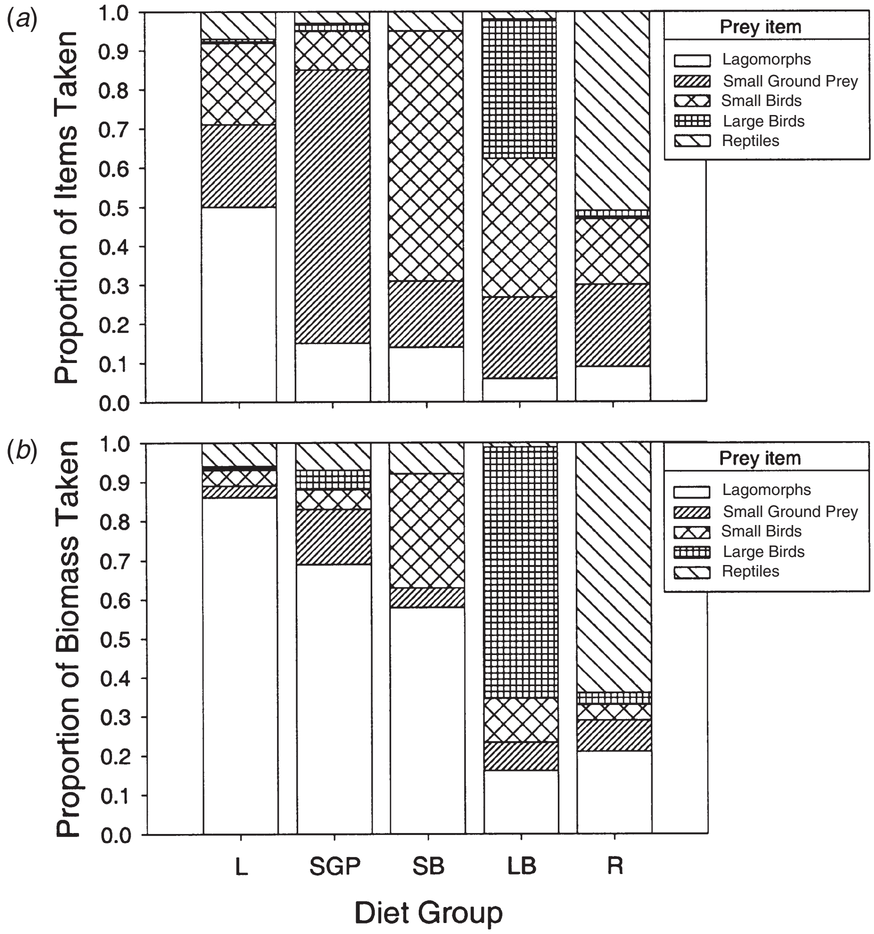

Fig. 2. The proportion of prey items in the diet of different pairs of brown falcons according to: (*a*) abundance (percentage of total number of prey items taken) and (*b*) biomass (percentage of total captured biomass). Pairs were classified as predominantly taking either lagomorphs (L), small ground prey (SGP), small birds (SB), large birds (LB) or reptiles (R).

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 bet-hedging theory, 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, yet in all years clutch size was unaffected by conditions. When storms were severe (2000 and 2001), smaller broods 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. Note that reductions in brood size were not a passive process due to low food availability but instead involved the selective allocation of resources amongst the brood by the female parent according to the sex and hatching order of the chicks (authors' unpublished data).

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 1984*a*). 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 2001*a*; 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 that 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 (M^{c}Donald, unpublished).

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, 1984*a*, 1984*b*; Marchant and Higgins 1993; Aumann 2001*a*). 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^{c}Donald, unpublished), 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^{c}Donald 2004). 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 that 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 after 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 territory fidelity were not apparent in brown falcons. Most individuals of both sexes occupied the same territory year after year, even after 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 that 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^{c}Donald

2004) 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 have been recorded more frequently outside the breeding season in other studies (Baker-Gabb 1984*a*, 1984*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^{c}Donald *et al.* unpublished), a relationship expected if females routinely captured larger prey items than did males.

Overall, the population had a very broad diet (B_{STA} = 0.721), with significant numbers of prey items being taken from such diverse groups as mammals, reptiles, birds and invertebrates. By comparison, most falcons have a relatively narrow diet breadth (Marti *et al.* 1993; Marchant and Higgins 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^{c}Donald, unpublished). 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 (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 (~150 km^2) 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 *et al.* (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 the availability and/or vulnerability of prey, 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 six birds 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 population's mean reproductive success as pairs that specialise upon small ground prey and small birds tend to have a lower reproductive success than those that prey upon other prey items, particularly lagomorphs (M^{c}Donald *et al.*, in press).

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

Prey items marked with an asterisk have not previously been recorded in the diet of brown falcons. Diet groups: 1, lagomorphs; 2, small ground prey; 3, small birds; 4, large birds; 5, reptiles; 6, miscellaneous. Source of biomass: 1, Baker et al. (1997); 2, Baker-Gabb (1982); 3, Clemann and Beardsell (1999); 4, personal communication, Jodi Rowley, Long Reef Frog Conservation Group; 5, Strahan (1995); 6, this study; 7, Watharow (2002); 8, Watharow and Reid (2002); 9, estimated from mean weights of possible species

Item	Age/size	No. taken	Biomass per item (g)	Diet group	Source of biomass
Mammals					
House mouse, *Mus musculus*		159	17	2	5
Black rat, *Rattus rattus*	Adult	16	280	2	5
	Juvenile	1	100	2	5
Rabbit, *Oryctolagus cuniculus*	Juvenile	177	500	1	2
Birds					
Cattle egret, *Ardea ibis*		1	332	4	1
Black-shouldered kite, *Elanus axillaris*		1	290	4	1
Australian spotted crake, *Porzana fluminea*		3	67	3	1
Baillon's crake, *Porzana pusilla**		1	18.5	3	1
Unidentified crake/rail		2	52	3	1
Purple swamphen, *Porphyrio porphyrio**	Chick	1	50	3	9
Eurasian Coot, *Fulica atra*		3	429	4	1
Black-tailed native-hen, *Gallinula ventralis**		1	410	4	1
Unidentified Charadriidae		3	50	3	1
Black-winged stilt, *Himantopus himantopus**		1	151.5	3	1
Silver gull, *Larus novaehollandiae*		34	328.1	4	1
Spotted turtle-dove, *Streptopelia chinensis**		2	157.7	3	1
Feral pigeon, *Columba livia*		4	465	4	2
Crested pigeon, *Ocyphaps lophotes*		2	206.9	3	1
Yellow-rumped thornbill, *Acanthiza chrysorrhoa**		1	9.34	3	1
Willie wagtail, *Rhipidura leucophrys*		1	20	3	1
Australian magpie, *Gymnorhina tibicen*		8	317.2	4	1
Richard's pipit, *Anthus novaeseelandiae*		56	27	3	2
Common skylark, *Alauda arvensis*		4	39	3	2
Unidentified pipit/skylark		3	33	3	2
House sparrow, *Passer domesticus*		6	26.81	3	1
Welcomeswallow, *Hirundo neoxena**		1	14.68	3	1
Fairy martin, *Hirundo ariel**		1	11.49	3	1
European starling, *Sturnus vulgaris*		90	77.76	3	1
Unidentified passerine		28	40	3	10
Amphibians					
Eastern banjo frog, *Limnodynastes dumerilii**		5	25	2	4
Southern bell frog, *Litoria raniformis*		1	30	2	2
Unidentified frog	Large	2	27.5	2	2
	Small	2	10	2	4
Reptiles					
Swamp skink, *Egernia coventryi**		3	20	2	3
Blue-tongued lizard, *Tiliqua scincoides**	Adult	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

(*continued overleaf*)

Appendix (*continued*)

Item	Age/size	No. taken	Biomass per item (g)	Diet group	Source of biomass
Eastern tiger snake, *Notechis scutatus*	>1 m	15	300	5	7
	15–75 cm	1	75	5	7
	~15 cm	8	30	5	7
Unidentified large reptile		5	300	5	9
Invertebrates					
Coleoptera		6	2	2	2
Orthoptera		1	2	2	2
Unidentified invertebrate		19	2	2	9
Carrion					
Chicken leg, *Gallus gallus*		3	100	6	6
Sheep, *Ovis aries*		10	100	6	6
Unidentified		25		6	