Assessment of band recoveries for four Australian falcon species

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Available band recoveries from 1958 to 2015 were analysed for the Nankeen Kestrel *Falco cenchroides* (n = 97, recovery rate 3%), Brown Falcon *F. berigora* (n = 78, recovery rate 6%), Australian Hobby *F. longipennis* (n = 13, recovery rate 11%) and Peregrine Falcon *F. peregrinus* (n = 97, recovery rate 8%). Nankeen Kestrels banded as adults (including age 1+) were recovered up to 732 km (mean 42 km) from the banding site and up to 7 years (mean 1.6 y) after banding; those banded as pulli/juveniles were recovered up to 822 km (mean 63 km) away and up to 5 years (mean 0.8 y) later. Adult Brown Falcons were recovered up to 409 km (mean 27 km) away and up to 11.7 years (mean 2.4 y) later and juveniles up to 2,047 km (mean 68 km) away and up to 18 years (mean 3.1 y) later. Hobbies were recovered up to 322 km (mean 45 km) from the banding site and up to 6.7 years (mean 1 y) after banding. Peregrine Falcons banded as pulli/ juveniles were recovered up to 7 years (mean 1.4 y) later and females up to 293 km (mean 79 km) away and up to 15 years (mean 3.2 y) post-banding. Most recoveries (42–85%, depending on the species) were of birds either found dead (cause unknown) or sick/injured/exhausted; human-related mortalities, either deliberate (persecution) or accidental (e.g. collisions, interactions with infrastructure), largely formed the balance of the reported public recoveries of each species.

INTRODUCTION

Available banding recovery data for the Nankeen Kestrel Falco cenchroides, Brown Falcon F. berigora, Australian Hobby F. longipennis and Peregrine Falcon F. peregrinus as at the early1990s were summarised by Marchant and Higgins (1993). A 25-year update was therefore sought, to ascertain whether further band recoveries had been obtained for these falcon species, and thus whether their movements could be further elucidated. In the interim, reports of studies of banded Kestrels around Canberra, Australian Capital Territory (Baker et al. 1997), Brown Falcons in southern Victoria (McDonald 2003; McDonald et al. 2003, 2004) and Peregrine Falcons in Tasmania and Victoria (Mooney and Brothers 1993; Emison et al. 1998) were published, and a noteworthy recovery of a Hobby has also been reported (Goodwin 2017; Anon. 2018). The few band recoveries for the Black Falcon F. subniger were discussed by Debus and Olsen (2011), and band re-sightings/recoveries and satellite tracking of the Grey Falcon F. hypoleucos were reported by Sutton (2011) and Schoenjahn (2018). It is acknowledged that other datasets for the four focal falcon species around Canberra and for Peregrines in Victoria (the latter foreshadowed by Hurley 2013a, b), will be published separately elsewhere by the researchers involved.

The present paper collates publicly available band recoveries to date for the four most numerous Australian falcon species, derived from the banding efforts of 53 banders (including SD and JO; Appendix 1). As well as summarising data on dispersal distances, dispersal directions and longevity, this compilation elucidates mortality factors. Region-specific dispersal distances, site fidelity, life tables, survival and/or mortality have already been calculated for Peregrines from the present dataset (Mooney and Brothers 1993; Emison *et al.* 1998). Some relevant aspects of Peregrine Falcon sociobiology based on individually-marked birds have also been published (e.g. Olsen and Stevenson 1996; Olsen *et al.* 2006).

METHODS

Recovery data for the four species of falcon from 1958 to 2015 were provided by the Australian Bird and Bat Banding Scheme (ABBBS, courtesy of D. Drynan); they resulted from the banding activities of 53 registered banders whose data were not under embargo (Appendix 1). The usable data exclude short-term (<1 month) recoveries of rehabilitated birds where the attempt to return them to the wild clearly failed (i.e. birds returned to care). For dispersal distance and direction, only those recoveries at least 5 km from the banding site were mapped (the appropriate resolution for the mapping scale in Figures 1-3). Distances are simple linear displacements, with no implication being made about the routes taken or where the birds may have been in the interim; they are therefore minimum distances travelled from the banding site. Here, 'road-killed' means known (not assumed) to have collided with a moving vehicle, as in the ABBBS definition. Ageing is as defined by the ABBBS codes, e.g. 1 + = first year or older, 2 = second year and 2+ = second year or older etc.

There were 97 usable recoveries for the Nankeen Kestrel (1996–2009), 78 for the Brown Falcon (1963–2008), 13 for the Australian Hobby (1975–1996) and 96 for the Peregrine Falcon (1958–2015). For the Kestrel, all but three individuals were banded before 2000 (mostly in the 1970s to 1990s); for the Brown Falcon, all but one were banded before 2000 (mostly in the 1990s); for the Hobby, all were banded before 2005 (mostly

in the 1990s), and for the Peregrine, all but six were banded before 2000 (mostly in the 1970s to 1990s).

For the Kestrel, almost half (n = 41) were aged at banding as a pullus/juvenile/first year bird (age 1), and of those about half were unsexed and the rest distributed quite evenly between the sexes. For the remainder (n = 56), the sexes were evenly split (with nine unsexed), and almost all were aged 1+ (two males 2+, one 3+; two females 2+).

For the Brown Falcon, almost half (n = 35) were aged at banding as a pullus/juvenile/first-year bird, and of those about one-third were unsexed and more were sexed as females (n = 15) than males (n = 9). Of the adults (n = 43), a few were aged 1+ but most were specifically aged as 2+ to 4+, with more females (n = 22) than males (n = 15) (and six unsexed).

For the Hobby, only three were aged at banding as a pullus/ juvenile/first-year bird (two of these unsexed), and five males and five females were aged 1+ or older (one male 2+, two females 2+). Age and sex classes were therefore pooled for analysis.

For the Peregrine, almost all were banded as pulli (n = 78), juveniles (n = 3) or first-year birds (n = 7), with the sexes being quite evenly represented (and 16 unsexed). Eight were aged as 1+ or older: one male 1+, two females 1+ and two females 2+, and the other three birds were unsexed.

Almost all recovered falcons originated in south-eastern Australia (eastern and southern New South Wales, Victoria and south-east South Australia), Tasmania and south-western Australia, and most were also recovered within these regions. Stated causes of recovery, as per ABBBS status codes, are enumerated herein, other than retraps or resightings (band number read in the field or inferred from colour bands) by banders of their 'own' birds. For the Kestrel, Brown Falcon and Peregrine, stated reasons for recovery (as per ABBBS codes in the dataset) were, in a few cases (n = 1-4 per species), given as 'captive bird (was from wild)', and so are excluded from analysis of recovery, as the circumstances were unclear (e.g. possible misinterpretation by rehabilitators of method of encounter codes). For Peregrine pulli, there were three cases in which only the band was returned without accompanying data (in the 1960s to 1980s, i.e. during the persecution era); we assumed that these individuals had been killed by, for example, pigeon fanciers or duck hunters and the time elapsed and distance travelled since banding were assumed to be valid (two of these were short, <1 year, 4 km and 52 km, and the third unexceptional in both respects, 12 km and <5 years).

The term 'migration' is used here in the usually accepted sense of regular biannual return movements between breeding and wintering areas.

Data analysis

Small sample sizes and many zero values precluded meaningful comparisons of the recovery distances by analysis of variance. We therefore present summary data which we interpret conservatively, particularly as standard deviations were usually large. Means are given ± 1 standard deviation.

Table 1

Distance (linear displacement) and time elapsed (years) of three falcon species and their age/sex classes banded and recovered in Australia. Juvenile = banded at age 1 (includes pulli); adult = banded at age 2+ or assumed so (i.e. aged as 1+ or older by bander; see text). M = male, F = female; *n* in parentheses. For median distances, see text.

Species	Distance (km)		Time (y)	
	range	mean	range	mean
Nankeen Kestrel:				
All (97)	0-822	51	0-7	1.3
Juveniles (41)	0-822	63	0-5.1	0.8
Juv. M (9)	0-267	39	0.02-2.4	0.9
Juv. F (11)	0-822	89	0-5.1	1.7
Adults (56)	0-732	42	0-7	1.6
Ad. M (23)	0-732	75	0-7	1.9
Ad. F (24)	0-110	15	0.01-6	1.1
Brown Falcon:				
All (78)	0-2,047	45	0-18	2.7
Juveniles (35)	0-2,047	68	0.01-18	3.1
Juv. M (9)	0-2,047	231	0.1-8.7	2
Juv. F (15)	0-47	8.4	0.01-15	2.2
Adults (43)	0-409	27	0-11.7	2.4
Ad. M (15)	0-41	9.8	0-11.7	2.7
Ad. F (22)	0-409	40	0.01-10.9	2.3
Peregrine Falcon:				
Juveniles (88)	0-333	62	0-15.3	2.2
Juv. M (34)	0-184	32	0.02-7.2	1.4
Juv. F (38)	0–293	79	0.1-15.3	3.2

RESULTS

Nankeen Kestrel

The recovery rate was 99 birds out of 3,634 banded (3%). Overall, Kestrels (n = 97) were recovered up to 822 km (mean 50.6 ± 145.5 km) from the banding site and up to 7 years after banding (Table 1). Of individuals that were aged (n = 96), those banded as juveniles (n = 41) appeared to be recovered farther from the banding site than those banded as adults (n = 55) (means 62.6 ± 156.6 km vs 42.4 ± 139.0 km). Of those that were sexed, juvenile females (n = 11) appeared to be recovered farther from the banding site than juvenile males (n = 9) (means 118.9 ± 255.8 km vs 39.3 ± 86.9 km), but adult males (n = 23) appeared to be recovered farther from the banding site than from the banding site than adult females (n = 24) (means 74.6 ± 209.3 km vs 15.0 ± 31.1 km). Dispersal directions varied widely, but with a possible slight north–south bias in south-eastern Australia and a notable movement from King Island to the Victorian mainland (Figure 1).

The median distance of recovery for adults of both sexes was 2 km; the median for all juveniles (including unsexed individuals) and for juvenile males was 4 km, and that for juvenile females was 24 km. For adult males, 78% were recovered within 20 km and 65% within 2 km of the banding site (48% *at* the banding site). For adult females, 88% were recovered within 20 km and 54% within 2 km of the banding site (33% *at* the banding site). For juveniles, 88% were recovered within 100 km and 83% within 50 km of the banding site (53% at or within 5 km of site: males 67% within 5 km and females 36% within 5 km).



Figure 1: Band recoveries for the Nankeen Kestrel in south-eastern Australia (>5 km, n = 42).

Kestrels banded as adults had a greater average and maximum longevity than those banded as juveniles. However, juvenile females appeared to have a greater survival rate than juvenile males, whereas adult males appeared to have a greater survival rate than adult females (Table 1). From limited datasets, 73% of Kestrels banded as pulli or juveniles were recovered in their first year; this percentage declined to 10% in their second and third years and to 2% in their seventh year. Of Kestrels banded as adults, 54% were recovered within a year (48% of males and 67% of females), but this percentage declined to 4% by the seventh or eighth year.

Even allowing for some cases of 'found dead' being euphemistic for clandestine persecution, most Kestrel recoveries were of birds found sick/injured etc. or the result of accidental interactions with vehicles or human infrastructure (Table 2).

Brown Falcon

The recovery rate was 80 birds out of 1,425 banded (6%). Overall, Brown Falcons (n = 78) were recovered up to 2,047 km (mean 45.5 ± 235.7 km) from the banding site and up to 18 years (mean 2.7 ± 3.9 years) after banding (Table 1). Of those that were aged, individuals banded as juveniles (n = 35) seemed to be recovered farther from the banding site than those banded as adults (means 68.2 ± 344.7 km vs 28 ± 71.8 km). Of the Brown Falcons sexed, juvenile males (n = 9) appeared to be recovered farther from the banding site than juvenile females (n = 15)(means 231.4 ± 680.9 km vs 8.4 ± 14.2 km), but this difference is more dubious because it is inflated by one exceptional long-distance recovery. Adult females (n = 22) seemed to be recovered farther from the banding site than adult males (n =15) (means 39.6 ± 94.6 km vs 9.8 ± 13.5 km). Excluding the outlier (a single movement from the arid zone to the tropics), for the temperate zone the mean recovery distances become 19.5 \pm 53.8 km (all individuals), 9.7 \pm 15.1 km (all juveniles) and 4.5 ± 12.7 km (juvenile males). Dispersal directions in southern Australia appear to be widely scattered, but with a north-south

Table 2

Reasons for band recoveries of four Australian falcon species, excluding re-traps/re-sightings of their 'own' birds by researchers.

Reason	Kestrel	Br Falcon	Hobby	Peregrine
Found dead ^A	14 (26%)	12 (28%)	7 (54%)	34 (41%)
Sick/injured/exhausted	14 (26%)	6 (14%)	4 (31%)	11 (13%)
Vehicle collision	3 (6%)	8 (19%)		5 (6%)
Found on/near road ^B	3 (6%)	3 (7%)	1 (8%)	9 (11%)
Window collision	2 (4%)		1 (8%)	
Collision with solid object				1 (1%)
Collision with wire etc.		1 (2%)		6 (7%)
Inside man-made structure	8 (15%)	1 (2%)		
Protect domestic animals	1 (2%)	1 (2%)		
Prevent aircraft strike		1 (2%)		
Trapped				4 (5%)
Poisoned ^C	3 (6%)			
Shot	1 (2%)	1 (2%)		3 (4%)
Seized by law enforcement ^D				1 (1%)
Electrocuted		1 (2%)		
Found near powerlines ^E		1 (2%)		3 (4%)
Taken by animal	1 (2%)			
Found dead in fresh water	1 (2%)			1 (1%)
Band/col. marking read in field	2 (4%)	3 (7%)		
Band found on bird, no data		3 (7%)		2 (2%)
Band only found, no data				1 (1%)
Total	53	43	13	83

^ACause unknown

^BNot certainly collided with vehicle

^cUnknown if intentional

^DWas dead

ENot certainly electrocuted/collided

bias and including notable movements from north-east South Australia to the south-west Kimberley (a juvenile) and from southern Victoria to Tasmania (a female aged 2+ at banding) (Figure 2).

The median distance of recovery of adult males was 6 km and of females 0 km; the median recovery distance for all juveniles including unsexed individuals was 4 km, but for juvenile males and females it was 0 km. For adult males, 87% were recovered within 20 km and 47% within 2 km (33% at the banding site). For adult females, 68% were recovered within 20 km and 59% within 2 km of the banding site (all the latter at the banding site). For juveniles, all except one (i.e. 97%) were recovered within 100 km and 94% within 50 km of the banding site (57% at or within 5 km of the banding site: males 78% within 5 km, females 60% within 5 km).

Longevity was similar across age and sex classes (Table 1), but was substantially influenced by re-sightings of colour-banded birds at one long-term study site. From the limited data, 40% of Brown Falcons banded as pulli or juveniles were recovered in their first year, declining to 23% in their second year, 11% in the third year and 3% by their eighteenth year. For those banded as adults, 44% were recovered within a year (40% of males and 41% of females), declining to 7% by the eleventh year.



Figure 2: Band recoveries for the Brown Falcon in Australia (>5 km, n = 35); Victoria and Tasmania.

At least some instances of 'found dead' (with bands reported or returned with no accompanying data) may be euphemistic for clandestine persecution. Nevertheless, most recoveries were either of birds found sick/injured etc. or the result of accidental interactions with vehicles or human infrastructure, including several interactions with wires and powerlines (Table 2).

Australian Hobby

The recovery rate was 15 out of 143 birds banded (11%). Overall, Hobbies were recovered 0-322 km (mean 45 km) from the banding site and 0.02-6.7 years (mean 1 year) after banding (n = 13). Three banded as juveniles were recovered 0–71 km from the banding site up to 0.9 year later. Combining all ages, five males were recovered 0-61 km (mean 25 km) away from the banding site within a year of banding (mean 1.4 years), but with one record (age 1+ at banding) of 6.7 years. Six females were recovered 0-322 km (mean 60 km) away from the banding site 0.02-3.3 years (mean 0.8 year) after banding (the oldest female was aged 2+ at banding, i.e. > 5 years old at recovery). A male aged 2+ (61 km) and a female aged 2+ (322 km) were recovered farther away from the banding site than those aged 1 or 1+ at banding (\leq 41 km, n = 9), except for one pullus recovered 71 km away from the banding site. These records are eclipsed by a juvenile having moved 920 km (in a northerly direction) during its first month of independence (Marchant and Higgins 1993), and a later record of a juvenile recovered 10.2 years after banding and 18 km away from the banding site (Goodwin 2017; Anon. 2018). Dispersal directions appeared to be widely scattered, with a slight north-south bias in southeastern Australia.

Recoveries were mostly of birds found dead or injured/sick/ exhausted, with cases also of a probable road kill and a window strike (Table 2). The Hobby reported by Goodwin (2017) was also fatally road-injured (*contra* 'released alive with band' as misreported by Anon. (2018), perhaps a status error in the ABBBS database).

Peregrine Falcon

The recovery rate was 96 out of 1,215 birds banded (8%). Overall, Peregrines (n = 96) were recovered up to 333 km (mean 60.17 ± 74.08 km) from the banding site and up to 15.3 years (mean 2.25 ± 3.27 years) after banding (Table 1). These birds were mostly banded as pulli or juveniles (n = 88). Juvenile females (n = 38) appeared to be recovered farther from the banding site than juvenile males (n = 34) (means 78.7 ± 75.5 km vs 32.2 ± 44.1 km; medians 58 vs 15 km). Most juveniles (80%) were recovered within 100 km of, and 18% at or near (i.e. within 5 km), the banding site; 32% of males and 8% of females were recovered at or near the banding site. Of eight banded at 1+ or an older age, a male (1+) was recovered 2 km away, two females aged 1+ were recovered 109 and 113 km away, respectively, and two females aged 2+ were recovered 0 and 8 km away, respectively. Dispersal directions appeared to be widely scattered, but with notable movements from Flinders Island to Tasmania but no detected movements between Tasmania and the Australian mainland (Figure 3). These movements are eclipsed by one additional record of a recovery at 500 km from the banding site, i.e. Canberra to Melbourne (Olsen and Debus 2014).

Longevity records were 15.3 years for a female and 7.2 years for a male (both banded as pulli), with juvenile females apparently surviving longer than juvenile males (Table 1). Fiftynine percent of the individuals banded as pulli or juveniles were recovered in their first year (68% of males, 50% of females).



Figure 3: Band recoveries for the Peregrine Falcon in south-eastern Australia (≥ 5 km, n = 78); Tasmania.

It is highly likely that the substantial number of recoveries of birds 'found dead', together with band recoveries having no accompanying data, and the number trapped, shot and confiscated (Table 2), reflects persecution by, for example, pigeon fanciers. Birds found injured etc., together with collisions (or probable collisions) with vehicles, wires and powerlines, collectively also figure prominently.

DISCUSSION

Recoveries and their interpretation are affected by small initial sample sizes and various other limitations in the datasets. Notable among these deficiencies are low recovery rates and the substantial proportion of birds not aged (other than 1+), despite the distinctive juvenile (first-year) plumage being moulted to adult or adult-like plumage at the end of the first year in Falco. Further, many recovered birds were not sexed, despite the existence of adult sexual dichromatism in Nankeen Kestrels and to some extent Brown Falcons, and sexual size dimorphism that is evident by banding age, especially in the Peregrine Falcon (Marchant and Higgins 1993; McDonald 2003; Hurley et al. 2007). Interpretation of recoveries by age or sex class is thus affected by the possibility that some birds aged as 1+ (lumped as 'adult' here) were either still juvenile or were 'floaters' not yet settled on a territory. Thus, the movements of the different age classes may be obscured. Furthermore, recoveries are biased by the continental distribution of both banding effort and human population densities conducive to the finding of banded birds by the public, i.e. a heavy bias towards south-eastern and southwestern Australia, with little chance of recoveries happening in the arid zone or tropics (Figures 1-3).

The band recoveries showed that all four species are capable of movements of hundreds of kilometres from the

banding site and, in one case, across the continent (>2,000 km). A larger dataset, analysed for season of recovery, might demonstrate seasonal movements or migration. Conversely, the data for all four species seem to suggest female-biased dispersal and male-biased philopatry, which is consistent with the findings of previous studies on these species (Olsen and Olsen 1987; Mooney and Brothers 1993; Baker *et al.* 1997; Emison *et al.* 1998; McDonald *et al.* 2004; Hurley 2013a, b). Overall, the available recoveries up to 2015 do further elucidate the movements, longevity and mortality factors of these four species beyond what was summarised for the period up to *c.* 1990 by Marchant and Higgins (1993).

Nankeen Kestrel

The recovery data suggest that juvenile females probably disperse farther than juvenile males, that some adults apparently move almost as far as juveniles, and that some adult males appear to move (migrate?) farther than adult females. Conversely, many adults appear to remain on, or return to, their territories. These findings are consistent with (a) indications of seasonal movement or migration at a continental scale, including an 'Inland, Mid to Top North' pattern (Marchant and Higgins 1993; Griffioen and Clarke 2002; Barrett et al. 2003; Johnstone et al. 2013), (b) dispersal or altitudinal migration from high latitudes and altitudes (i.e. cold regions) of some of the population, including breeding adults, in winter (Olsen and Olsen 1987; Baker et al. 1997; Cooper et al. 2014), and (c) previous conclusions about the movements (or philopatry) of age and sex classes (Olsen and Olsen 1987). The recovery data suggest that there is high juvenile mortality in human-inhabited landscapes in the first year and rather high annual adult mortality (minimum adult survival being 57 or 58% in a colour-banded population: Baker et al. 1997).

Brown Falcon

The recovery data suggest that (a) juveniles probably move farther from the banding site than adults, (b) juvenile males probably move farther than juvenile females, and (c) adult females probably move farther from the banding site than adult males. However, the juvenile and adult samples are both skewed by gender, and the single long-distance recovery (arid zone to the tropics) tentatively suggests that Brown Falcons in the arid zone may move farther than those originating in the temperate humid and sub-humid zones. Exclusion of this outlier, and the use of median rather than mean distances, modify these conclusions somewhat and suggest that in the temperate zone juvenile females may disperse farther than juvenile males. These findings are generally consistent with (1) inferred continentalscale or regional-scale movement of juveniles and other age classes, including altitudinal movements at high elevations and an 'Inland, Mid to Top North' movement pattern, and (2) site fidelity (or philopatry) and local winter movements of breeding adults (Marchant and Higgins 1993; Griffioen and Clarke 2002; Barrett et al. 2003; McDonald et al. 2003, 2004; Johnstone et al. 2013; Cooper et al. 2014; Corbett et al. 2014). In productive temperate environments, breeding adults are sedentary on their home ranges (M^cDonald 2003). The recovery data suggest that high juvenile mortality occurs in human-inhabited landscapes in the first year and that there is rather high annual adult mortality (~40%).

Australian Hobby

The few available data suggest that some adults disperse or migrate and that females apparently disperse or move farther than males. There is little to add to previous inferences that Hobbies make continental-scale or regional-scale seasonal migrations, including altitudinal migration and a north–south movement (Marchant and Higgins 1993; Barrett *et al.* 2003; Johnstone *et al.* 2013; Cooper *et al.* 2014). However, Griffioen and Clarke (2002) found only suggestive evidence of local movements. Nevertheless, over three survey trips to Sumba in the austral winter (June–July) and summer (December–January), Hobbies resembling Australian birds (rather than the smaller *F. l. hanieli* resident on other Lesser Sunda Islands) were observed, apparently wintering, only in July (Olsen and Trost 2007).

Peregrine Falcon

The data show that juvenile females probably disperse farther than juvenile males, and suggest that other than two birds (aged 1+) which may have been 'floaters', adults tend to remain near the banding site. These findings, and the high mortality of juveniles (especially males), are consistent with findings in previous studies (Marchant and Higgins 1993; Mooney and Brothers 1993; Emison *et al.* 1998; Hurley 2013a).

One of the Peregrine recoveries was a re-sighting of a male, banded by JO as a pullus in a cliff nest, breeding in a stick nest in a tree ~ 20 km from its natal site. This record represented, at the time, the first published report of a banded Peregrine Falcon fledging from a cliff nest and breeding successfully in a treenest, i.e. changing its nesting 'tradition' (see further discussion by Olsen *et al.* 2006 and Hurley 2009). Olsen *et al.* (2006) postulated that cliff and tree nests were close together in their study area, so Peregrines fledged from cliffs could readily move to nests in trees; their study 'did not confirm Kirmse's (2004) claim that selection of tree-nest sites by breeding Peregrines is totally determined by imprinting to the natal nest-site' and that, because cliff sites are saturated in Australia, 'tree-nesting pairs remain sparsely distributed among cliff-nesting pairs and... the two types of nesters may mix more often than was once believed'. This conclusion was confirmed with a larger sample by Hurley (2013b), who recorded that 9% of natal dispersals were from a cliff to a stick nest, and that 'atypical' natal dispersals from one nest type to another accounted for 30% of dispersals (n = 101).

There is evidently some continental-scale movement by Australian Peregrines, apparently particularly of juveniles and floaters (Marchant and Higgins 1993; Barrett et al. 2003; Johnstone et al. 2013). However, Griffioen and Clarke (2002) found only suggestive evidence of a confused pattern of movements. The situation may be confounded by the occurrence in the austral summer of Northern Hemisphere migratory subspecies from northern Asia (notably F. p. calidus and possibly japonensis) in northern Australia mainly, but potentially anywhere in Australia, including the far southern mainland (Johnstone et al. 2013; Anon. 2014, 2015, 2017). These boreal migrants may be overlooked among Australian Peregrines, although they are recognisable by their narrow malar stripe, white auriculars and less chunky build (e.g. Menkhorst et al. 2017). Migratory F. p. calidus certainly reach southern Africa (Meyburg et al. 2018), so the same thing may happen in Australia. It is worth noting that the high mobility of Australian Peregrines, among other evidence, argues against the recognition of alleged, but invalid, south-western Australian F. p. submelanogenys (see Olsen and Debus 2014, contra White et al. 2013).

Conclusions

The different causes of mortality among the four falcon species are consistent with aspects of their ecology and foraging behaviour. For instance, the Nankeen Kestrel is a slow-flying, perch-hunting and hovering, roadside-frequenting generalist that commonly inhabits managed farmland (crops etc.) and thus may be susceptible to agricultural poisons (rodenticides, insecticides), and it frequents buildings. The similar, but larger Brown Falcon, with its larger wingspan, sometimes scavenges road-kill and may be more prone to collisions with or electrocutions on power poles or lines. The Australian Hobby and Peregrine Falcon are fast-flying bird-chasers, more prone to collisions with poorly visible human-created hazards (wires etc.) and vehicles, and they may be more vulnerable to injury because they take more prey that are more difficult to capture. The Peregrine is (or was) also prone to persecution (e.g. Marchant and Higgins 1993; Olsen and Stevenson 1996; Scuffins 2003; Olsen 2014), which was partly driven by pigeon-fanciers' myths concerning the supposed origin of killed Peregrines found to be wearing ABBBS bands (Mooney 2013).

It is apparent that there has been a general decline in research on Australian raptors, except for the charismatic and secure species such as the Peregrine Falcon and Wedge-tailed Eagle *Aquila audax*, precisely at a time when many other species, even those common in farmland, are declining (e.g. Barrett *et al.* 2003; Cooper *et al.* 2014). This reduction in research is self-evident from the decade(s) in which members of the species examined here were banded, i.e. mostly pre-2000 (see 'Methods'). The decline in research somewhat reflects increased bureaucracy (mainly animal ethics and other permit requirements and fees), the consequent demise of the enthusiastic amateur, and perhaps other technologies replacing banding. For instance, traps with live lures cannot now be used in some States at least, but models and wind-up lures do not sufficiently attract the interest of, for example, Brown Falcons (N. Mooney pers. comm.). On the other hand, radio/GPS tracking is becoming popular and its use is attractive to funding bodies and students, although it is expensive.

To better understand the ecology and life history of the declining species, further banding/colour-banding research is required to obtain estimates of survival and mortality and life tables etc., and to further elucidate movements of age classes. For instance, with larger datasets incorporating the currently researcher-embargoed ones, it is already possible to 'animate' seasonal recovery maps of the more frequently banded/recovered species to reveal dispersal or migration patterns (Drynan 2014). Satellite telemetry, as well as helping in documenting homerange and habitat use at the local scale, can reveal hitherto unsuspected continental-scale movement by breeding adults (e.g. Little Eagle Hieraaetus morphnoides: Drynan 2017), which have since been confirmed as return migration to the breeding territory through the sighting of colour-bands and from transmitters (Dabb 2018; Olsen and Trost 2018). It is likely that similar return migration would be detected by satellite telemetry of some of the Australian falcons now that satellite transmitters are small enough to be fitted to kestrel-sized, adult raptors.

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REFERENCES

- Anon. [=Editor, S. Debus] (2014). Northern Hemisphere Peregrine subspecies in Australia. *Boobook* 32, 38.
- Anon. (2015). Siberian Peregrine in southern Victoria. Boobook 33, 14.
- Anon. (2017). Another Siberian Peregrine in south-eastern Australia. Boobook 35, 8.
- Anon. (2018). Recovery round-up. Corella 42, 107-109.
- Baker, G. B., Olsen, P., McCulloch, R. and Dettman, E. B. (1997).
 Preliminary results of a long-term study of the Nankeen Kestrel:
 Population density and turnover. In *Australian Raptor Studies II* (Eds. G. Czechura and S. Debus), pp. 108–113. Birds Australia Monograph 3, Birds Australia, Melbourne.
- Barrett, G., Silcocks, A., Barry, S., Cunningham, R. and Poulter, R. (2003). *The New Atlas of Australian Birds*. RAOU, Melbourne.
- Cooper, R.M., McAllan, I.A.W. and Curtis, B.R. (2014). An Atlas of the Birds of New South Wales & the Australian Capital Territory, Volume 1: Emu to Plains-wanderer. NSW Bird Atlassers Inc., Sydney.

- Corbett, L., Hertog, T. and Estbergs, J. (2014). Diet of 25 sympatric raptors at Kapalga, Northern Territory, Australia 1979–89, with data on prey availability. *Corella* 38, 81–94.
- Dabb, G. (2018). An inconvenient eagle. Canberra Bird Notes 43, 132–137.
- Debus, S. J. S. and Olsen, J. (2011). Some aspects of the biology of the Black Falcon *Falco subniger*. *Corella* **35**, 29–36.
- Drynan, D. (2014). Results from raptor banding. *Corella* 38, 48. [Abstract of conference presentation, ABSA/BirdLife Southern NSW, Canberra, March 2014.]
- Drynan, D. (2017). Billboard. Flightlines 32, 5.
- Emison, W. B., Hurley, V. G., White, C. M. and Brimm, D. J. (1998). Results from a banding study of Peregrine Falcon chicks in Victoria, 1972–1997. *Corella* 22, 87–91.
- Goodwin, W. (2017). Band recovery of an Australian Hobby in Perth. *Boobook* **35**, 8.
- Griffioen, P. A. and Clarke, M. F. (2002). Large-scale bird-movement patterns evident in eastern Australian atlas data. *Emu* 102, 99–125.
- Hurley, V. G. (2009). An assessment of nest site imprinting in Peregrine Falcons Falco peregrinus macropus in Australia. In: Peregrine Falcon Populations: Status and Perspectives in the 21st Century (Eds. J. Sielicki and T. Mizera), pp. 263–274. Turul Publishing and Poznań University of Life Sciences Press, Poznań, Poland.
- Hurley, V. G. (2013a). Peregrinations: Patterns of natal dispersal and nest selection by Peregrine Falcons *Falco peregrinus macropus* and lifetime consequences [conference abstract]. *Boobook* **31**, 73.
- Hurley, V. G. (2013b). Factors affecting breeding success in Peregrine Falcons (Falco peregrinus macropus) across Victoria from 1991– 2012. PhD thesis, Deakin University, Burwood, Melbourne.
- Hurley, V. G., Hogan, F., White, J. G. and Cooke, R. (2007). A morphological model for sexing nestling Peregrine Falcons (*Falco peregrinus macropus*) verified through genetic analysis. *Wildlife Research* 34, 54–58.
- Johnstone, R. E., Burbidge, A. H. and Darnell, J. C. (2013). Birds of the Pilbara region, including seas and offshore islands, Western Australia: distribution, status and historical changes. *Records of the Western Australian Museum* 78, 343–441.
- Kirmse, W. (2004). Tree-nesting Peregrines Falco p. peregrinus in Europe did not recover. In Raptors Worldwide (Eds. R. D. Chancellor and B.-U. Meyburg), pp. 271–277. World Working Group on Birds of Prey and Owls, Berlin and BirdLife Hungary, Budapest.
- Marchant, S. and Higgins, P. J. (Eds.) (1993). Handbook of Australian, New Zealand and Antarctic Birds, Volume 2: Raptors to Lapwings. Oxford University Press, Melbourne.
- M^cDonald, P. G. (2003). Variable plumage and bare part colouration in the Brown Falcon, *Falco berigora*: The influence of age and sex. *Emu* **103**, 21–28.
- M^cDonald, P. G., Olsen, P. D. and Baker-Gabb, D. J. (2003) Territory fidelity, reproductive success and prey choice in the Brown Falcon, *Falco berigora*: A flexible bet-hedger? *Australian Journal of Zoology* **51**, 399–414.
- M^cDonald, P. G., Olsen, P. D. and Cockburn, A. (2004). Weather dictates reproductive success and survival in the Australian Brown Falcon *Falco berigora*. *Journal of Animal Ecology* **73**, 683–692.
- Menkhorst P., Rogers, D., Clarke, R., Davies, J., Marsack, P. and Franklin, K. (2017). *The Australian Bird Guide*. CSIRO Publishing, Melbourne.

- Meyburg, B.-U., Paillat, P., Meyburg, C. and McGrady, M. (2018). Migration of a Peregrine Falcon *Falco peregrinus calidus* from Saudi Arabia to Cape Town as revealed by satellite telemetry. *Ostrich* **89**, 93–96.
- Mooney, N. (2013). The falcon wars. *Wildlife Australia* Summer 2013, 9–13.
- Mooney, N. and Brothers, N. (1993). Dispersion, nest and pair fidelity of Peregrine Falcons *Falco peregrinus* in Tasmania. In: *Australian Raptor Studies* (Ed. P. Olsen.), pp. 33–42. Australasian Raptor Association, RAOU, Melbourne.
- Olsen, J. (2014). Australian High Country Raptors. CSIRO Publishing, Melbourne.
- Olsen, J. and Debus, S. (2014). Some misconceptions about Australian Peregrines. *Boobook* **32**, 42–44.
- Olsen, J. and Stevenson, E. (1996). Female Peregrine Falcon *Falco peregrinus* replaces an incubating female and raises her young. *Australian Bird Watcher* **16**, 205–210.
- Olsen, J. and Trost, S. (2007). Diurnal raptors on the island of Sumba, Indonesia, in June/July and December/January 2001–2002. *Australian Field Ornithology* **24**, 158–166.

- Olsen, J. and Trost, S. (2018). Little Eagle returns from Daly Waters to Canberra. *Boobook* **36**, 7.
- Olsen, J., Fuentes, E., Dykstra, R. and Rose, A. B. (2006). Male Peregrine Falcon *Falco peregrinus* fledged from a cliff-nest found breeding in a stick-nest. *Australian Field Ornithology* 23, 8–14.
- Olsen, P. D. and Olsen, J. (1997). Movements and measurements of the Australian Kestrel, *Falco cenchroides*. *Emu* 87, 35–41.
- Schoenjahn, J. (2018). Adaptations of the rare endemic Grey Falcon Falco hypoleucos that enable its permanent residence in the arid zone of Australia. PhD thesis, University of Queensland, Brisbane.
- Scuffins, M. (2003). Injury and illness in wild Victorian birds of prey. Australian Field Ornithology 20, 85–93.
- Sutton, A. J. G. (2011). Aspects of the biology of the Grey Falcon Falco hypoleucos in the Pilbara region of Western Australia. Corella 35, 11–15.
- White, C., Cade, T. and Enderson, J. (2013). *Peregrine Falcons of the World*. Lynx, Barcelona.

Appendix 1

List of people who banded falcons in the dataset used in this study.

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N. J. Favaloro J. L. Gardner D. J. Geering J. W. Hardy J. G. K. Harris K. Henderson M. C. Holdsworth J B Hood B. R. Hutchins J. Klapste W. L. Klau N W. Kurtz S. G. Lane R.G. Lonnon K. W. Lowe I. McCallum P. G. McDonald E. J. McKenzie

N. Mooney O. P. P. Mueller M. T. Murn J Olsen P. R. Pain G. R. Park D. C. Paton M. R. Pople D. I. Smedley Taronga Zoo Rehab Program M. T. Templeton G. H. Underwood M. H. Waterman OAM R. M. Warneke Wild Bird Rehabilitation Group J. T. Willows S. J. Wilson