# Breeding biology, behaviour and foraging ecology of the Black Falcon Falco subniger near Tamworth, New South Wales

# S. J. S. Debus<sup>1</sup>, A. L. Bauer<sup>1</sup> and G. I. Mitchell<sup>2</sup>

<sup>1</sup>Division of Zoology, University of New England, Armidale, New South Wales 2351 (Email: sdebus@une.edu.au) <sup>2</sup>17 Kyooma Street, Hillvue, New South Wales 2340

> Received: 10 May 2017 Accepted: 24 July 2017

The breeding biology and behaviour of the Black Falcon Falco subniger were studied in the Tamworth district (northern inland New South Wales) through 146 hours of observation over 47 days in 2015 (one pair, pre-laying to early incubation) and 261 hours of observation over 69 days in 2016 (four pairs, pre-laying to fledging, with checks through the post-fledging period). Pellets were collected from under vacated nests. Aerial displays (e.g. agility, V-dives, 'undulatory roll,' 'high winnowing'), nest-site selection and occupation, courtship and mating are described. Adopted stick nests were high in tall or emergent riparian or paddock eucalypts; nearest-neighbour distances averaged 10.25 km (range 9-12 km). Eggs were laid in July, and the incubation period appeared to be 34 ± 1 days at one nest. Males took a minor share of incubation (1-3% of daylight) and brooding of hatchlings (1%). Interspecific conflict or nest-site defence was strongest against corvids in the pre-laying phase, and against Wedge-tailed Eagles Aquila audax during the nestling phase. Feeding rates and estimated biomass provision were 0.09-0.26 item/h and ~4-28 g/h at nests that failed during the incubation or hatchling phase, and 0.19 item/h and ~23 g/h to a single nestling that fledged, albeit underweight. Nest failure appeared to be related to cold, wet weather and poor hunting success around hatching time. Breeding productivity was 0.25 young per attempt in 2015–16, and 0.5–0.6 young per attempt for 10 nests since 2004, with up to half of fledglings failing to reach independence. The observed breeding diet was 98% birds and 2% rodents, although insects appeared in pellets. Hunting success on birds was 36% of observed attacks. Demographic and ecological research on this species is required. As the threatened and declining Black Falcon faces human-related impacts in the sheep-wheat belt, some possible management strategies are suggested (e.g. artificial nests).

# **INTRODUCTION**

The breeding behaviour and parental time-budgets of the Black Falcon Falco subniger have been partly described, with quantification for the second half of the nestling period (Debus et al. 2005; Charley et al. 2014). Some males share incubation and brooding of downy nestlings, but the relative contribution of the sexes to parental care is unquantified (Debus and Zuccon 2013; Charley et al. 2014; Whelan et al. 2016). Some aspects of aerial displays, courtship (including supplementary feeding of the female by the male) and mating have been described briefly, with limited data on copulation rates in the pre-laying period being documented (Debus et al. 2005; Debus and Tsang 2011; Whelan 2013; Whelan et al. 2016). The post-fledging dependence period has also been described (Charley et al. 2014; Whelan et al. 2016). Although much is thus known about the breeding biology of this species, there are still significant gaps in our knowledge.

The present study attempted to fill remaining gaps on parental behaviour and time-budgets by quantifying pre-laying behaviour and sex-roles during the incubation and early nestling phases. A comparable study has been published on the related Grey Falcon *F. hypoleucos* (Ley and Tynan 2016). The Black Falcon belongs in the heirofalcon ('great' or 'desert' falcon group – Lanner Falcon *F. biarmicus* and relatives) and the Grey Falcon is basal to the heirofalcon/Peregrine Falcon *F. peregrinus* divergence (Fuchs *et al.* 2015).

During our attempt to more completely document the breeding cycle and ecology of the Black Falcon in an agricultural environment, one observed breeding attempt in 2015 failed early in incubation, so we resumed the study in 2016. Here we report observations on four pairs in 2016 and include observations from other territories in the study area where they supplement existing published information. The observations presented here are either novel for the pre-laying, incubation and early nestling periods or confirm with data from previously unstudied pairs that certain behaviours are apparently typical for the species.

## **METHODS**

The study area in the Peel Valley near Tamworth ( $31^{\circ}05'S$ ,  $150^{\circ}55'E$ ), in the sheep–wheat belt of northern inland New South Wales, extended to the localities of Warral, Bithramere and Bective (up to ~20 km from Tamworth), as described previously (Debus *et al.* 2005; Debus and Tsang 2011; Debus and Zuccon 2013; Charley *et al.* 2014). In this region, the summer of 2015–16 was notably hot and dry, whereas late winter–early spring of 2016 was cold, with extended rainy periods.

The observation protocol comprised focal-animal sampling from an unconcealed position on the ground outside the falcons' alert distance using telescopes and binoculars, and occasionally digital photography. Initially, observations were conducted from approximately 200 metres (m) away, but then we gradually moved over the next two weeks to approximately 100 m away from the nest when it was clear that the falcons were not alarmed by non-threatening human presence (e.g. in a car used as a hide). Observation distances, and tree and nest heights, were measured with a range finder after nests were vacated.

In 2015, after monitoring the Warral site since April, we observed the pair there (Pair/Site 1) for 102.5 hours over 31 days from the date of the first observation of copulation until the last day that the male was present (21 July) (Table 1), and then until the female abandoned the nest. In the inferred laying phase and at the start of incubation, daily watches finished at dusk and started at first light to determine the female's overnight location. We observed for a further 25 hours over the following 10 days from 22 July, observations being spread fairly evenly through daylight hours (3-6 h per day). When a new male appeared in late August, we observed the nest for a further 18 hours over six days (28 August to 4 September), with our observations again being spread fairly evenly through daylight hours (2-4.5 h per day), until the falcons were out-competed for the nest (see later) and left the vicinity. The new male was readily distinguished by having much paler cheeks than the original male.

In 2016, we monitored Site 1 from late April and Pair/ Site 2 (the airport site of Debus et al. 2005) by conducting a fortnightly transect from 14 May along a circuit taking in these two sites and a third one (see below and Fig. 1 of Bauer and McDonald, in press). When a pair was clearly occupying each site, we commenced timed nest-watches (Table 1). The Pair 1 female was apparently the same individual as in 2015 based on plumage, behaviour and other characters, and the male was apparently the new one of August 2015 with pale cheeks. The female was the more pale-cheeked member of Pair 2; thus both pairs were somewhat plumage-dichromatic as well as sizedimorphic, enabling identification of sitting individuals when only the head was visible over the nest rim. We observed Pair 2 for 123.5 hours over 25 days (17 July to 27 August) from the pre-laying (two days) and laying stages (three days) through incubation (20 days) and to nest failure at the point of hatching (Table 1). Incubation was inferred from behavioural cues; early in this phase the female visibly rolled eggs beneath her as she settled in the nest.

In early August 2016, we found the nest of a pair at Bithramere (Pair/Site 3) (the 'Tamworth' site of Charley *et al.* 2014) during incubation and observed the nest of a further pair at Bective (Pair/Site 4) from the downy chick stage in mid-September, as follows:

Nest 3: 68 hours over 13 days (27 August to 13 September), until nest failure four days after hatching.

Nest 4: 28.33 hours over 11 days (17 September to 13 October), from the end of Week 2 of nestling development until fledging (Table 1), with casual observations or weekly checks being made thereafter until the fledgling could no longer be located.

Pair 4 was plumage-dichromatic (male with pale cheeks and 'scaled' upperparts). Hatching at Nest 3 was indicated by behavioural cues; the female for the first time took prey to the nest rim, tore food and offered small pieces into the nest cup, and also moved eggshell with her bill. The age of the chick in Nest 4 was estimated assuming a median fledging age of 40 days (after Charley *et al.* 2014 and Whelan *et al.* 2016).

#### Table 1

Observation schedule (hours of observation) at Black Falcon nests, Tamworth (NSW), during each two-hour interval of daylight: pre-laying phase to egg-laying or early incubation period (Nest 1, May–July 2015); laying and incubation period (Nest 2, July–August 2016); incubation and hatchling stage (Nest 3, August–September 2016); and nestling stage (Nest 4, September–October 2016). See text for nest site locations.

<08:00	08:00-10:00	10:00-12:00	12:00-14:00	14:00-16:00	>16:00
Nest 1:					
11.5	19.5	18.5	18	20	17
Nest 2:					
9.75	14.5	20.67	30.58	27.5	20.5
Nest 3:					
8.75	11.25	9	15.5	13.5	10
Nest 4:					
4.5	3.75	4	7	5.75	3.83

Adult vocalisation types (cackle, creaking call and begging whine) and vocal behaviour are described and quantified by Debus *et al.* (2017). Agonistic (inter-and intraspecific) encounters were quantified as the number of separate incidents, within each of which there could be multiple, repeated swooping attacks by one or both members of a pair of Black Falcons until the episode against the intruder finished. Further analysis of interspecific interactions is provided by Bauer and M<sup>c</sup>Donald (in press).

Prey species in orts and regurgitated pellets collected from under active Black Falcon (BF) nests were identified and biomass of delivered prey was estimated as previously described (e.g. Debus *et al.* 2005; Charley *et al.* 2014). Biomass estimates herein are crude, being heavily biased by unidentified, partlyeaten items seen delivered to the female or young and assigned (on relative size) a mass of 50 grams (g) or, for small items, 30 g.

# RESULTS

#### Aerial displays in the pre-laying period

The following chronological sequence was observed through the months and weeks preceding egg-laying through observations on the various pairs:

- (1) Pair re-formation: in March, within sight of Site 1 (although 4 km away), a high-soaring female BF stooped to join a low-circling male; they appeared to track each other, interacting, and then as the female closely approached the male, he dodged away and they separated to hunt alone.
- (2) Male courtship/advertisement: in late May, during synchronised soaring by Pair 1 over their nest area, the male performed a power dive and sharp upswing (V-dive) with exaggerated slow-flapping and canting from side to side at the apex; he then repeated the performance, before both pair members glided off together.
- (3) High-aerial agility display: in early June, during synchronised soaring by a fifth pair (neighbour of Pairs 1 and 2), the female made a 'jinking' manoeuvre (brief, twisting dive below the male), before they departed together.



Figure 1. Pair 2 female Black Falcon performing 'high winnowing' display with dihedral towards intruding raptor, incubation period. Photo: Keith D. Fisher

- (4) Unilateral slow-flapping: in mid-June, a BF (sex unknown) flew with bursts of slow wing-flapping, interspersed with slightly anhedral wings in glide, towards Site 3 (~3.5 km away); the display was similar to normal flight of Brown Falcons *Falco berigora* except for the wing attitude during gliding.
- (5) Food offering: in mid-June, in the P1 female's absence from the nest area, the male arrived with prey, then soared high over the nest area, dangling and picking at the small prey item in his foot as if offering it for collection.
- (6) Low-aerial agility display: in late June, both members of Pair 1 perched in their nest tree and the female then made a low, fast flight away from and back to her perch. Then, as both birds left on a low hunting flight, the male rose above the female with exaggerated slow-flapping flight, apparently after having passed low over her.
- (7) Female advertisement display: in mid-July, the Pair 2 female left her nest-side perch with bursts of rapid, shallow flapping of the wings above the plane of the back ('high winnowing'), soaring with wings held in a slight dihedral (Figure 1), as she circled up to join the high-soaring male.

In the newly formed Pair 1 (with a new male), after a lapse of a month in the female's attendance at the nest or nest tree, the following behaviours were observed a few days after the pair was first seen reoccupying the site (late August):

- (1) Female courtship: as the male appeared soaring higher overhead, the circling female made sudden random changes of direction and short stoops, with deep, slow flapping and banking with wings held well forward; she then flew rapidly to the nest and peered up at the male (K. Fisher pers. comm.).
- (2) Male low-aerial agility display: as an intruding Brown Falcon flew past their territory, the pair arrived and the male flew with exaggerated slow-flapping, canting from side to side, as he briefly followed the retreating Brown Falcon, before diving into a tree and then flying onto the perched female's back (on the adjacent dead tree) to copulate.

#### Table 2

Nest-site characteristics of four Black Falcon pairs, Tamworth district (NSW), 2016. For tree species, YB = Yellow Box *Eucalyptus melliodora*; WB = White Box *E. albens*; GB = Western Grey Box *E. microcarpa*. For position in landscape, 'creek' = creek line or creek flat; 'No' = lower slope. 'Dead trees' = dead trees/dead branches in vicinity of nest, used by falcons. ht = height, dbh = diameter at breast height and m = metres.

Nest #	Tree sp.	Tree ht (m)	Tree dbh (cm)	Nest ht (m)	Creek	Dead tree(s)
1	YB	30	167	28	Yes	Yes
2	YB	27	81	23	Yes	Yes
3	WB	24	123	19	No	Yes
4	GB	23	60	20	No	Yes

#### Aerial displays in the incubation period

Several times in the incubation period the Pair 2 female left the nest to perform the 'high winnowing' aerial display, with accompanying loud cackling, once oriented towards a Wedgetailed Eagle *Aquila audax* that approached within about 400 m, and in circuit(s) of the nest site, with long bouts of creaking calls on the nest or branch, as an intruding female BF circled over the nest area. The Pair 3 incubating female performed this display below a soaring Peregrine Falcon.

# Nest sites and spacing

The stick nest of Pair 1 was in the top of a living emergent eucalypt (Table 2). The nest was in one half of the double-trunked tree and was the vacant nest of a pair of Australian Ravens *Corvus coronoides*; the other half of the tree contained an older nest of these ravens, which continued to occupy the area.

Pair 2's nest was also built by Australian Ravens (in winter 2015) and was also high up in the top third of a living, emergent eucalypt. The nest trees of Pairs 1 and 2 were in creek-line remnant woodland in flat to gently undulating agricultural land (used for cropping and grazing), 80 and 125 m from public roads, respectively.

Pair 3's nest in 2016 was near the base of the dense canopy of a mature remnant eucalypt in sparse paddock woodland, on a low rise upslope from the 2010 creek-flat woodland site of Debus and Tsang (2011) and 400 m from roads. Australian Ravens had built and defended a nest against BFs and Brown Falcons in this tree in 2013 (SD pers. obs.).

The stick nest of Pair 4 was situated in a Box Mistletoe *Amyema miquelii* in the crown of a eucalypt in an extensive stand of woodland (a travelling stock reserve) on a gentle rise from, and contiguous with, the wooded flats of the Peel River, and 117 m from a minor backroad. This nest was apparently built by ravens, which had older nests and an active nest in the area.

All four nest sites had emergent or horizontal dead branches in the nest tree and/or surrounding trees and dead trees within 100 m, all of which were used by the falcons for perching, mating, prey transfers/consumption and nest-guarding. Nest 2, and part of the nest tree, were destroyed by a storm in December 2016. The limbs supporting Nests 1 and 3 had broken off, and Nest 4 had disintegrated, by July 2017.

In 2016, inter-nest distances among all four pairs, which appeared to be nearest neighbours to one another, averaged 10.25 km (range 9–12 km). The former nest site of another pair, known to have bred in the area previously, was also 10.5 km from Pair 2's nest and Pair 4's 2016 nest. All three near-roadside nests were readily visible to the human observer.

#### Nest occupation

In 2015, Pair 1 occupied the nest site three months before egg-laying (in mid-July); the male initially perched in the nest tree or stood on the nest and the female joined him in the tree through April-May. The pair frequently occupied the site from mid-May and were seen copulating in the tree from 22 May onwards. From this stage (early June), the male also 'advertised' the nest to the female e.g. they would arrive together; the female, with prey or a full crop, would fly to her favoured perch in the nest tree and the male would alight on the nest and give creaking calls there; alternatively, the female or both birds perched in the nest tree, the male would fly to the nest and give creaking calls or sat in it, before they copulated at her favoured perch. The female occupied the nest tree and increasingly the nest from mid-May to early July as laving approached, thus effectively counterbalancing the male's declining attendance at the nest and tree over that period (Table 3).

In 2016, Pair 1 first appeared in their nest tree in late April and the male was observed to stand on the nest in mid-May. However, the pair was often absent in the ensuing weeks, appearing at the site only occasionally through June and early July, and then frequenting the nest site more regularly and copulating there from mid-July. The behaviour of June 2015 or a variant of it was repeated in late July 2016. However, after conflict with ravens nesting in the same tree (see below), the pair was last seen defending the nest and nest tree and copulating there on 23 July, after which they abandoned the site.

#### Courtship behaviour

Early in the pre-laying period at Site 1 in 2015, the pair frequently departed on co-operative hunting flights. Typically, the male left first and the female followed immediately or within a few minutes. She apparently readily located him, as they often returned together with a prey item or full crop(s). In this period, courtship (or supplementary) feeding took the form of apparent enticement of the female to the nest e.g. in mid-June the male brought prey to the nest, whining softly, and gave it to her, bill to bill, when she joined him there from her perch in the nest tree; in late June they arrived together at the nest and he gave her prey there, amid creaking calls, before she took it whilst uttering whining calls to her favoured perch; in early July this behaviour was repeated, although with frequent female begging (i.e. whining calls) before and after the exchange.

In the pre-laying period, the female appeared to gorge herself on the male's kills, being frequently seen (a) with a full crop, (b) feeding on his next delivery while still engorged from the previous one, or (c) feeding on his next delivery immediately

#### Table 3

Occupation of Black Falcon nest and (separately) the nest tree (% daylight observation time), pre-laying phase (May–July 2015), Tamworth (NSW, Site 1). First half of pre-laying period = 22 May–19 June (n = 10 observation days); second half = 20 June–6 July (n = 8 observation days; start of laying inferred to be 7 July). Hours of observation in parentheses.

	May–June (30 h)	June–July (28 h)
Male:		
Nest tree	19	10
Nest	5	1
Female:		
Nest tree	35	28
Nest	2	9

after having finished the previous one. The pair also cached surplus food during this phase, and the male sometimes departed to hunt with a full crop.

The female was first seen visiting the nest on her own three weeks before laying. In mid-June, she visited for four minutes, giving creaking calls, leaning into the nest and sitting in it, but from early July she visited at an increasing frequency and for a greater duration. For example, in early July she spent 8-10+ minutes sitting and shuffling in the nest, with soft 'chittering', clucking or 'ticking' calls, or creaking as the male arrived in the tree, and she frequently whined in long bouts from her favoured perch in the nest tree. She sat in the incubation posture for 45 minutes on 3 July, and on 6–7 July for up to 1.3 hours, sometimes nibbling or pushing sticks on the rim. The first egg appeared to be laid on 7 July, and from that date the male transferred prey to her at their perch in the tree. The clutch was apparently complete or nearly so on 13 July when the female incubated overnight for the first time, although copulation continued for a further five days.

The new male also offered food at the nest; a few days after he arrived in August and after synchronised soaring by the pair, he took prey to the nest and held it there for five minutes before eating it himself when the female failed to arrive (K. Fisher pers. comm.).

In 2016 in the pre-laying phase at Site 2, both pair members shared a large prey item side by side on their feeding perch: as one, apparently the female, held the prey in its foot, both took and ate pieces, until the female went with a full crop to the nestside branch in the adjacent tree while the male finished the prey.

## Copulation

In 2015 mating was observed at Site 2 in late February. After the pair had soared together, the female landed in a tree, the flying male alighted directly on her back and they copulated whilst emitting whining calls within about 200 m of the nest subsequently built by ravens. A female BF was first seen perching beside this nest in early July 2016, and from mid-July the BF pair was observed occupying the nest.

In 2015 Pair 1 started copulating on their favourite perch, a horizontal dead branch, in the nest tree almost seven weeks before laying. In May-June they were observed to copulate on five days at a rate of 0.18 times per hour over 15 days (22 May to 29 June) (n = 49.5 observation h). In July, they were observed to copulate 0.24 times per hour (on eight days) over 14 days (2-18 July), almost daily over the inferred laying period to the start of full-time incubation (6–13 July) (n = 45 h). During our fairly evenly spread observations over two-hour blocks of daylight, including three all-day watches and three half-day watches, the falcons typically mated in early to mid-morning and in mid- to late afternoon, but rarely in late morning. Copulation duration appeared to increase through June, from 2-3 sec early on (n =2) to 4–5 sec in mid to late June (n = 2) and to 10–11 sec in the inferred laying phase in early to mid-July (n = 5). The female invited copulation with a head-low, bowing posture and creaking calls, and the male typically alighted directly on her back from flight, balancing with flapping wings. In May, copulation was accompanied by creaking calls or creaking and whining calls together. In June and July, copulation was accompanied by whining calls definitely given by the female, which sometimes also gave creaking calls as the male dismounted, and once in July it was accompanied by creaking calls, apparently given by the male, as she whined.

In 2016, at the nest re-establishment stage (17-23 July), matings by Pair 1 were accompanied by creaking calls given by the female or creaking and whining calls apparently given by the female and male, respectively. They mated three times in 12.75 hours (= 0.24/h). In the week leading up to laying, Pair 2 copulated in the nest tree and the adjacent tree twice in 10.75 hours (= 0.19/h). During one post-laying copulation by Pair 2, four days after full-time incubation commenced, the male alighted on the female's back as she was eating his prey on a branch of the nest tree; brief mating ensued with whining then creaking calls apparently given by the female.

# Breeding chronology

In 2015, the Pair 1 female appeared to lay eggs over the period 7–13 July; this timing is consistent with a clutch size of 3–4 and laying occurring on alternate days, e.g. Marchant and Higgins (1993). In 2016, the Pair 2 female appeared to complete laying during the period 23–26 July, and the Pair 3 female appeared to be incubating by 6 August, with hatchling(s) being present on 10 September. Nest 4 was occupied by 28 July and the juvenile fledged on 14 October; assuming from previously recorded values a nestling period of six weeks and an incubation period of five weeks, hatching was estimated to have occurred in early September and laying in late July.

#### Roosting

During the inferred laying phase of 2015, the Pair 1 female roosted in a leafy eucalypt canopy within about 50 m of the nest tree. The male was once seen going to his roost site in a different leafy eucalypt, also  $\sim$ 50 m from the nest-tree, at dusk. The day after she abandoned her clutch, on a rainy evening the female was on her favourite nest-tree perch and then at dusk retreated to a more sheltered position against the trunk, in the lee of the wind and rain.

## Table 4

Responses of breeding Black Falcons to other bird species intruding in the breeding territory or nest tree (within ~400 m): defensive attack bouts by falcons (n), and instances of intrusion eliciting no defensive attacks (= Nil), falcons' pre-laying phase to start of incubation (Pair 1, 2015) and pre-laying phase to post-fledging period (all pairs combined, 2016). The non-raptors were all in or within 50 m of the nest tree.

Species		2015		2016	
		Nil	n	Nil	
Black Kite Milvus migrans	3 <sup>A</sup>	2	1	4	
Whistling Kite Haliastur sphenurus	1	2	2 <sup>A</sup>	1	
Brown Goshawk Accipiter fasciatus		2	2	3	
Spotted Harrier Circus assimilis	1	3		1	
Swamp Harrier Circus approximans				1	
Wedge-tailed Eagle Aquila audax			18	7в	
Little Eagle Hieraaetus morphnoides		2	1	1	
Nankeen Kestrel Falco cenchroides	1	2		2	
Australian Hobby Falco longipennis	2 <sup>A</sup>	2		7	
Brown Falcon Falco berigora	2	1		7	
Peregrine Falcon Falco peregrinus		2	2		
Little Corella Cacatua sanguinea			1		
Sulphur-crested Cockatoo Cacatua galerita	2		1		
Red-rumped Parrot Psephotus haematonotus	1				
Laughing Kookaburra Dacelo novaeguineae			1		
Noisy Miner Manorina melanocephala	1				
Australian Magpie Gymnorhina tibicen			1	1	
Australian Raven Corvus coronoides		2	14	8	
Total observed attacks	14		44		

Aone attack on each of these species was kleptoparasitism

<sup>B</sup>three of these were soaring high, and three cases were juvenile eagles flying past (in two cases chased by ravens and magpies): all in the falcons' incubation period or (once) at the hatching stage.

During the incubation phase of 2016, the Pair 2 male sometimes arrived to roost in the nest tree at dusk. Similarly, the Pair 3 male sometimes roosted in the nest tree at dusk, and on one frosty morning he did not leave to hunt for two hours after sunrise.

## Interspecific interactions and defence

In the pre-laying phase through to the start of incubation in 2015, 71% of defensive attack bouts by Pair 1 were directed at other similar-sized raptors that might use a stick nest of raven size or larger (Table 4). Nevertheless, one or both of a pair of Australian Hobbies Falco longipennis occasionally visited the falcons' nest or nest tree in the falcons' absence from early May. Also in the falcons' absence, a pair of Spotted Harriers Circus assimilis briefly visited the older raven's nest in the other half of the tree until they were repelled by the pair of ravens. Neither of these intrusions prompted return or defence by the falcons. On one occasion when the falcons were absent, a raven also perched low down in the nest tree without eliciting a response. However, in 2015 the ravens apparently nested in another tree about 400 m away, and both repelled the female BF when she approached it. The female BF performed 64% of the 14 observed defensive attacks, and both falcons attacked together once. One attack was directed at a Sulphur-crested Cockatoo Cacatua galerita that was on the falcons' nest, pulling out and discarding material.

Between nesting attempts by Pair 1, during the month that the nest was unattended by the falcons, a pair of hobbies claimed the nest, and when eventually the falcon pair (now including the new male) attempted to reuse the nest, the hobbies defended it strongly and together routed the female falcon when she tried to visit it. The falcons then went elsewhere, leaving the hobbies to successfully raise a brood.

Considering all pairs combined from the pre-laying period through to the post-fledging period in 2016, most defensive attacks on other birds by BFs were directed at Wedge-tailed Eagles (41%) and Australian Ravens (32%), followed by other raptor species (18%) and various other bird species (9%; n= 44). Members of these other species were chased from the nest tree or its vicinity (Table 4). Females performed 80% of the defensive attacks, some were conducted jointly by both pair members (16%; on ravens and especially eagles), and the rest were executed by the male (5%; on ravens). The hourly attack rate on ravens was greatest in the pre-laying (i.e. nest establishment) phase (0.10 attack/h, n = 31.5 observation h) versus 0.05/h in the laying and incubation periods (n = 163 h) and 0.04/h in the nestling period (n = 51.33 h). The hourly rate of attacks on Wedge-tailed Eagles was greatest in the falcons' nestling period (0.18 attack/h vs 0.04/h in the laying/incubation period and zero in the pre-laying phase). An incubating female BF also cackled at soaring Wedge-tailed Eagles without leaving her nest or feeding perch, and other females arrived, sometimes cackling, at their respective nest or guard tree when an eagle flew or soared near the nest containing chick(s). One or both falcon pair members effectively routed eagles, causing them to retreat, sometimes rolling and parrying the falcons' stoops. In the post-fledging period, a strongly defending female falcon briefly grappled feet with a flying raven.

In the pre-laying phase, interactions between Pair 1 and ravens took the form of skirmishes over the nest tree, when the ravens built a new nest in the other half of the doubletrunked tree. Both ravens together routed the male falcon when he attacked them at their new nest, but the pair of falcons in concert had the ravens retreating, the female raven to her new nest where she sat tightly. Nevertheless, the falcons abandoned this site when the ravens started incubating in the new nest.

## Intraspecific interactions

In 2015, during Pair 1's first breeding attempt, there was one observed intrusion by a pair of BFs. The incubating female stood, creaking in long bouts, then left still creaking, to join the male in a 1 min-long, weaving and diving chase of the intruding pair through the nest patch and around the nest tree. The female, creaking, and male returned to the nest tree as the intruders retreated and the male then incubated. During the second nesting attempt at this site in 2015 (with the new male), the female flew to the nest giving a long creaking bout as the male glided past high overhead, followed by an intruding female, until both were out of sight.

Throughout the 2016 breeding cycle, single intruding BFs appeared in the territory of each of the four breeding pairs at rates of 0.05 intrusion per hour in the pre-laying phase (Pair 1, n = 40.75 observation h), 0.03 per hour in the laying/incubation period (Pairs 2 and 3, n = 163 h) and 0.04 in the nestling period (Pairs 3 and 4, n = 51.33 h). Two intrusions at Site 1 (in the



**Figure 2.** Pair 2 female Black Falcon fighting with intruding Black Falcon, incubation period.

Photo: Keith D. Fisher

pre-laying period) involved the pair skirmishing aerially with a third falcon, with chasing, stooping and display flights. Three intrusions by a female falcon at Site 2 involved: (a) the breeding female directing a display flight ('high' winnowing and dihedral, as in 'Aerial displays', above) with creaking calls at the high-soaring intruder, (b) the female chasing and attacking the intruder in flight, causing it to fend her off with its feet, followed by a display flight (as above) (Figure 2), and (c) both pair members creaking from the nest and branch and then soaring, the female performing two curving V-dives then giving creaking calls while diving at, and grappling brieffy with the intruder, which whined with a squealing quality while under attack. The female continued chasing and stooping at the intruder until it was high up and distant, pursuing it with slow flapping and canting; the male meanwhile incubated.

Two intrusions at Site 3 involved: (a) both falcons chasing the intruder, the female breaking off giving creaking calls to return to the nest, while the male continued the pursuit, and (b) the male flying below the intruder and cackling, while the incubating female creaked from the nest. Two intrusions at Site 4 in the nestling period involved: (a) opportunistic piracy by the intruder after the resident male had given prey to the breeding female, after which the female chased and grappled the intruder to the ground; the male then chased it, cackling, although the intruder retained the prey, and (b) one of the pair attacking the intruder with creaking calls, attempting to grapple, until all three continued the chase out of sight.

#### Incubation regime

In 2015, the Pair 1 female gradually increased her incubation stint duration over the inferred laying period from 11 minutes on 7 July to 49 minutes on the 9th to 62 and 42 minutes on the 10th and 35+ minutes on the 11th. She incubated in the mornings, perhaps when laying, as suggested by her behaviour, but not in the afternoons when she was either on the nest rim or in the nest tree. On the 15th she stepped carefully into the nest and visibly shuffled down on eggs. Over the first six days after inferred clutch completion, she incubated for 62% of daylight observation time (n = 21 observation h), and was otherwise on the nest rim (17%), in the tree (20%, sometimes feeding on the

male's prey) or flying (1%, in absences of ~2 min). Six complete stints averaged 47 minutes (range 18–109 min, with others of up to >75 min). The male only incubated for one stint of one minute, after the clash with the intruding pair of BFs (see above); this stint was interrupted by chasing a Black Kite *Milvus migrans* that approached the nest tree, after which he stood on the nest for six minutes. During the laying phase and early incubation period, he attended the nest tree for 40% of daylight observation time (n = 45 h) and stood on the nest for 1%.

After the intense clash with the intruding pair (see above), the female incubated for only one-third of the remainder of that day (7.5 h) in short stints (2–66 min, mean 18 min, n = 8) and spent the afternoon perching on the remains of the male's prey delivery. She cached the remains at dusk, visited the nest briefly, but roosted in a neighbouring tree (as did the male) until it was too dark to see if either of them went to the nest. Two to three days later the pair appeared to have resumed their normal parental roles, but the female then ceased incubating when the male disappeared; he was presumed dead or injured, although no BF passed through the local wildlife carer network at the time (S. Pullman pers. comm.). On his first day of absence, the female retrieved a food scrap from her cache tree and robbed a hobby of prey that she saw it catch, and otherwise perched in the nest tree where she also roosted that night. Over the next two days she foraged for herself, returning to the nest tree between sorties, but then abandoned the site.

In 2016 incubation was only partial during Pair 2's laying stage, which is consistent with what is known for other Falco species (e.g. Marchant and Higgins 1993). In Pairs 2 and 3 the male took only a minor share in incubation throughout the incubation period (Table 5). The small difference between the sexes' relative contributions in the two pairs (Table 5) appeared to be related to weather. Thus, the Pair 2 female left her clutch near hatching after several days of cold wind and rain, when it was clear from her begging that she was hungry and she was often absent, apparently hunting. The male when present at the nest site covered the eggs in her absence, but they ultimately abandoned the clutch. Overall, eggs were uncovered for 7-8% of daylight observation time (data for both pairs, before the Pair 2 female abandoned her eggs), occasionally in periods of up to an hour, although usually 1-14 minutes and commonly 1-6 minutes, unless the female was feeding on the prey brought by the male. Females sometimes interrupted incubation by perching on the nest branch or making short, circuitous flights around the nest tree or display or defence flights against intruders.

Throughout the incubation period as a whole, the Pair 2 female incubated for complete stints of 1–146 minutes (mean 47 min, n = 53), and the male for stints of 5–123 minutes (mean 34 min, usually 5–16 min, n = 7). Often the female incubated beyond the start and/or finish of nest watches for periods of up to more than 1 hour or even 2.5 hours.

In the final fortnight of incubation, the Pair 3 female incubated for complete stints of 6–200 minutes (mean 64 min, n = 9), and the male for one stint of seven minutes. On several occasions the female incubated beyond the start and/or finish of nest watches for periods of up to 2+ or even 3.5 hours.

During incubation changeovers, the male typically relieved the female after she had collected and fed on his prey, usually in the nest tree or surrounding trees, although once the male brought

### Table 5

Parental time-budgets of breeding Black Falcons, Tamworth (NSW), 2016: laying and incubation periods of Pairs 2 and 3, hatchling stage of Pair 3, and downy chick stage (weeks 2–3) of the nestling period of Pair 4 (see text): % daylight observation time spent in various activities (*n* observation hours in parentheses).

Gender/stage	Incubate/ brood	Stand on nest	Perch in nest tree	Defend
Pair 2, laying (10.25 h):				
Female	22	7	56	0
Male	1	1	8	0
Pair 2, incubation (107.75 h):				
Female	77 <sup>A</sup>	<1	11	1
Male	5 <sup>A</sup>	0	5	<1
Pair 3, incubation (45 h):				
Female	92	<1	3	<1
Male	<1	0	12	<1
Pair 3, brooding (23 h):				
Female	86	5 <sup>в</sup>	5	0
Male	1	0	16	<1
Pair 4, brooding (18.08 h):				
Female	8	6	17 <sup>c</sup>	3
Male	0	0	7 <sup>c</sup>	3

<sup>A</sup>89% and 3% (of 92.75 h) before female abandoned the eggs near hatching (see text)

<sup>B</sup>includes feeding chick(s)

<sup>C</sup>includes guard trees next to nest tree

prey to the nest. The returning female simply displaced him from the nest or he left as she approached with cackling. On one early morning at Nest 2, the male went to the nest rim, but the female continued incubating and he retreated. Half an hour later he approached and incubated while the female perched for an hour elsewhere in the nest patch. He remained on the nest when she then returned and perched, whining, on the nest branch for the next hour, until she finally displaced him and he left to hunt.

From behavioural cues at Nest 3, namely inferred incubation on 6 August, incubation on 8 September and hatchling(s) being present on 10 September, a minimum incubation period of  $34 \pm 1$  days was estimated.

## Brooding regime

The Pair 3 male performed a minor share of brooding the chicks in their first few days. In Week 1 of the nestling period his mate brooded for complete stints of 6–284 minutes (mean 75 min, n = 10) and he brooded for two observed stints of four and six minutes. There were also several occasions on which the female brooded beyond the start and/or finish of watches for periods of up to more than one hour or two hours. From the end of Week 2 through Week 3, only the female of Pair 4 brooded and for a fairly small proportion of daylight observation time (Table 5).

During brooding changeovers at Site 3, the female collected the male's prey and he brooded until either she brought the prey to the nest and he moved aside into the nest tree, or he rose and defended her against mobbing birds while she fed in the tree. The chick(s) were left unattended for 8% of daylight observation time; the female's absences from the nest were usually short (1–12 min, commonly 1–3 min), but extended to 13–43 minutes when she foraged and/or fed on prey off the nest. She herself foraged from early in the chick phase: thus, on Day 1 she left for 43 minutes and returned with prey and fed the chick(s). On Day 4 the pair hunted co-operatively before she returned with, and fed on, their captured prey, as well as on the male's next two deliveries that morning, without feeding the chick(s). Nest failure appeared to be related to cold, wet weather in Week 1 and the resultant depressed hunting success, because the female was clearly hungry as she fed herself instead of the chick(s).

In the latter half of Week 3, the Pair 4 female brooded for complete stints of 8–36 minutes (mean 18 min, n = 5) and one stint on *c*. Day 19 of more than 26 minutes; the final observed stint on *c*. Day 22 was for 16 minutes in cold, wet weather. In Week 3 the chick was attended for only 14% of daylight observation time. Otherwise, from Week 3 onwards the parent(s) when present, most often the female, guarded the chick from nearby perches or by soaring overhead (Table 5). In Weeks 2 to 4 the male delivered prey to the female, which then fed the chick bill to bill. In Week 5 the female stood on the nest while the chick fed itself on prey, and the male carried food towards the nest as if to deliver it in the female's absence. From the end of Week 3 (*c*. Day 21), the female started foraging with the male.

# Development of a nestling

On *c*. Day 14 the Nest 4 chick was downy and during parental feeding it picked at prey in the nest with its bill. On Day 19 it was large and downy with dark feathering around its eyes, and occasionally fed itself during parental feeding. On Days 20–21 its remiges and rectrices were emerging through its down; it was active, standing but overbalancing, and it stretched and flapped its wings and pecked at nest material in possible exploratory object play. On Days 32–33 (5–6 October) it was mostly feathered, with well-grown primaries and tail, and fed itself on prey in the nest. On Day 40 (13 October) it was fully feathered, had lost its down except under the wings, and fledging appeared imminent.

### Fledging of a juvenile

The Nest 4 juvenile left the nest on 14 October, but then suffered misadventure. It was found on the ground next morning, unable to fly (Figure 3), and was thin (prominent sternum) and underweight (470 g, cf. mean for male BF of 582 g: Debus and Olsen 2011). It was taken for veterinary assessment, but the only sign of illness or injury was minor soft-tissue damage (thickening) on one shoulder, suggesting impact or strain injury. It was assessed as being male, based on relative size and bill massiveness in comparison with its parents. It was banded and released at the nest site weighing 593 g after 10 days in care and having regained the capacity to fly.

# Post-fledging period

Three and four days post-release, the Site 4 juvenile had adopted a vacant stick nest about 600 m from its natal nest and was being defended and fed by its parent(s). A week later it occupied the adults' food-caching tree about 500 m from its natal nest, sometimes made short flights, and was being fed and guarded by its parents. It was sometimes seen in that tree up to



**Figure 3.** Site 4 fledgling Black Falcon on its fledging/rescue day (see text); nest tree in left background.

## Photo: Alice Bauer

five weeks post-fledging, its band sometimes being visible by telescope. Over the first five weeks post-fledging, it gained in competence and appeared well fed. It was not located six weeks post-fledging, although its mother defended the nest woodland area against a Wedge-tailed Eagle, suggesting the fledgling was possibly in the vicinity. Neither juvenile nor adults could be located a further week later, suggesting that the juvenile had become independent or nearly so.

## Breeding productivity

One fledgling from three breeding attempts with known outcomes translates into a productivity of 0.33 young fledged per pair in 2016. However, without human intervention at Nest 4 the outcome would have been no young raised to independence from those three pairs. There was also no evidence that Pair 1 raised young to fledging from an alternative nest in 2015 or 2016. Thus success for four known breeding attempts in 2015–16 gives a productivity of 0.25 young fledged per breeding attempt.

# Hunting and prey

In 2015, early in the pre-laying phase in late April, Pair 1 plus two Australian Hobbies, at least four Nankeen Kestrels *Falco cenchroides* and two Brown Falcons all hawked for swarming flying insects in a thermal column on a warm afternoon. Otherwise, all identified prey items of Pair 1 were

avian (Table 6). Similarly, most identified prey items in 2016 were avian (96%), except for one rodent (4%); however, a few insects were found in a minority of pellets during the breeding cycle (Table 6), but being small they may have been in the stomachs of vertebrate prey. In 2016, seven intact pellets measured  $30.7-39.7 \times 15.3-23$  mm (mean  $34.7 \times 18.9$  mm), and eight pellets weighed 1.3-2.7 g (mean 2.2 g).

In 2015 and 2016 seventeen attacks on prey, including three cases of kleptoparasitism, were observed (see Figure 4). Almost all observed attacks on prey were shallow, direct flights initiated, apparently opportunistically, from perches in or near the nest tree, at prey on the ground or in the tree canopy (Table 7). However, these observations were probably biased by the observers' nest-watching positions. Five of 14 attacks by breeding adults on avian prey succeeded (36%).

## Feeding rates

From the pre-laying phase to early in the incubation stage in 2015, the Pair 1 male delivered or provided 0.14 prey items/h, of which one small item (~30 g, pre-lay phase) was not collected by the female, and an additional item (also prelay phase) that he brought he did not share with her. This rate approximated to a roughly estimated 11 g/h per of prey biomass provided, to which the female added one kill of her own to bring her estimated observed intake to 12 g biomass/h. Excess prey was cached either in a branch fork of the nest tree or in the horizontal, hollow limb of a live eucalypt about 50 m from the nest tree, and was retrieved from both sites.

In the pre-laying period at Nest 2 in 2016, the male's preydelivery rate to the female was 0.29 item/h (estimated biomass 19 g/h). In the incubation period, it was 0.15 item/h (biomass  $\sim 9$ g/h), to which the female added one observed kill of her own, making her intake  $\sim 10$  g/h. In the incubation period at Nest 3, the male's delivery rate was 0.09 item/h (~4 g/h). In Week 1 of the nestling phase, the parental delivery rate was 0.26 item/h (~28 g/h), but the female consumed much of it. In Weeks 2–4 of the nestling phase at Nest 4, the parental delivery rate was 0.23 item/h (~25 g/h), of which one item was lost to piracy before it could reach the nest, giving an effective delivery rate of 0.19 item/h or ~23 g/h. Prey transfers usually occurred in the nest tree or neighbouring trees, or sometimes aerially as the male approached the nest site; in one case the female started plucking at the the prey in flight en route to the nest tree. Pair 4 had one known cache tree, a large living eucalypt (see 'Post-fledging period', above), but the precise nature of the cache site was not determined.

## Reaction to disturbance

Pair 1 did not overtly respond to routine farm activity, road traffic or helicopter flights near the nest tree, although the pre-laying female became alert and flushed when the farmer, pushing logs with a small bulldozer, approached to about 50 m. Incubating Pair 2 (off the airport runway) did not overtly respond to low overflights by light aircraft or the grading and gravelling of the nearby road. The female at Nest 3, located farther from regular human activity, flushed off hatchling(s) as the farmer, riding a motorbike down the fence line, drew level with the nest tree (~200 m away). Pair 4, nesting even farther from regular human activity, flushed from the nest area if approached within about 120 m by pedestrians.

#### Table 6

Identified prey items of Black Falcons, Tamworth (NSW), Pair 1 in 2015 and all four pairs combined in 2016: n by direct observation, and occurrence in pellets (n = 13).

Prey species	n obs. 2015	<i>n</i> obs. 2016	In <i>n</i> pellets 2016
Stubble Quail Coturnix pectoralis		1	
Rock Dove Columba livia	1		
Crested Pigeon Ocyphaps lophotes	1		
Probable Crested Pigeon	3		
Galah Eolophus roseicapilla	1	1	2
Probable Galah		1	
Cockatiel Nymphicus hollandicus	1		
Eastern Rosella Platycercus eximius		2	1
Red-rumped Parrot Psephotus haematonotus	2	1	
Noisy Miner Manorina melanocephala		1	
Australian Magpie Gymnorhina tibicen		1	
Magpie-lark Grallina cyanoleuca		2	1
Common Starling Sturnus vulgaris	3	6	8
Probable starling	1	1	
Common Myna Acridotheres tristis		1	
Passerine sp.	2	1	
Bird sp.	2	5	3
Black Rat Rattus rattus		1	
Insects			3
Total	17	25	



Figure 4. One of the Tamworth Black Falcons hunting feral Rock Doves, May 2016.

Photo: Michael Perkins.

#### Table 7

Target	Attack type	Outcome
Rock Doves	M, F co-operative alternating stoops at milling flock	Fail
Red-rumped Parrot in tree	F direct flying attack around tree canopy, flushed parrot	Success
Common Starlings on ground	M direct flying attack	Fail
Bird sp. on ground	F direct flying attack	Fail
Bird sp. in tree	M direct flying attack	Fail
Starling on ground	M direct flying attack	Success
Starlings on ground	M direct flying attack	Fail
Black Kite	M kleptoparasitism	Success, but rejected food (road carrion?)
Australian Hobby	F kleptoparasitism of starling: hobby caught starling near falcon's nest tree, F immediately chased hobby and snatched prey from it in flight	Success
Whistling Kite	M, F joint kleptoparasitism of Eastern Rosella (road kill?)	Success
Starling flock on ground	F direct flying attack	Fail
Starling on ground	F direct flying attack	Success
Unknown	M flushing dives around trees and ground	Fail
Australian Magpie	M, F co-operative prolonged chase	Success
Starling on fence	M direct flying attack	Success
Australian Magpie	M, F co-operative attempts (alternating swoops) to flush incubating bird	Fail (magpie remained on nest)
Starling flock on ground	M, F co-operative alternating stoops at fleeing flock	Fail

Hunting episodes of breeding Black Falcons, Tamworth (NSW) 2015–16, pre-laying phase to nestling period as applicable (see Table 1), all pairs combined. M = male falcon, F = female. Scientific names in Tables 4 and 6.

#### DISCUSSION

#### Aerial displays, courtship and mating

The BF's aerial displays, including diving, exaggerated slowflapping and canting display flights (by both sexes), are similar to the 'undulatory roll' and other aerial displays of the Gyrfalcon *Falco rusticolus* and Lanner Falcon (both hierofalcons; see Potapov and Sale 2005; Leonardi 2015; Black Falcon: Debus *et al.* 2005; Debus and Tsang 2011; Whelan 2013; Charley *et al.* 2014; Whelan *et al.* 2016; this study). Our observations of aerial displays, courtship (e.g. supplementary feeding) and mating behaviour confirm and expand previous accounts by Debus *et al.* (2005), Debus and Tsang (2011) and Whelan *et al.* (2016); these behaviours are similar to those of other hierofalcons and large falcons in general, e.g. Peregrine (allowing for stick nests rather than ledge nests) (cf. Cade 1982; Ferguson-Lees and Christie 2001; Potapov and Sale 2005; Leonardi 2015).

#### Agonistic interactions

Interspecific conflicts were similar to those described in previous accounts (Charley *et al.* 2014; Whelan *et al.* 2016; see also Bauer and M<sup>c</sup>Donald in press) and appear to be functionally related largely to nest-site selection, competition with other falcons and corvids for nest sites and defence of nestlings against large raptors (as in other hierofalcons, e.g. Potapov and Sale 205; Leonardi 2015). Defensive actions were similarly variable in intensity, as in the Grey Falcon (Ley and Tynan 2016). The frequency of intraspecific conflicts suggests that there was a floating population of BFs in the study area and some competition for breeding territories.

#### Breeding biology and behaviour

Our study reaffirms and extends findings for the study area and elsewhere on the BF's nest-site characteristics: i.e. tall or emergent eucalypts in lower, flatter parts of the landscape, including lower slopes above riparian zones, and with dead trees near the nest tree (e.g. Debus et al. 2005; Debus and Olsen 2011; Debus and Tsang 2011; Charley et al. 2014; Whelan et al. 2016). Nest trees occurring on lower slopes suggest that a broadening of the search criteria would be productive in future studies. Inter-nest distances also confirm and extend previous local data (Debus and Tsang 2011), but there is little to compare with elsewhere in the sheep-wheat belt. Breeding chronology at Tamworth confirms early breeding, with nest occupation in April and laying in mid-winter, in south-eastern Australia (see also Charley et al. 2014; Whelan et al. 2016), which is perhaps an adaptive, evolutionary response to nest availability ahead of the corvid breeding season.

Our study confirms, although still with limited quantification for the early nestling period, the male's minor role in incubation and brooding, and the decline in maternal nest attendance with chick age, as may be expected and which is in accordance with the Peregrine, hierofalcons and the Grey Falcon (e.g. Turner *et al.* 1993; Potapov and Sale 2005; Leonardi 2015; Ley and Tynan 2016). It also supports an estimated incubation period of 34 days for the BF (Cupper and Cupper 1980), although this value could bear confirmation; it is similar to that of the Grey Falcon (~34–35 days; Ley and Tynan 2016) and Peregrine (33 days; Marchant and Higgins 1993). Growth of the Pair 4 chick agrees well with prior data (Charley *et al.* 2014; Whelan *et al.* 2016), and supports its estimated age at fledging and the estimated hatching date. The juvenile's behaviour and development in the post-fledging dependence period were also consistent with prior knowledge (Charley *et al.* 2014; Whelan *et al.* 2016), but its progress was influenced by human intervention. After rehabilitation, it was successfully reunited with its parents, which resumed feeding and defending it.

Black Falcon productivity and recruitment are relatively low in the study area (Debus 2015b), compared with productivity for this species elsewhere and for other Australian falcons (cf. Debus 2012a; Charley *et al.* 2014; Whelan *et al.* 2016). Combining our 2016 data gives a total of only four successful nests out of 10 monitored attempts (40%) since 2004, from which only five or six young fledged (0.5–0.6 per attempt) and at least one juvenile, perhaps up to three, failed to reach independence. Without rescue, the 2016 fledgling would also have failed to reach independence.

## Foraging ecology

The BF's breeding diet mostly of birds at Tamworth in 2015–16 was similar to that in previous years, and to that elsewhere in agricultural landscapes in south-eastern Australia (cf. Debus *et al.* 2005; Debus and Olsen 2011; Debus and Tsang 2011; Charley *et al.* 2014; Whelan *et al.* 2016), but it contrasts with the higher proportion of mammals taken in arid and tropical Australia (Marchant and Higgins 1993; Corbett *et al.* 2014). Pellet size and mass were within the previously recorded range (cf. Debus *et al.* 2005; Charley *et al.* 2014; Whelan *et al.* 2014; Corbett *et al.* 2014; Whelan *et al.* 2016). Collectively, the various samples potentially provide diagnostic criteria for distinguishing BF pellets versus those of some other raptors; further systematic collections may provide an index of food intake when calibrated by feeding trials on captive birds.

Hunting behaviour was consistent with previous observations on the falcon's search and attack methods, allowing for the nestsite focus of the observers (cf. Debus et al. 2005; Debus and Tsang 2011; Debus 2012b; Debus and Zuccon 2013; Charley et al. 2014). Combining our 2015-16 data with a larger sample (Debus 2015a; Whelan et al. 2016) yields a hunting success rate of seven of 35 attacks on birds (20%) and nine of 37 attacks on all vertebrates (24%), but includes data for falcons of unknown age and social status. Weather-affected feeding rates and biomass provision at the hatching stage and for a single nestling were lower than for older nestlings and larger broods, respectively, in other studies (cf. Debus et al. 2005; Charley et al. 2014), and may have been implicated in nest failure at Site 3 and the poor condition of the Site 4 fledgling (cf. Brown Falcon and Peregrine Falcon: McDonald et al. 2004; Robinson et al. 2017). The frequency of caching appears to be related to food abundance and hunting success (cf. the high rate of caching, and the abundant prey and large brood size in the study by Charley et al. 2014), but this deserves further investigation.

# Conclusions

The BF's breeding biology and behaviour and foraging ecology are now well known in general terms, although the incubation period and parental time-budgets in the early nestling period warrant further confirmation. Diet composition, feeding rates and biomass provisioning deserve investigation in relation to prey abundance, and further data are required on hunting success. The falcon's reactions to human activities suggest that, although some pairs habituate to routine farming and other practices, those nesting in secluded woodland may be warier and adversely affected by sudden novel, major disturbances. Future research could usefully focus on population aspects e.g. long-term monitoring of breeding density, nest occupation and breeding success, and on home range, habitat use, dispersal and movements, using banding, colour-banding and telemetry.

The BF is listed as *vulnerable* in New South Wales. Its main problems in the sheep-wheat belt appear to be the loss of tall eucalypts in degraded riparian zones and sparsely treed paddocks, loss of nest sites to storms and abundant, competing native corvids, and collisions with vehicles and human infrastructure (Zuccon 2014; Debus 2014, 2015b; this study). All these factors appear to be contributing to its low breeding productivity and recruitment, so part of a recovery strategy might profitably include provision of artificial nest sites, and release of captive-bred offspring from 'unreleasable' injured falcons that are currently euthanased (Debus 2015b). These issues at least deserve discussion and a review of government policy. Some aspects of habitat management in the agricultural zone, and competition with a thriving Peregrine Falcon population, may also be relevant (cf. Lanner Falcon: Sarà 2014; Sarà *et al.* 2016).

## ACKNOWLEDGEMENTS

The 2016 component of this study contributed to a UNE Zoology Honours project by Alice Bauer, supervised by Dr Paul McDonald and supported by a research grant from BirdLife Northern NSW and the School of Environmental and Rural Sciences, UNE. We thank the landholders for permission to watch the falcons on their land; Joan Dunne, Eric Fair, Denise Kane (Tamworth Birdwatchers Inc.), Keith D. Fisher and Michael Perkins for supplementary observations and photographs; and Greg and Madelon Blaxland, Gavin Hombsch and Matt and Sarah Berlyn for their generous accommodation. We also thank North West Local Land Services (courtesy of Mitch Palmer) for funding a raptor survey of travelling stock reserves that resulted in the discovery of Pair 4; and Sharon Pullman and Jae Price (WIRES) and staff at the Piper Street Vet Clinic (Tamworth) for their role in rehabilitating the fledgling. This study was conducted under UNE Animal Ethics authority AEC16-02. We thank Paul McDonald, David Baker-Gabb and an anonymous referee for comments on a draft.

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