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Delayed juvenile behavioral development and prolonged dependence are adaptations to desert life in the grey falcon

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Abstract

Rapid learning in the young of most endothermic animals can be expected to be favored by natural selection because early independence reduces the period of vulnerability. Cases of comparatively slow juvenile development continue, therefore, to attract scientific attention. In most species of birds, including raptors, the young depend on their parents for some time after fledging for the provisioning of food and for protection while they learn to become nutritionally and otherwise independent. Among raptors, post-fledging dependence periods that exceed 6 months are exclusive to the largest species and these have reproductive cycles that exceed 12 months. By contrast, young of the medium-sized grey falcon *Falco hypoleucos* have been reported in close company with their parents up to 12 months after fledging, that is, at a time when the adults are expected to breed again. We investigated the occurrence and characteristics of prolonged adult–juvenile association relative to other falcons and similar-sized raptors. We found that the behavioral development of grey falcon young is extremely delayed, and that they even depend nutritionally on their parents for up to 12 months after fledging. We suggest that these 2 distinctive features are, ultimately, adaptations of the grey falcon to its extreme environment, Australia's arid and semi-arid zone, one of the hottest environments in the world.

Key words: arid environment, behavioral adaptation, bird of prey, post-fledging period.

In most species of birds, including raptors, the young depend on their parents for some time after fledging for the provisioning of food and for protection while they learn to become nutritionally independent (Lack 1954; Fogden 1972; Burger 1980; Heinsohn 1991). Skills that the young birds have to learn include recognition and localization of foraging areas and suitable food or prey, foraging or hunting behaviors, and food handling (Nelson 1971; O'Connor 1984; Varland and Klaas 1991; López-López et al. 2014).

Rapid learning can be expected to be favored by natural selection because early nutritional independence reduces the period of vulnerability, whether from predators or environmental extremes. Further, thermoregulatory and other metabolic requirements necessitate a dependable and regular food supply, in line with most endothermic animals. Cases of comparatively slow juvenile development have, therefore, attracted scientific attention, for example, in primates including humans (reviewed by Jones 2011). In birds, cases of relatively long juvenile dependence in a species have usually been attributed to the juveniles requiring a long time to attain foraging independence (e.g., Heinsohn 1991; Hunt et al. 2012). The difficulties may stem from having to learn foraging techniques that require extended learning periods, including tool use (e.g., New Caledonian crow *Corvus moneduloides* [Hunt et al. 2012]) or the location and securing of scarce food types (e.g., frigatebirds [Burger 1980]).

The post-fledging dependence periods of young diurnal raptors (Cathartiformes, Accipitriformes, Falconiformes) tend to increase with the size of the species. For falcons, genus *Falco*, this period ranges from a few days to 4 weeks for small species and 4–6 weeks for most large species (Newton 1979). Examples for other raptors are post-fledging dependence periods of 5–12 weeks for buzzards and kites and about 6 months for some large eagles and vultures (Newton 1979). Post-fledging dependence periods that exceed 6 months are exclusive to the largest raptors (Newton 1979), ones that have reproductive cycles that exceed 12 months, resulting in breeding only every second or third year. The harpy eagle *Harpia harpyja* has probably the longest post-fledging dependence period of any raptor, around 1.5 years, and it also has the longest breeding cycle among raptors, exceeding 2 years (Brown and Amadon 1989; Muñiz-López et al. 2012, p. 510; Aguiar-Silva and Sanaiotti 2013).

The juvenile dependence period of raptors has been studied from several perspectives, including whether the parents or the young determine the end of this period, whether the young hunt for themselves during this period, and the influence of weather and prey availability (Brown 1966; Newton 1979; Alonso et al. 1987; Mínguez et al. 2001; Arroyo et al. 2002; Walls et al. 2005; Balbontín and Ferrer 2009). Also, the comparative duration of the juvenile dependence period across similar species has received consideration (e.g., Donázar and Ceballos 1990).

Only anecdotal information is available on the post-fledging behavior of the grey falcon, as collated by Schoenjahn et al. (2020). That is, young grey falcons have been reported to be in close company with their parents up to 12 months after fledging. By contrast, the young of all other species of *Falco* are independent at about 2 months after fledging. We therefore investigated the occurrence and characteristics of prolonged juvenile dependence of the grey falcon, to test these earlier reports. First, we collated information (own observations and those reported to us by reliable observers) on the extent of the juvenile dependence period in this species to establish whether it is as long as the available anecdotal reports seem to suggest. We quantified 1) how grey falcon parents support their young during that period and the extent to which they do this and 2) the development of key survival skills in juveniles. We then compared the results with published behaviors of other *Falco* species. In this article, we demonstrate that grey falcons differ significantly from other falcons and similar-sized raptors with regard to the duration during which a family stays together and the time required for juveniles to develop survival skills. These findings strongly suggest that an ecological explanation for these 2 behaviors exists and we develop this in the discussion.

Materials and Methods

Study species

The grey falcon is a rare Australian endemic raptor. It is a medium-sized falcon with a median body mass of adults captured from the wild of 412 g ($N = 7$; range 339–448 g) for males and 502 g ($N = 9$; range 486–582 g) for females (Schoenjahn 2018). The species breeds at most once a year and invariably between June and November, that is, across midwinter and spring, in line with most of its congeners (Schoenjahn 2013). Grey falcons of all ages and throughout the year feed almost exclusively on birds (reviewed by Schoenjahn et al. 2020).

The species is distributed at very low density across parts of Australia's vast arid and semi-arid zone, an area of about 5 million km^2 or 70% of the Australian mainland (Australian Museum 2002; Pavey and Nano 2006; Schoenjahn 2013). Specifically, the species is restricted to areas that are classified as "hot desert" and "hot savannah," the hottest climate zones recognized by the Köppen-Geiger Climate Classification (Peel et al. 2007; Schoenjahn 2013). The grey falcon appears to be the only *Falco* species that is virtually entirely (i.e., all individuals) and permanently confined to arid-hot conditions (Schoenjahn et al. 2020).

Study area and study period

The study presented here is part of an ongoing research project that commenced in 2004 and is conducted across the arid/semi-arid zone of Australia and adjacent areas. It thus encompasses the entirety of the species' distribution (for which see Schoenjahn et al. 2020). Sites are undisclosed to protect the birds of this threatened species (which is listed nationally as Vulnerable under the *Environment Protection and Biodiversity Conservation Act 1999*). Data for the study presented here were collected between 15 March 2007 and 31 October 2016 and between 15 March and 1 August 2021.

Data collection

The data on family groups remaining together for extended periods are based both on our own observations ($N = 21$), and those unpublished reports of others ($N = 23$) that were supported by photographic evidence or conclusive descriptions of field marks consistent with those provided by Schoenjahn (2010). Only those observations made between 15 March and 31 October are included, to cover the 5–12 month period after fledging of the young (median fledging date was found by Schoenjahn [2018] to be 12 October). At the age of 5 months after fledging, the young of all other raptors of similar size to grey falcon have long left their parents, including all *Falco* species specifically studied in this respect (Table 1). The threshold of 5 months after fledging leaves no room for misinterpretation of the data.

A group of grey falcons was considered to be a family group if it consisted of 2 or more individuals, with at least 1 juvenile and 1 adult clearly associated with one another, for example, roosting closely together on the same tree or artificial structure (such as telecommunication repeater tower and powerline pylon). Groups containing more than 2 adults (i.e., aged 2 years and older) were never observed. Each family record contained at least the following information: confirmed identification of the species, date, location, number and age of individuals, and sex (if known). These details were assessed through direct observation in the field or from photographs made available to us. Distinguishing young grey falcons from adults is straightforward for several months after fledging (Schoenjahn 2010). Young grey falcons at the age of about 1 year, "yearlings," may be recognized by remnants of juvenile plumage and their bare parts not being as bright orange-yellow as in adults (Schoenjahn 2010; Schoenjahn J, personal observation).

Observations of groups within 200 km of each other at different times of the same year were considered to have a high enough probability of involving the same family, so only the latest record in the year was included in the data set and analysis. The threshold of 200 km was chosen on the basis of the movements of a satellite-tracked grey falcon in its first year that remained within 155 km of its natal site during April–October 2014 (Schoenjahn 2018). We are, therefore, confident of the independence of our group-based observations.

The interactions of the juveniles aged 5–12 months after fledging with their parents, and also the key motor skills of these juveniles,

Table 1. Post-fledging periods of *Falco* species, as reviewed by Newton (1979) unless indicated otherwise

Species of *Falco*	Common name	Post-fledging period (wk)	Body mass (g)
naumanni	Lesser kestrel	<1[a]	90–208
vespertinus	Red-footed falcon	1–3	130–197
subbuteo	Eurasian hobby	2–3	131–340
Sparverius	American kestrel	3	80–165
tinnunculus	Common kestrel	3.5–4	136–314
rusticolus	Gyrfalcon	4	961–2,100
berigora	Brown falcon	1–6	405–860[b, c]
biarmicus	Lanner falcon	4–6	500–900
cherrug	Saker falcon	4–6	730–1,300
peregrinus	Peregrine falcon	5–6	550–1,500
subsp. *macropus*[d]		≥10[e]	505–960[b, c]
subniger[d]	Black falcon	8[f]	510–1,000

Note: Body mass (sexes combined) according to White et al. (1994), unless indicated otherwise, [a] Bustamante and Negro (1994). [b] Marchant and Higgins (1993), [c] Live adult birds (banding data). [d] Endemic to Australia. [e] Sherrod (1983) ($N = 1$). [f] Charley et al. (2014) ($N = 1$).

were recorded exclusively by a single observer (J.S.), thus ensuring that the behaviors of the birds involved were determined consistently. Eighteen of the aforementioned 21 family groups were thus assessed; the remaining 3 families could not be assessed because their members remained inactive when observed. All observations were carried out from the ground with binoculars (10 × 42 BN, Leica, Germany) and telescope (Apo-Televid 77 with 32 × WW eyepiece, Leica, Germany).

A juvenile was presumed to be night-roosting together with its parent(s) when the individuals were observed roosting closely together at around sunset or sunrise. This definition was used because these birds remain, until sunrise, where they settled the previous evening (Schoenjahn J, personal observation). Food-soliciting was recorded when juveniles begged (vocally) or harassed (behaviorally) a parent. Motor skills of juveniles were assessed by comparing these to those of adults. Skills included flying skills (e.g., avoiding collision with obstacles in the flight path); selecting a suitable perch (e.g., a horizontal perch); precision landing; and perching successfully and securely on the perch, food handling, and food passing. A total of 383.75 h (median 17.5 h, range 1.0–74.0 h) was spent observing young–parent interactions in the 18 family groups.

Ethical standards

The fieldwork was approved by the Animal Ethics Committees of the Australian States and Territory concerned and the University of Queensland. These details are listed in Supplementary Material S1.

Results

Family groups

Forty-one independent family groups were recorded in the period 15 March to 31 October of the years 2007–2016, and a further 3 during 15 March to 1 August 2021 (Table 2). Fifteen (37%) of the 41 family group observations were in the months September and October, the core of the breeding season (Figure 1). The juveniles in these families were, therefore, aged about 11–12 months after fledging. One of the adult pairs (No. 38 in Table 2), while being closely associated with a yearling, was breeding with 3 young in the nest.

That pairs are capable of breeding in successive years, and partners may stay together for more than 1 breeding event, was evidenced by the observation of a pair of individually color-banded grey falcons that bred successfully in 2010 and 2011, using the same nest. Breeding more often than once in a year was never recorded.

Behaviors of parents and juvenile offspring

The behaviors of adult and juvenile grey falcons aged 5–12 months after fledging that were observed in individual family groups are presented in Table 3 ($N = 18$). In all families that could be assessed for night-roosting ($N = 15$), the juveniles roosted together with their parent(s) during most nights (89%; $N = 34$ of 38). This behavior was evidently independent of the age of the juveniles. Of note, a family roosted together at night even after the male parent had attacked its single 1-year-old offspring; the begging yearling was attacked several times on 6 and 7 October 2007. This was the only instance in this study of a parent attacking a closely associated offspring. The family group was clearly associated with a nest in good repair but the adults did not breed in that year.

Begging or harassing a parent for food was observed in juveniles in most family groups (83%; $N = 15$) and this was seen frequently in these birds. The behavior was independent of the age of the juveniles and was seen in individuals even about 12 months after fledging, that is, within 2 weeks before and after the median fledging date (12 October). The young of the 18 family groups assessed were never observed catching their own food. Further, cooperative hunting involving individuals of any age was never observed.

Parents providing food to their offspring 5–12 months after fledging was recorded in 3 family groups (17%) (Table 3). Each of these feeding instances ($N = 13$) involved an adult pair associated with 1 or 2 offspring at the age of about 12 months after fledging, and these young were begging and harassing their parents, strongly at times. During 4 (31%) of these 13 instances, the adult parent fed the offspring piecemeal. In the remaining 9 instances (69%), the offspring removed a whole prey item, or a part of it, from the parent's talons while both birds were perched (see below). The first pair listed in Table 3 (No. 10) that was involved in such feeding was not breeding at the time but was clearly associated with a nest in good repair which might have been the yearling's natal nest. The second pair (No. 11 in Table 3) was breeding at the time and had 3 nestlings. On 15 September 2015, the adult female fed the yearling piecemeal while both birds stood on the active nest. Later that day the yearling received a whole dead bird from the adult male. The third pair (No. 17 in Table 3) was closely associated with 2 yearlings; on 1 October 2016 feeding of one or the other offspring was observed 7 times. The location was a nesting site of 2015 where a pair had raised 2 young; the incidence almost certainly involved the same individuals.

Table 2. Records ($N = 44$) of independent individual family groups of 2 or more grey falcons observed by us and reliable observers, between 15 March and 31 October 2007–2016 ($N = 41$) and between 15 March and 1 August 2021 ($N = 3$)

No.	Date (if known)		Year	Number of birds in the group	Age and sex (as far as known)	State or territory[a]
1	March	23	2015	2	1 ad. ♀, 1 juv. ♂	QLD
2		27	2015	2	1 ad. ♀, 1 juv. ♂	QLD
3		31	2008	4	2 ad., 2 juv.	QLD
4	April	04	2014	3	2 ad., 1 juv. ♀	WA
5		06	2016	2	1 ad., 1 juv.	QLD
6		Mid	2013	4	2 ad., 2 juv.	QLD
7		16	2021	2	1 ad., 1 juv.	NT
8		17	2011	2	1 ad., 1 juv.	NSW
9		24	2021	3	2 ad., 1 juv.	WA
10		26	2014	3	2 ad., 1 juv.	NSW
11	May	02	2007	3	1 ad., 1 juv.	QLD
12		10	2016	4	2 ad., 2 juv.	WA
13		13	2013	5	2 ad., 3 juv.	NSW
14		15	2008	3	2 ad., 1 juv.	WA
15		18	2013	4	1 ad., 1 juv.	WA
16		Second half	2012	4	2 ad., 2 juv.	QLD
17		21	2011	3	1 ad., 2 juv.	QLD
18		Late	2012	4	2 ad., 2 juv.	QLD
19		Late	2012	3	2 ad., 1 juv.	QLD
20		31	2011	4	1 ad., 1 juv.	QLD
21	June	Early	2014	3	2 ad., 1 juv.	NT
22		02	2008	4	2 ad., 2 juv.	WA
23		First half	2016	4	2 ad., 2 juv.	NT
24		30	2015	2	1 ad., 1 juv.	QLD
25	July	06	2008	3	2 ad., 1 juv.	QLD
26		10	2012	3	1 ad., 1 juv.	QLD
27	August	01	2014	3	1 ad., 1 juv.	NT
28		01	2021	3	2 ad., 1 juv.	NT
29		09	2008	2	1 ad. ♀, 1 juv. ♂	WA
30	September	11	2011	3[b]	2 ad., 1 juv.	QLD
31		19	2009	2	1 ad. ♀, 1 juv. ♂	NT
32		28	2008	2	1 ad. ♀, 1 juv. ♂	QLD
33		29	2012	2	1 ad. ♀, 1 juv. ♂	NT
34	October	01	2015	3	2 ad., 1 juv. ♀	NT
35		02	2012	3	1 ad., 1 juv.	QLD
36		02	2016	4	2 ad., 2 juv.	QLD
37		04	2012	3	2 ad., 1 juv.	QLD
38		05	2015	3[c]	2 ad., 1 juv. ♀	SA
39		07	2007	3	2 ad., 1 juv.	QLD
40		07	2012	4[d]	2 ad., 2 juv.	QLD
41		12	2012	2	1 ad., 1 juv.	QLD
42		16	2009	2	1 ad. ♀, 1 juv. ♂	QLD
43		17	2012	3[e]	2 ad., 1 juv.	QLD
44		31	2009	3[f]	1 ad., 2 juv.	QLD

Notes: Groups consisted of 1 or 2 adults (ad.) in close company of 1 or more juveniles (juv.). It was not always possible to determine age and sex of all birds in a group. [a] The Australian States and Territory are abbreviated as follows: "NSW," New South Wales; "NT," Northern Territory; "QLD," Queensland; "SA," South Australia; "WA," Western Australia. [b] At the same location on 31 May 2011, a family of 2 adults and 2 juveniles was recorded. This was almost certainly the same family. [c] This pair was breeding at the time with 3 young in the nest. [d] At the same location in late May 2012, a family of 2 adults and a juvenile was recorded. This was presumably the same family as observed on 7 October 2012 but with 1 of the 2 juveniles not having been detected in May. [e] At the same location in mid-March 2012, 2 adults accompanied by 2 juveniles were recorded, almost certainly the same family. Further, at a location 175 km to the south-east a family of 2 adults and 1 juvenile was observed on 10 October 2012, that is, within the 200 km distance that may be covered by juveniles at that age. The observation 10 October 2012 was, therefore, excluded from the analysis., [f] This group was observed at that site until 2 November 2009, that is, beyond the cut-off date 31 October.

During all 13 feeding instances both birds were perched and the prey was already dead. Aerial food-transfers, which are often used by, for example, peregrine falcons *F. peregrinus* (Sherrod 1983), were never observed in this study. Occasionally the yearling would fly a short distance to meet the food-delivering adult in the air and molest the adult, sometimes even trying to get hold of the prey. Invariably, the adult would not let go of the prey but evaded the juvenile until all birds were perched. For example, a perched adult

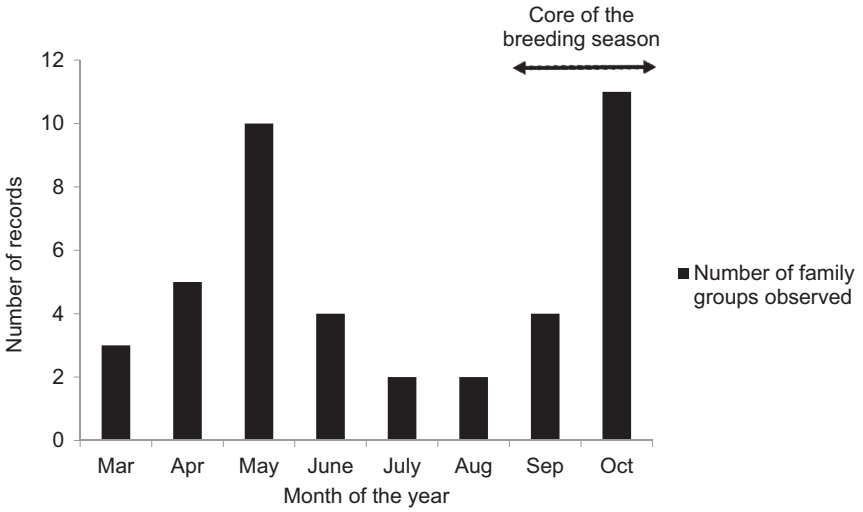

Figure 1. Frequency of records of grey falcon family groups, that is, 1 or more adults associated with 1 or more 5–12 month-old young, observed between 15 March and 31 October 2007–2016 ($N = 41$).

female did not let her 1-year-old female offspring have the whole prey despite the yearling attacking the item; the adult then commenced feeding the yearling piecemeal.

Motor skills of juveniles

Key motor skills of young grey falcons aged 5–12 months after fledging could be assessed in 9 of the 18 families observed. Consistently in all these 9 cases, the young had at least one key motor skill not fully developed (Table 3). Specifically, the young performed below adult-standard in 3 crucial skills, namely flying, choosing a suitable landing spot and landing securely on it, and food handling. These results were independent of the age of the juveniles.

Observations ($N = 14$) were also made of juvenile grey falcons 5–12 months after fledging, in the absence of adults (Table 4). Note that in 8 cases, adults were not searched for. Motor skills could be assessed in 3 of the 14 cases. The first case involved an individual aged about 6 months after fledging. It had below adult-standard motor skills and appeared emaciated. The second case involved 2 closely associated individuals, presumably siblings, aged 8–9 months after fledging. One of these 2 young successfully captured a small parrot and subsequently fed on it. The third case involved a yearling with poor flying skills. It flew, while begging vehemently, toward an active grey falcon nest and was driven away by both adults. Further details of these 3 cases are provided in the footnotes in Table 4.

Juvenile motor skills of below adult-standard were presumably under-recorded. This is because some tasks were not observed being performed or their performance did not require great skill. For example, food-handling skills could not be assessed in the cases when the juveniles were fed piecemeal, and flying in open, treeless environments may not often require difficult maneuvres.

Discussion

Juvenile behavioral development in the grey falcon was found to be slower and juvenile–adult dependence significantly longer than in any other species in the genus *Falco* and diurnal raptors of similar size (Tables 1 and 3). Cases of slow juvenile development in birds tend to be explained with reference to the difficulty in learning to become nutritionally independent, and invoke often time and practice needed to learn intricate foraging skills and the difficulty in locating and securing scarce food types (Table 5). We propose that the slow juvenile development and uniquely prolonged dependence in the grey falcon may be best explained as an adaptation to the species' extreme environment, Australia's arid and semi-arid zone, one of the hottest environments in the world.

The grey falcon stands out among its congeners by its specializations in 2 fundamental ecological aspects, namely diet and the environment it inhabits throughout its life (Schoenjahn et al. 2020). Its diet is the most restricted of any species in the genus *Falco*, consisting throughout the year and independent of age virtually exclusively of birds (Schoenjahn et al. 2020; this study, see Supplementary Table S1). In regard to its environment, the grey falcon is the only species of *Falco* that is entirely restricted to a zone of arid climate with some of the highest average annual temperatures globally (Schoenjahn et al. 2020). It is in this context that the grey falcon's extreme post-fledging period, the longest of any *Falco* species (Table 1), needs to be interpreted.

The grey falcon is an extreme food specialization and adults and young never switch to prey types that may be easier to obtain at a given time, such as insects (Supplementary Table S1). Significantly, this precludes young grey falcons from building their skills gradually on prey that is less difficult than birds to pursue. From the outset, then, they have to learn to hunt birds in flight, perhaps the most difficult and physically demanding food types to obtain (Newton 1979). Many practice attempts will surely be needed before their success rates are high enough to sustain their independence. By contrast, young of the peregrine falcon, also a bird-hunting specialist (Zuberogoitia et al. 2013), are known to pursue flying insects within a week of fledging and thus build their hunting skills (Cade 1960; Ratcliffe 1980; Sherrod 1983; Schoenjahn et al. 2020). The young of many other raptor species also learn hunting in a staged process (e.g., red-shouldered hawk *Buteo lineatus* [Snyder and Wiley 1976], Australian hobby *Falco longipennis* [Metcalf 1989], greater kestrel *F. rupicoloides* [McCann and Kemp 1994], lanner falcon *F. biarmicus* [Leonardi 2015]). The *Falco* species mentioned above are known to live and breed in arid environments, but not exclusively so, and have significantly broader diets than the grey falcon.

The environment within which the young grey falcons' learning takes place imposes extreme heat loads, for the species' breeding is

Table 3. Behavior of grey falcons in family groups ($N = 18$)

No.	Month	Year	Number and age (if known) of the birds in the group	Adult behavior			Family night-roosted together (n/m)	Juv. solicited	Motor skills in juv.			
				Breeding	Aggressive toward juv.	Fed juv.			Flying	Selecting a suitable Perch	Precision landing	Food handling/ passing
1	March	2015	1 ad., 1 juv.	N/A				Yes	B/A		B/A	B/A[a]
2	April	2014	2 ad., 1 juv.	N/A				Yes				
3	April	2008	2 ad., 2 juv.	N/A			4/4	Yes	B/A	B/A	B/A	
4	May	2008	2 ad., 1 juv.	N/A			4/4	Yes		B/A	B/A	
5	August–October	2007	2 ad., 1 juv.	No	Yes		9/9	Yes				
6	August	2008	1 ad., 1 juv.	No			1/1	Yes				
7	August–September	2011	2 ad., 1 juv.	No			1/2	Yes	B/A			
8	September	2009	1 ad., 1 juv.	No			1/4		B/A	B/A		
9	September	2008	1 ad., 1 juv.	No			1/1					
10	September–October	2015	2 ad., 1 juv.	No		Yes[b]	4/4	Yes	B/A			
11	September–October	2015	2 ad., 1 juv.	Yes[c]		Yes[b]	3/3	Yes	B/A		B/A[d]	
12	October	2012	2 ad., 1 juv.	No			1/1	Yes			B/A	B/A[e]
13	October	2012	2 ad., 2 juv.	No			1/1					
14	October	2012	2 ad., 1 juv.	No			1/1	Yes				
15	October	2012	1 ad., 1 juv.	No			1/1	Yes				
16	October	2009	1 ad., 2 juv.	No			1/1	Yes				
17	October	2016	2 ad., 2 juv.	No		Yes[b]	1/1	Yes	B/A		B/A	B/A[f]
18	October	2009	1 ad., 1 juv.	No				Yes				
	Total			1 of 14	1 of 18	3 of 18	34/38	15 of 18	Juv. skills below ad.-standard in 9 families			

Notes: Groups involved 1 or 2 adults (ad.) and 1 or more of their presumed offspring from the previous year (juv.). Observations were made from 15 March to 31 October 2007–2016, to cover the juvenile ages of 5–12 months after fledging. Adult behavior was assessed in relation to breeding and their interactions with the juvenile present. That of the juveniles was assessed for the level of execution of their motor skills, as listed. "N/A," not applicable because outside breeding season; " "(blank), indicates that a behavior or skill could not be assessed because the task was not observed being performed or its performance did not require great skill; "n/m," n out of m nights of observation, that is, number of nights, n, during which at least 1 juvenile and 1 parent roosted together, against the number of nights, m, at which at least 1 member of the respective family was recorded roosting; "B/A," below adult-standard execution of skills and maneuvers. [a] The juvenile fed on a small passerine bird when the observer (J.S.) arrived at the site. It took the juvenile 20 min to consume the item which appeared to have been an Australasian pipit *Anthus novaeseelandiae* (body mass 26 g [Higgins et al. 2006]). For comparison, adults were repeatedly observed in this study taking about 1 min to consume a budgerigar *Melopsittacus undulatus* (body mass 30 g [Higgins 1999]). [b] A juvenile received food from a parent, that is, either the parent fed the juvenile piecemeal or a whole prey item was passed from adult to juvenile. In all cases, both birds were perched and the prey was dead. [c] This pair was breeding at the time with 3 young in the nest. Whether grey falcons bred in this area in the preceding year, 2014, is not known. [d] The situation concerned the active nest of the parents of this juvenile. The nest was about 80 m above ground on a repeater tower. The 1-year-old juvenile was perched on the structure at nest level when the adult male parent arrived with prey, landing at nest level but on the side opposite of the juvenile. For more than 3 min, the juvenile tried clumsily to find a way to walk, climb, and hop along the structure to the adult male before it succeeded and took the food off the male parent. The juvenile did not attempt to reach the parent by flying, as an adult bird would likely have done. [e] The yearling fed clumsily on a food item, repeatedly taking it into the bill and making a few steps back or forth, then passing it back to a foot and pulled at it again, often failing to tear off meat. Holding it in one foot, the yearling looked at the item and tilted its head from one side to the other, a behavior that we have not observed in feeding adults. [f] One of these 2 yearlings, while soaring with a whole dead bird (that it had received from its male parent) in its talons, pulled with its bill on the item, dropped the item twice, each time catching the falling item in mid-air.

restricted to the hot arid and semi-arid zone of Australia (Schoenjahn et al. 2020). These birds therefore face extreme and unpredictable climatic events, which are most severe in summer, and include extremely high temperatures, prolonged heat waves, dust storms, prolonged droughts, deluges of rain, and, in the northern parts of the grey falcon's distribution, tropical cyclones. The first season that newly fledged grey falcons face is summer. For them to find, let alone catch, live birds at a rate that would allow them to live independently, seems extremely unlikely. Indeed, passerine and other prey species are reported to seek shade and fly less during periods of high heat loads (Carroll et al. 2015; Martin et al. 2015). Further, during droughts, heat waves and tropical cyclones prey abundance may be reduced through mortality and migration (Wiley and Wunderle 1993; Perdomo-Velázquez et al. 2017; Conradie et al. 2020). Although rain is rare in grey falcon environment, when it does come, usually in summer, it is likely to reduce foraging opportunities for grey falcons. That is, wet plumage seems to reduce dramatically the grey falcon's flight performance (Schoenjahn 2013; Mullin et al. 2020). And inexperienced (but independent) juveniles are likely to perish at significantly higher rates than dependent young, as quantified in young yellow-eyed juncos *Junco phaeonotus* when summer storms reduced their foraging time (Sullivan 1988). Even a few successive missed opportunities by an inexperienced young grey falcon could be life-threatening (e.g., bird No. 2 in Table 4), and especially so during periods of high heat loads.

The inexperience of juvenile grey falcons under the summer conditions described above would endanger them. We predict that this is why adult grey falcons keep the activity levels of their young low, primarily by hunting for them. And even the aerial adult–juvenile food-transfers that are so common in raptors including *Falco*

Table 4. Records ($N = 14$) of juvenile grey falcons without the presence of adults (with the exception of No. 13, see footnote 4), made between 15 March and 31 October 2007–2016 ($N = 10$) and between 15 March and 1 August 2021 ($N = 4$)

No.	Month	Day	Year	Number of juveniles	Motor skills (if assessed)	Observer
1	April	18	2010	1		T. Mutton
2	April	22	2021	1[a]	Poor flying and hunting skills	J.S.
3	May	13	2013	1		S. Vernon and S. Knights
4	June	9	2015	1		R. Waring
5	June	26	2021	2		W. Palmer
6	June	29	2012	2		P. Waanders
7	July	5	2021	2[b]	Captured prey and fed on it	A. Newey (video footage)
8	July	7	2016	1		P. Barratt
9	July	18	2012	2		R. Clemens
10	July	29	2021	1		C. Schoenjahn
11	August	6	2008	1		JS
12	August	26	2014	1[c]		A. Boyle
13	September	23	2009	1[d]	Poor flying skill	J.S.
14	October	19	2009	2		J.S.

Notes: The records by observers other than J.S. were supported by video or photographic evidence. Adults were searched for only in the cases of the juveniles numbered 2, 7, 13, and 14. Note that motor skills were assessed exclusively by J.S., during in situ observation and from video footage in the case of the juveniles numbered 7. [a] This individual, aged about 6 months after fledging, was observed for 45 min at a telecommunication repeater tower. It appeared emaciated with an empty crop, and had below adult-standard motor skills, specifically involving avoiding obstacles in its flight-path and choosing an appropriate perch. Repeatedly it stooped clumsily and without success at passerines that moved among bushes along the perimeter fence of the repeater, returning to the repeater between the attacks. After one such unsuccessful stoop it came within half a meter of the ground and hit, seemingly by accident, a grasshopper that had launched itself into the air, presumable in response to the approaching falcon. The grasshopper fell to the ground, the young falcon landed next to it, picked it up with its bill, and manipulated it. Whether the young fed on the insect remains unclear. [b] The 2 closely associated young, aged about 9 months after fledging, were observed on several days in late June and early July 2021 at an artificial waterbody and no adults were encountered during any of the visits despite being looked out for. On 5 July, the 2 young were video-recorded and photographed hunting. One of the 2 birds captured a mulga parrot *Psephotellus varius* and subsequently fed on it (Newey A, personal communication to J.S., 5 July 2021). [c] The photographs show a juvenile in poor condition; its age was about 10 months after fledging. It was emaciated, had an empty crop, on both wings some primaries were missing and some others broken, and some rectrices were broken. The location was near Broome, north-western Australia, about 390 km north-east of the nearest breeding location recorded during this study and outside the breeding distribution determined during this study. [d] The incidence involved a yearling male with below adult-standard motor skills and an adult breeding pair that were not closely associated as a family group. None of these individuals was marked and it remains unclear whether they were parents and offspring. The yearling flew toward the pair's active nest 80 m above ground on a repeater tower while both adults were present. The yearling begged incessantly and flew with inefficient wing-beats, lost height, and barely avoided collision with one of the cable guys of the repeater tower. The yearling was instantly driven away vigorously by both adults. The site might have been the yearling's natal nest site and the yearling might have been the offspring of one or both of these adults because a pair had nested at that site in 2008, raising a single male young.

Table 5. Selected examples of bird species with long post-fledging periods during which adults support their young with food, and for which an explanation has been offered

Species	Duration (months)	Explanation	Sources
Forest red-tailed black cockatoo	≥6	Handling of difficult food	Johnstone et al. (2013)
Great frigatebird	≥6	"The specialized frigate feeding technique of snatching food in flight and piracy . . . takes a long time to perfect"	Nelson (1967, p. 318)
New Caledonian crow	≤10	Use of specifically fabricated tools to extract food from crevices	Hunt et al. (2012)
Grey falcon	12 or more	Locating and capture of difficult prey in extreme aridity and heat	This study

(summarized by Sherrod [1983]; see also Metcalf [1989], Barnes and Debus [2014]) were never observed in grey falcons (see the "Behaviors of parents and juvenile offspring" section). It is perhaps surprising, though, that even 6 months after the end of summer the 1-year-old grey falcons are still fed by their parents, and their flight and other survival skills are not fully developed (Tables 2 and 3). Again, this contrasts dramatically with the complete independence (for 9 months or longer) of the young of all similar-sized raptors, including falcons (see above). To explain this extraordinary discrepancy, the year-round behavior of adult grey falcons needs to be

considered. We predicted previously that grey falcons across all ages should have low activity levels in all key activities (Schoenjahn et al. 2021). Indeed, adult grey falcons have been proposed to be adapted to living exclusively in hot arid environments by maintaining low activity levels throughout the year and even when most active (Schoenjahn et al. 2022). That is, by keeping physical exertion low they minimize endogenous heat production and thus ease their thermoregulation during periods of high heat load, which are unpredictable in occurrence and severity.

The dietary and environmental specializations result in a suite of interacting circumstances which together impact on the duration of the juvenile dependence period in this species. Their dietary specialization on prey that is difficult to capture (which cannot yet be explained) prevents the young from hunting easier prey and gradually building hunting skills. The environmental specialization results in extreme threat to the recently fledged young grey falcons and reduced learning opportunities for them because bird prey may be more difficult to find, pursue, and secure in summer than at other times. Finally, the behavior of the grey falcon parents actively reduces the learning opportunities for their young because the parents do not entice them to practice crucial skills, such as hunting (see above, and also the "Behaviors of parents and juvenile offspring" section). This and other adult–juvenile interactions prevent the young from elevated physical exertion, which eases their thermoregulation during periods of high heat load. Maintaining low activity levels even when most active is in line with the year-round behavior of the adults. The young grey falcons seem to have to learn this behavior, which has been suggested to be an adaptation to the hot arid environment to which the species is restricted (Schoenjahn et al. 2021).

Authors Contributions

J.S.: conceptualization, methodology, investigation, funding acquisition, writing—original draft, and review and editing. C.R.P.: conceptualization and writing—review and editing. G.H.W.: conceptualization and writing—review and editing.

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Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

Conflict of interest

None declared.

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