

Parental Care by Lone Male Ferruginous Hawks (*Buteo regalis*), Rough-legged Hawks (*Buteo lagopus*), and Great Horned Owls (*Bubo virginianus*) was Limited to Providing Food

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In three long-term studies of Ferruginous Hawks (*Buteo regalis*), Rough-legged Hawks (*Buteo lagopus*), and Great Horned Owls (*Bubo virginianus*), we observed rare but regular occurrences of superabundant prey at nests where nestlings were hungry, emaciated, or dead. In these cases, a male appeared to be the lone parent; the female parent was found dead, kept away by disturbances, or simply absent. We conclude that the male parents, whose normal role is to provide food, were unable to expand their care to include morseling, feeding, and brooding. Faced with the stress of incessant food begging by nestlings, the male parents responded by bringing more and more food to the nest, to the point where food spoiled while the young starved amid plenty. We provide and interpret detailed observations for 11 such cases and suggest several variables that would influence the nestlings' chances of survival.

Key Words: Ferruginous Hawk; *Buteo regalis*; Rough-legged Hawk; *Buteo lagopus*; Great Horned Owl; *Bubo virginianus*; parental care; food provisioning; feeding; brooding; starvation; Rankin Inlet; Nunavut; Hanna; Alberta; Saskatoon; Saskatchewan

Introduction

Studies of birds have revealed fascinating patterns of mate choice and parental care, including elucidation of the apparent ecological correlates that predictably lead to such patterns (e.g., Cockburn 2006). Typical patterns include brood parasitism; male only, female only, and bi-parental care; and cooperative breeding (Cockburn 2006).

Care of young by monogamous pairs is the most common pattern among raptors and birds in general; 81% of all species exhibit it. Among raptors, three overlapping phases occur: at first, the female assumes brooding and shading duties almost continuously; later, the female leaves the partly grown young for part of the time to roost or even hunt nearby; and, finally, both male and female may be away hunting when the young approach fledging (Newton 1979, page 160).

A difference in body size influences the way in which dominance relationships and parental roles are apportioned within a raptor pair. Although a difference in size between females and usually larger males is common among animals (e.g., Blanckenhorn 2005), this is reversed among raptors with females about a third larger than males (e.g., Olsen and Olsen 1987). The nest is the female's domain, and it is common among broad-winged hawks, and possibly less so among falcons, for the male to spend little time at the nest (Newton 1979, page 159).

Using an inductive style of inquiry (e.g., Schmutz 1992), we report on observations at nests and emphasize context and detail in our field observations and related literature. We examine a male's limits in parental care and ask whether a male parent can adequately compensate for the loss of a female and under what conditions this may be possible.

Study Area and Methods

Ferruginous Hawks (*Buteo regalis*), studied near Hanna, Alberta, were in moist, mixed-grass prairie where rangeland grazing of cattle was the dominant land use. Richardson's Ground Squirrel (*Urocitellus richardsonii*) was the hawks' main prey. Our observations were part of a long-term population study varying in intensity from banding and monitoring of breeding densities each year to detailed monitoring of prey, growth of nestlings, and survival and dispersal of colour-marked young and breeding adults (Schmutz *et al.* 2008). The number of nests and visits to nests varied accordingly, from near daily during the nestling period to once a season. The use of an intensively studied core area and a peripheral area also affected the number of visits.

Observations of Rough-legged Hawks (*Buteo lagopus*) were made in the vicinity of Rankin Inlet, Nunavut, within an area defined for the long-term investigation of the breeding biology of Arctic Peregrine Falcons (*Falco peregrinus*; Court *et al.* 1988).

Great Horned Owl (*Bubo virginianus*) studies were conducted from a base in Saskatoon, Saskatchewan. Nests were reported by area residents or spotted from roads while trees were still devoid of foliage. Once located, nesting areas were visited annually to determine occupancy. Owlets were banded and prey items recorded (Gérard *et al.* 2009).

For convenience, we refer to cases or nests by number, preceded by F, R, or G, for Ferruginous Hawks, Rough-legged Hawks, and Great Horned Owls, respectively (Table 1).

Results

Observations of parental care deficits were rare in our studies (< 1% in over 5000 visits to all nests) and occurred at different stages in the nestling period and in different years.

Ferruginous Hawk nests

F-1: On our arrival at the study site on 9 June 1975, two nestlings less than 1 week old were peeping as if hungry, although prey was in the nest and a dark morph female, judging by size, was roosting on the nest rim. On 11 July, both nestlings were dead, a light morph Ferruginous Hawk was circling overhead, and the dark morph bird was not seen. In the nest, we found 14 dead Richardson’s Ground Squirrels. Our interpretation was that the nestlings vocalized out of hunger, to which the male parent responded by bringing more food but did not feed them.

F-2: On 30 June 1989, a mass of about 20 Richardson’s Ground Squirrels was found in a nest used during that year, but without young or adults visible at the time. Many of the squirrel bodies were whole. They had decayed and dried, suggesting that they had been captured and deposited 2–3 weeks earlier. This would have placed the prey deliveries about mid-way through the normal nestling period for Ferruginous Hawks in that year.

F-3: On 11 June 2002, a nest with two nestlings and no prey was attended by a light morph Ferruginous Hawk circling overhead. On 4 July, one nestling was dead and one alive. The live nestling gave monosyllabic, flutelike calls suggesting hunger (see Powers 2003, page 98). Of 30 partial or whole ground squirrels in the nest, 11 were gutted but otherwise uneaten, yet no parent was visible. The live nestling weighed 905 g at a primary length of 150 mm, the dead nestling 600 g at 132 mm (see Schmutz 1977, Appendix 3 for age determination). Assuming that the emaciated nestlings were smaller-bodied males, they were still 180 and 470 g below normal weight for their age, respectively. The most plausible interpretation was that one nestling had starved to death and the second was near death.

F-4: On 8 June 1976, a single, distant adult called in defence of a nest where a 410-g nestling emitted peeping sound (presumed hunger), although seven Richardson’s Ground Squirrels were present. On 10 June, the nestling was dead with the prey still in the nest. We

TABLE 1. Summary of nestling care deficits and reproductive outcomes for four Ferruginous Hawk (*Buteo regalis*) nests near Hanna, Alberta, two Rough-legged Hawk (*Buteo lagopus*) nests near Rankin Inlet, Nunavut, and five Great-horned Owl (*Bubo virginianus*) nests near Saskatoon, Saskatchewan.

Nest no.	Parents	Nestling age	Nestling status	Prey in nest	Nestling outcome
<i>Ferruginous Hawk nests</i>					
F-1	Male, possibly both	1 week	Hungry then died	In excess	Died
F-2	None, nest abandoned	Unknown	Unknown	In excess	Presumed dead
F-3	Male only	28 and 30 days	Starving	In excess	1 died, 1 fostered
F-4	Lone parent	11 days	Hungry, dead 2 days later	In excess	Died
<i>Rough-legged Hawk nests</i>					
R-1	Parents known present	3 weeks	Unfed for lengthy photography periods	In excess	Lived
R-2	Male only female presumed dead	3 weeks	Starving	In excess	2 of 3 dead
<i>Great-horned Owl nests</i>					
G-1	Male only Female electrocuted	2–3 weeks	Hungry	1 meadowlark	Survived ≥ 7 days
G-2	Male only	3 weeks	1 dead, 1 snow covered and hungry	1 magpie	Unknown
G-3	Male only Female dead 10 days	4 weeks	No apparent care	2 birds 1 rabbit	Survived 3 weeks to fledging
G-4	Male only	4 weeks	1 dead 3 hungry	In excess	Unknown
G-5	Male only	4 weeks	No apparent care	In excess	Apparently healthy 6 days later

assumed that a nestling reared to 11 days must have had a female parent initially, and, later, the remaining adult was a male unable to feed the nestling.

Rough-legged Hawk nests

R-1: From 29 to 31 July 2000, a blind was installed for photographic purposes approximately 15 m from the nest of a pair of Rough-legged Hawks, about 10 km north of Rankin Inlet, Nunavut. The pair had three young, approximately 3 weeks of age. Each member of the pair was easily identified to sex based on plumage. The adult male was apparently not affected by the installation of the blind and delivered several Siberian Brown Lemmings (*Lemmus sibiricus*) to the nest each day when photographers were present. At no time was the male observed attempting to feed nestlings, and the nestlings did not feed themselves. The adult female did not attend the nest when photographers were in the blind, and no feedings were witnessed during photographic sessions lasting up to 6 h. The young were apparently fed by the female after the photographers' departure; when the photographers arrived to film each day, the previous day's food was absent and the female flushed on their arrival. We recorded several prey deliveries by the adult male over the 3 days. Our interpretation at the time was that male Rough-legged Hawks do not feed young despite ample opportunity and apparent need.

R-2: On 8 August 2005, a visit to a Rough-legged Hawk nest on the Barrier Islands, Rankin Inlet, revealed only an adult male present. The female parent was not recorded at the territory during the visit, which lasted more than 1.5 h, unusual for this species at this location and time of year. The nest contained one live but emaciated nestling and two dead nestlings that were extremely emaciated and had apparently starved to death (Alastair Franke, Research Associate of the Circumpolar Institute at the University of Alberta and the Principal Investigator for Arctic Raptors, personal communication, 8 August 2005). The living nestling was standing on or beside the carcasses of at least five uneaten Arctic Ground Squirrels (*Spermophilus parryi*) and one Siberian Brown Lemming. We concluded from these observations that the female had died and that the male was not feeding the starving young, despite the availability of ample prey.

Great Horned Owl nests

G-1: On 29 April 2002, a telephone call alerted us to three orphaned Great Horned Owl nestlings. On 26 April 2002, a female had been electrocuted on a transformer, which subsequently required repair. On MAG's arrival, a male flushed from a roost and came to within 5 m of the nest tree in a farm shelterbelt. Three young, approximately 12, 16, and 20 days old, were in the nest, along with a whole, fresh, male Western Meadowlark (*Sturnella neglecta*). As the young were making hunger calls, MAG fed the meadowlark to the two larger owlets. The youngest owlet was removed

and introduced into a foster nest with only one nestling near Saskatoon. On 1 and 3 May 2002, the remaining two young were reportedly doing well. We assume that the two nestlings were large enough to feed themselves, possibly by consuming small prey whole.

G-2: On 6 May 2002, a nest 6 m above ground in a Trembling Aspen tree (*Populus tremuloides*) was snow covered after a snowstorm the previous day. The nest contained a freshly dead, 400-g Great Horned Owl nestling and a shivering 660-g nestling, plus the whole, fresh carcass of a Black-billed Magpie (*Pica hudsonia*). The living chick appeared to be cold and was "chittering" continuously. It readily ate offered morsels of the magpie. A shy adult male owl was observed nearby — apparently the sole survivor of the nesting pair — and was behaviourally unable to brood and tear prey for the nestling. We believe we saved or prolonged the life of the second nestling by removing snow and feeding it.

G-3: On 13 May 2005, a female owl that had been banded at this nesting area in 2002 was found dead below a nest containing one young. The female was partly decomposed and estimated to have been dead for 7–10 days. Prey, including a blackbird (Icterinae), a rabbit head (Lagomorpha), and a Grey Partridge (*Perdix perdix*), were on the ground below the nest, and a shy Great Horned Owl, judged by size to be a male, was nearby. At banding time on 2 June 2005, the estimated 7-week-old fledgling owl flew poorly. The adult male was still present and being mobbed by American Crows (*Corvus brachyrhynchos*). It was protective of the young and aggressive toward our black Labrador dog. By removing the dead female, we may have encouraged the male to place prey in the nest subsequently.

G-4: On 6 May 2008, we observed a nest containing one dead and three live owlets, estimated to be 25, 28, and 30 days old. An adult owl attended the nest, but without venturing from nearby cover. The young were vocalizing as though hungry. The nest contained three young Snowshoe Hares (*Lepus americanus*), five Northern Pocket Gophers (*Thomomys talpoides*), one Northern Shoveler (*Anas clypeata*), one Long-eared Owl (*Asio otus*), and the remains of a Northern Harrier (*Circus cyaneus*). The hungry young consumed a whole hare and part of the shoveler when these were offered in morsels. The smallest nestling was fed and introduced into a foster nest attended by two adults. We took signs of hunger despite superabundant food to indicate that parental care was compromised. All remaining prey appeared to be too large for the young to swallow whole or tear apart on their own.

G-5: On 5 May 2012, two 4-week-old owls were banded. Their nest contained eight American Coots (*Fulica americana*), one Gadwall (*Anas strepera*), one rabbit, and one Virginia Rail (*Rallus limicola*). Some of the coots contained maggots. A male adult owl was in attendance. Several days later, the nest was revisited and, again, only a male was in attendance. At 4 weeks

of age, we assumed that the young owls were able to feed themselves, possibly swallowing small prey when offered while leaving the large coots, ducks, and rabbit uneaten.

Discussion

Is the male's parental care role inflexible?

A common theme throughout these observations was food in all 11 nests and so much excess food that it spoiled in five of them (Table 1). Another common feature was the presence of a male parent only, except in nests R-1 and, possibly, in nest F-1 with F-2 unknown. Adult gender was judged based on raptor size, plumage, in-hand inspection (G-1, G-3), in-flight/roosting observation (F-1, G-2), or presumed based on the fact that the food-provision role (male) was satisfied while the brooding and feeding role (female; Bechard and Schmutz 1995; Houston *et al.* 1998; Bechard and Swem 2002) was not (F-3, F-4, R-2, G-4, G-5).

We know that two females had died (G-1, G-3). We assume that other females had also died (F-1, F-2, R-2, G-2, G-4, G-5) or that they were somehow kept away from the nest (e.g., R-1). Nestlings were starving, hungry, or cold, indicating that females were absent for at least several crucial hours (e.g., during a snowstorm) and for the days it took the males to amass excess prey, some of which had begun to spoil. We concluded that the female member of the pair was lost and that the male was induced to keep hunting by the hungry young. Males were unable to make the needed shift to feeding and brooding.

We are cognizant of the additional possibility that some nestlings may have died because of congenital problems or poisons in the environment (e.g., Schmutz *et al.* 1989) and that such nestlings voice physical pain, which would induce the male to continue hunting. This is unlikely in cases where nestlings survived or were transplanted (F-3, G-1, G-3, G-5). In case of F-3, the surviving nestling fledged from its foster nest, although, later, its long-dead carcass was found. Its early near starvation state may have compromised normal development, preventing this nestling from maturing normally and becoming able to hunt and survive on its own.

Flexible parental roles in related species

Kenward (2006) summarizes observations and reports that suggest some Northern Goshawk (*Accipiter gentilis*) males are also unable to care fully for their young when the female is lost. As in our cases, young starve in the face of ample food. Also similar to some of our owl cases, however, young Goshawks fledged from five nests where females disappeared at nestling age 12–20 days, when they begin to feed themselves.

When nestlings are very young and exposed to weather, the ability of their parents to brood is as important to their survival as the availability of food. In nest G-2, we believe that the failure of the male owl to brood the young during a snowstorm led to the death of one nestling; the other was likely saved by our clear-

ing snow off the nest. For comparison, RWN has observed a male Peregrine Falcon flying to a nest when the female had left temporarily and begin to cover and brood the young. Similarly, JKS observed a male Swainson's Hawk (*Buteo swainsoni*) cover the eggs in a nest after the male had brought prey which the previously incubating female accepted from him and ate atop a fence post.

In clear contrast to our observations of limited parental care, a study of a captive male Red-tailed Hawk (*Buteo jamaicensis*; Hamerstrom and Hamerstrom 1971) suggests that males of this species can participate in all facets of reproduction. The hawk studied had been taken from its nest at the nestling stage and used for falconry. Its gender was confirmed by ejaculation elicited by the falconer on whom the hawk was imprinted. The male hawk wove sticks into a nest base, formed a lined nest cup when straw was provided, covered a chicken egg, and developed a 5-cm × 6-cm brood patch, but without significant blood vascularization. The male hawk accepted a total of three Red-tailed Hawk nestlings 1, 6 and 21 days old offered over 2 years. Without prior experience, it responded positively to the vocalizations of the newly introduced 1 and 6-day-old nestlings and displayed great care closing its talons and sliding mostly on his tarsus over the nestlings to brood. It fed the nestlings pieces of flesh until they were 9 days of age. The pieces were not regurgitated, but still moist from saliva that seemed to flow more during feeding. After 9 days, the male tended to lay small pieces of meat on the nest rim for the nestlings to eat. By 24 days, the nestlings began to tear and consume mice and day-old chickens on their own. When the nestlings were 16 days old, the male gradually stopped brooding them at night, in a mid-May Wisconsin climate.

It may be surprising that hawks of the same genus differ so greatly in terms of parental care. The Red-tailed Hawk described above capably conducted all facets of parental care, including the development of a rudimentary brood patch. In contrast, we observed Ferruginous and Rough-legged Hawks, and Great Horned Owls, fail to tear prey and feed morsels to begging nestlings, a simple act that might have prevented their starvation. Species-specific behaviour repertoires may vary to that extent. Another possibility is that plasticity in parental care exists initially, but is lost through experience and discouraged by the dominant female.

Are female roles similarly inflexible?

At a different nest, a series of observations suggested that a female Ferruginous Hawk was able to assume the food provisioning role of males and raise her brood alone. Here, a male was observed with the female on two visits (6%) just before eggs hatched, then not again for the remaining 32 visits during the nestling period. This deviated from the typical pattern of two adults defending a nest in 38% of 164 visits in 1975 ($G = 9.42$, $P = 0.002$). Prey was less often present in the female-only nest, on only 21% of 29 nest checks

compared with 54% of 420 visits ($G = 10.77$, $P = 0.001$) to all other nests. Despite the lone attendance of the female parent and scarce prey in the nest, the young appeared as well fed as others. At least one young had food in its crop on 57% of 7 crop records, compared with 41% of 96 crop records ($G = 0.72$, $P = 0.396$) from nests with both parents in attendance.

These results suggest that this female Ferruginous Hawk was able to both hunt and care for her young, raising two young from four eggs to fledging. She likely left her young exposed during favourable weather, hunted when the young were hungry, and fed them immediately on return. This pattern would account for the reduced frequency at which food was found in the nest, yet also account for well-fed young with an average rate of food present in their crops. This male-loss or abandonment occurred in a year of exceptional food availability (Schmutz *et al.* 2008).

Is the mating system of Ferruginous Hawks female-centred?

In a female-centred mating system, the male is not only dependent on the female for reproduction, but also takes its cues from the female. Some observations suggest that this is the case in Ferruginous Hawks.

Observations from a blind in 1990, by Janet Foster (co-owner of John and Janet Foster Productions Ltd., personal communication, 26 June 1990) confirm the nestling-care role of females (see also Powers 2003). On several occasions, all four nestlings patiently waited their turn without struggle to be fed. Only once did two or more nestlings pull on the same piece of food offered by the female. When the offered piece of food was too large and the nestling struggled to swallow, the female took it back and ate the food herself. These nestlings were 28–31 days old at the time.

Older nestlings are able to feed on their own. Observing the same nest as above from a blind in 1989, Dan Wood (owned Wild Prairie Photographics Ltd., personal communication, 7 July 1989) observed a male, judging by size, leave a hill where it and the female had been roosting. The male returned 1 h later and delivered a ground squirrel directly to the nest, and then rejoined the female on the hill. One of the three young took the delivered ground squirrel from the nest rim and eventually all three nestlings fed on their own at ages 39 and 41 days.

A film sequence taken without audio in 1990 at the nest mentioned above shows male and female Ferruginous Hawks roosting side by side on the nest rim (Foster and Foster 1992*). Twice, the female turned her head toward the male with crown feathers erect and beak opening, suggestive of a dominance cue, whereupon the male left the nest to land on a branch in the same tree only 2 m away. This behaviour combined with the pattern of a male's rare and brief presence at nests with young, suggests that the female discourages the male from tending young.

Other observations support the female's primary role where the nest and young are concerned. In dozens of images obtained using time-lapse photography of nests (JKS, unpublished), in only one case did both male and female roost on the nest rim together; usually it is only the female. Similarly, Powers (2003) describes adult males delivering prey directly to the nest, as described by Dan Wood above, but "he never tarried at the nest but sat only briefly before departing within a few seconds of his food delivery, presumably to hunt for more food" (Powers 2003, page 67). Powers (2003, page 93) concluded that a male remained only 5–15 s at a nest after a prey delivery, and the longest observed stay was 5 minutes.

In the context of the female's primary care at the nest and, possibly, even enforced dominance over the male, the F-3 male's inability to channel its care away from excessive hunting to feeding is plausible. Repeated exclusion from the nest by a female, possibly over several years, likely reinforced nest avoidance, and flexibility in nestling care, if any, was lost through learning. This role development with experience and learned irreversibility could also apply to Great Horned Owls and Rough-legged Hawks.

Female loss and prey size

Our observations suggest that three broods of Great Horned Owls (G-1, G-3, G-5) survived in the absence of a female. Large owls and especially Great Horned Owls are known for their ability to swallow sizeable prey whole. This could have been a significant factor in the survival of some of the owl broods after female loss. Furthermore, the prey used by the owls was varied and included smaller items such as voles, mice, and songbirds.

In contrast, the diet of Ferruginous Hawks and Rough-legged Hawks (R-2) included primarily relatively large, tough-skinned ground squirrels. Our observations of the Ferruginous Hawks showed that 28–31-day-old nestlings still waited for the female to feed them. At 39–41 days, nestlings tore ground squirrels and fed on their own.

Nests F-3, F-4, R-2, G-2, and G-4 are noteworthy as nestlings were hungry and even starving amid plenty of food. The F-3 nestlings were an estimated 28 and 33 days old, and apparently could not tear and consume the ground squirrels that were present. The older starving nestling may have tried to eat on its own as it had dried blood on its beak.

Even with females present, a parental miscue was noted by Wayne and Alora Nelson (personal communication). A captive, 9-year-old, human-imprinted female Ferruginous Hawk incubated and tended to her hatchling normally, but persisted in presenting food morsels 5 cm above the nestling's beak. The Nelsons had to feed the young until it was 1 week old and able to touch the female's beak, which led to normal feeding by the female soon after.

In conclusion, we suggest that starving nestlings amid a superabundance of food in nests is a rare but widespread occurrence and that, in these cases, the loss of the female parent should be considered. We also provide evidence that male loss is less severe than female loss. Furthermore, we suggest several variables that might influence reproductive outcome after female loss: age of nestlings, prey size related to the ability of nestlings to swallow it whole, and, possibly, age of the male parent. We postulate that first-breeding males may exhibit more behavioural flexibility in feeding young than males whose role as a mere provider has been entrenched by the female over several breeding seasons.

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