

WESTERN BIRDS



Volume 53, Number 1, 2022

MERLIN PARENTAL BEHAVIOR AND CHICK DEVELOPMENT AS REVEALED BY WEBCAM

LYNN W. OLIPHANT, Box 80, Site 600, RR6, Saskatoon, Saskatchewan S7K 3J9, Canada

IAN G. WARKENTIN, Environmental Science, Memorial University of Newfoundland, Corner Brook, Newfoundland and Labrador A2H 6P9, Canada; ian.warkentin@grenfell.mun.ca (corresponding author)

KELLY KOZIJ, 803 Coteau Avenue, Weyburn, Saskatchewan S4H 0H1, Canada

ADAM P. SCHMIDT, Box 2714, Melville, Saskatchewan S0A 2P0, Canada

ABSTRACT: Previous knowledge of the Merlin's (*Falco columbarius*) nesting behavior was based on observation from the ground or data recorded during nest checks. Similarly, descriptions of chicks' behavioral development were restricted to studies of captive birds. We used a webcam to observe adult Prairie Merlins (*F. c. richardsonii*) and their four young on an artificial nest platform located in Weyburn, Saskatchewan, from 25 April to 22 July 2020. Our observations extended from prior to egg-laying until 12 days after fledging, being most intensive after hatching. Activities revealed by the webcam largely confirmed previous ground-based observations and studies involving either nest visits or captive rearing. Eggs were laid at roughly 2-day intervals followed by a 30-day incubation period and a 31-day nestling period. The female dominated activity at the nest until the chicks achieved homeothermy (7–10 days after hatching); the male was seldom seen except when delivering prey to the female. The female stopped brooding chicks during the night after day 14 and during daylight on day 16. The male began bringing food directly to the chicks starting 17 days after hatching. The chicks' development matched published reports with constant competition for food among chicks but also apparent efforts by the adult female to ensure that each chick received sufficient food. The webcam enabled us to gather more detailed information about the Merlin's behavior at the nest than previously possible and provided an opportunity for citizen science involving a common but little studied falcon.

The nature and quality of parental care provided for eggs and nestlings affects birds' success in breeding (Lack 1968, Newton 1979). This care is expressed through attendance at the nest to incubate the eggs, protection of eggs and chicks from the elements and potential predators, and providing food for the chicks' growth and development. Technological advances in cameras, power sources, and recording/broadcasting devices have greatly enhanced the opportunities for generating detailed, high-quality data linked to

parental care while reducing disturbance below the level possible with direct observation of raptors from blinds (Reif and Tornberg 2006). This improved capacity reflects progress from the initial time-lapse camera work of Temple (1972) to the highly effective and more affordable digital video surveillance that is becoming commonplace (e.g., Kross et al. 2012, Sonerud et al. 2014, Miller et al. 2020).

Studies of diverse raptor species over the past three decades using these technological approaches have assessed variation in nesting behavior and provided insight into raptors' capacity for adaptation to, or mitigation of, varying environmental conditions (Palmer et al. 2001, Watts 2014, Katzenberger et al. 2015). Outcomes have ranged from baseline descriptions of nesting behavior, as for the Mexican Spotted Owl (*Strix occidentalis lucida*; Delaney et al. 1999), Eurasian Kestrel (*Falco tinnunculus*; Steen et al. 2012), and Northern Saw-whet Owl (*Aegolius acadicus*; McCullough and Conway 2017), to detailed assessments of intersexual differences in nesting behavior of adults and the effect of nest-site quality on parental care, as for the Ferruginous Hawk (*Buteo regalis*; Keeley and Bechard 2017) and Gyrfalcon (*F. rusticolus*; Henderson et al. 2021).

Despite an extensive list of species examined with this technology, we are unaware of any critical examination of nesting Merlins (*F. columbarius*) by means of digital video camera monitoring. Consequently, knowledge of the Merlin's nesting behavior is limited to observations from the ground and data recorded during intermittent nest checks (see overview in Warkentin et al. 2005). Likewise, descriptions of chicks' behavioral development are restricted to studies of birds in captivity (Oliphant and Tessaro 1985, Ruttledge 1985). For tree-nesting species, ground-based observations typically lack fine details on the actual behavior of both parents and nestlings or the interactions among individuals, whereas studies of captives produce results that may reflect captivity rather than natural occurrences. Because of their intermittent nature and intrusiveness, behavioral observations from nest checks are limited, and the data are restricted largely to morphometrics, and to some extent the timing of development. Here we provide data on the behavior of adults and nestlings and the timeline of development in a single wild Merlin nest viewed via webcam from egg-laying through fledging.

METHODS

We monitored a Prairie Merlin (*F. c. richardsonii*) nest located in a White Spruce (*Picea glauca*) tree of a residential neighbourhood of Weyburn, Saskatchewan, Canada (49° 39' 48" N, 103° 51' 12" W), a city of about 11,000 people located along the Souris River in the moist mixed grassland ecoregion (Shorthouse 2010) of southeastern Saskatchewan. Merlins, along with other species of raptors, have nested in Weyburn for several decades (Kozij 2003). The focal tree for this study was the site of an American Crow (*Corvus brachyrhynchos*) nest built in 1999 that provided the initial platform subsequently occupied by Merlins in 2000. Several years later about 3 m was trimmed off the top of the tree, leaving it 13 m tall and creating a basket of branches within which Swainson's Hawks (*B. swainsoni*) nested in 2014; this nest was used by Merlins in 2015. An artificial nesting platform located 13

m up the now 18-m-tall tree replaced the unused and disintegrating hawk nest in 2016. Constructed of 2.5-cm wire mesh, this platform, diameter 60 cm, was covered with common flax (*Linum usitatissimum*) straw attached with cable ties and rimmed with flax bundles 10 cm thick and also attached to the base with cable ties to create a nest bowl. This nest was not occupied until 2019 when it was used by Merlins, and then again during 2020 when we made the observations we report here.

We installed continuous recording equipment to view the nest platform in 2016. The equipment included a home security camera (Swann DVR4-4600, Port Melbourne, Australia) positioned 60 cm from the center of the nest, facing to the east-southeast and angled downward 45° so that the field of view extended from the near edge of the nest but could still capture the full image of an adult perched on the far edge. A cable from the camera ran down the tree and into the adjacent house to a desktop computer. Beginning 25 April 2020, video was live-streamed to the Internet through Vimeo Livestream (Vimeo LLC, New York) so we and the general public could view real-time images, as well as review the most recent four hours from available recordings within the Vimeo Livestream platform; full recording of the entire study period was not an available option because of the platform's storage constraints and the limitations of our own computing capacity. The camera system used infrared illumination for night vision and automatically switched between daylight/color and infrared/black and white video as appropriate. The rate of video recording was set to 10 frames per second with resolution set to 1080P (progressive scan) and a maximum bit rate of 5120 kilobytes per second. The video had the capacity to be reviewed frame by frame.

We initiated observations on 25 April 2020 with periodic checking of the video feed (typically 4–5 times a day at early morning, midday, late afternoon and early evening) to assess activity in the nest during courtship, egg-laying, and incubation. Intensive observation started at hatching (9 June 2020), through our watching the video live and scanning the previous 4 hours of recorded material for the initial observations of each morning to examine nighttime activities (with the exceptions noted below when overnight observations were recorded explicitly). Observation from hatching onward was largely continuous each day from well before sunrise to about an hour after sunset (generally about 02:00 to 22:00 CST) and continued through 22 July 2020, at which point there was little activity at the nest. Additional observations were contributed by the public via a chat function of the Internet broadcast. We verified all public observations by re-examining relevant video sequences, when possible, for any activity missed during our own live observations. Additionally, we collected just over 600 video clips and screen shots of activities throughout the cycle to review and confirm observations drawn from daily notes.

We categorized the breeding cycle into three periods; courtship, during which a male establishes a territory and endeavors to attract a female to become resident on its territory through behavioral displays and provisioning of food; egg laying/incubation; and hatching/nestling, ending with fledging from the nest. We further split the nestling period into two segments based on the chicks' level of dependence on the adults for active direct care. When discussing the adults' roles and chicks' development we further subdivided

the nestling period to reflect the chicks' developmental stages as defined by Oliphant and Tessaro (1985) and detailed below. We established a time budget for the adult birds at the nest during the nestling period on the basis of four categories: brooding (including any direct physical contact with the young), feeding of young (direct bill-to-bill transfer of food from adult to chick), absence from nest (adult not visible in the video feed), and other (adult at the nest but not brooding or feeding). We readily distinguished between the breeding female and male by their differences in size and plumage; the male at this nest was at least 2 years old on the basis of its distinctive blue dorsal plumage (Warkentin et al. 2005). We attempted to identify the prey that were delivered to the nest within the view of the webcam, but the vast majority had already been plucked of identifying plumage (only avian prey were delivered to the nest) and so we could only estimate body size, except for six occasions when we determined the species as noted in the Results. We noted and quantified all prey deliveries (arrival at the nest of an adult bird carrying a carcass; note that parent responsible for the prey capture was not attributable from our data) and feedings at the nest (either beak-to-beak transfer of food torn from a carcass by the adult and given to a chick in one bout of feeding, or the transfer of a carcass from an adult to one of the chicks in the nest). As the chicks could not be individually identified, when reporting the timing of events we consider the chicks' average day of hatching (10 June 2020) as the hatch date (D0) for all four chicks. Phases of nestling development are based on the description of hand-raised Merlin chicks developed by Oliphant and Tessaro (1985) using morphological and behavioral criteria, with minor modifications reflecting differences for the nest monitored. All time references are Central Standard Time. Because sample sizes for most values presented are less than ten and thus too small to justify reporting error levels for these statistics, for consistency throughout we provide average measures along with the respective range of values.

RESULTS

The female we monitored laid five eggs from which four chicks hatched and eventually fledged. The unhatched egg remained in the nest until after the chicks fledged at which point we retrieved it: the shell had a hole and the egg's contents had largely dried out. The female was the primary attendant at the nest (Figure 1).

Courtship Period

We first detected adult Merlins at the nest site on 31 March. Nest displays between the male and female (as described by Feldsine and Oliphant 1985; see Figure 2) on the platform were observed only four times (25 April, 27 April, 1 May, 2 May). On 25 April, one female was seen on the nest for about 15 seconds, followed by a second female entering the nest quickly and aggressively. The first female reacted to the incoming female by rolling onto her back with talons extended to meet the attack. They grappled within view of the camera for about 5 seconds before rolling off the nest platform and out of view. During the courtship period, the male was seen to deliver prey to the empty nest once each on 26 April, 28 April (a male Yellow-rumped Warbler,

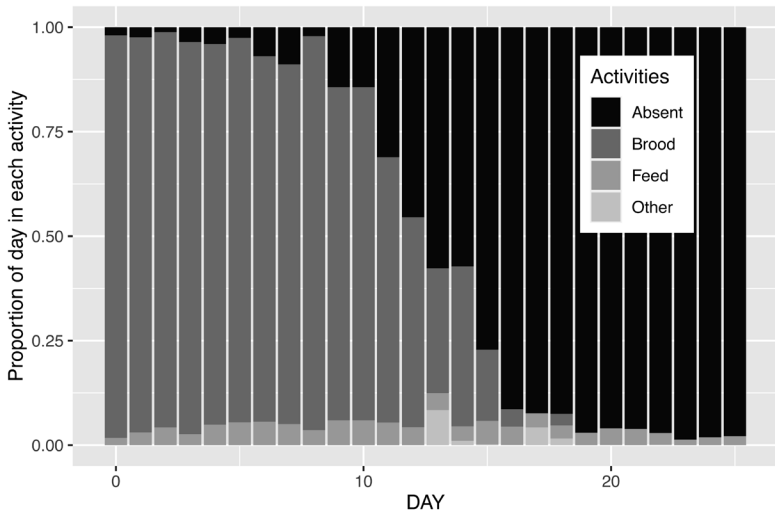


FIGURE 1. Proportion of 24-hour period spent in four activity types by a nesting adult female Merlin monitored for 25 days after the chicks hatched.

Setophaga coronata), and 30 April, twice on 1 May, and once again on 2 May. We never observed copulation or prolonged mutual displays at the nest. The female was seen lying in the nest and/or creating a scrape in the nest material by pushing down with her breast on 28 April.

Egg-Laying/Incubation Period

The eggs were laid at roughly 48-hour intervals, the first on 2 May (exact time unknown). The second egg was laid on 4 May between 18:46 and 19:15,



FIGURE 2. Nest display by female and male Merlin during courtship period.

the third egg 6 May at 17:23, the fourth on 8 May before 19:42, and the fifth on 10 May between 12:43 and 19:11. The female began lying on the nest starting 6 May (egg 3), but this activity was not continuous; the transition to steady incubation was unclear because our observations were not continuous at this point. We observed the male incubating only once, sitting on the first egg laid for 1 min following delivery of prey to the female on the nest on 3 May. We detected the male delivering prey to the female at the nest during incubation only four times (4 May, 30 May, 1 June, and 6 June).

Hatching/Nestling Period (D0–D25)

Four chicks hatched within an interval of 36–38 hr. The first chick hatched on 9 June (by 18:00), the second (02:56–04:30) and third (14:57–16:20) on 10 June (D0), and the fourth on 11 June (06:23–08:27). The female kept newly hatched chicks covered until they were completely dry. The first indication of hatching was the appearance of an eggshell in front of the female. We observed the female nibbling on eggshells several times, although it was unclear whether she was actually consuming fragments. But she was not observed carrying eggshells from the nest, so it appeared that the shells were either eaten or reduced to small fragments rather than carried away.

Female brooding. The female brooded the young and unhatched egg almost continuously during the day for the first nine days (D0–D8) and continuously overnight (Figure 1). For the latter, we determined the female's behavior every 1–2 min for an hour during the night of D2/morning of D3; she was observed with closed eyes and her head laid out on the nest 18 times and with eyes open, head up, and alert 21 times. The female did not leave the nest for periods exceeding 5 min for the first three days. About 20 min before sunrise, the female typically left the nest for less than a minute, returned without prey, and resumed brooding the young. During daylight hours from hatching to D8 the female averaged 14.4 absences per day (range 6–31) that lasted an average of only 4.0 min each (range <1–29 min). For 50 of 108 absences during this period, the female returned after 2–3 min with prey to feed the chicks. The female dozed or slept for periods lasting 5–10 min throughout the day while brooding although would often become alert and leave the nest abruptly, presumably in response to the male vocalizing as he brought in prey or in reaction to some disturbance near the nest but outside the view of the webcam. Her sleep pattern did not change significantly during the night. She frequently repositioned and shuffled the young, preened her feathers, and picked at the nest material both night and day.

Daytime brooding decreased steadily from D9 to D16 (Figure 1). The maximum length of intervals the female spent away from the nest increased during this period from 41 min on D10 to 340 min by D16 (total of eight daytime absences averaging 178 min). There was repeated reshuffling of position by the female who often appeared to be “bounced” by the chicks under her as they became larger and more active. The female continued to incubate the unhatched egg while brooding the chicks during this period, actively pulling it under her. When absent from the nest itself from D9 to D16, she frequently remained close, hopping to a perch just above the nest where she was mostly out of view of the camera except for an occasional glimpse of the end of her tail. After D14, nighttime brooding ceased entirely, whereas

previously nighttime brooding was continuous. By D16 all daytime brooding ceased except for a 40-min period on the morning of D18 after an overnight rain had soaked the chicks. Otherwise, from D16 to the end of the surveillance (D42), the female was continuously absent from the nest except when returning to feed the young or simply transfer prey to a chick.

Female feeding young. Chicks were fed as soon as 2 hours after hatching. There were four feedings on D0, four on D1, five on D2, three on D3, and five on D4 (Figure 3). These feedings were prolonged beak-to-beak transfers of food, typically taking 10–12 min. The female fed the young as long as they begged, although on D1 each chick took no more than 10 “bites” of food at one feeding. The chicks’ food intake and corresponding prey deliveries increased rapidly, and on D5 a count at one feeding yielded an average of 32 “bites” taken by each nestling. Sparrow-sized birds were the primary prey; most were likely House Sparrows (*Passer domesticus*), on the basis of research from other urban settings in the region (Warkentin et al. 2005). Along with the prey specifically identified above and below, we noted three House Sparrows and one Vesper Sparrow (*Poecetes gramineus*) among the carcasses brought to the nest. The hindquarters were left over after feedings finished in the first two days after hatching, and these were taken away by the female. After D2, any food not eaten by the young was consumed by the female at the nest.

The female was the sole adult responsible for the direct feeding of nestlings (either beak-to-beak or provisioning of whole carcasses) until D17, when the male began to bring prey to the nest (Figure 3). The number of daily feedings for D0 to D4 (during the newly hatched to early small downy stages, as defined below by level of development) was 4.2 deliveries per day (range 3–5)

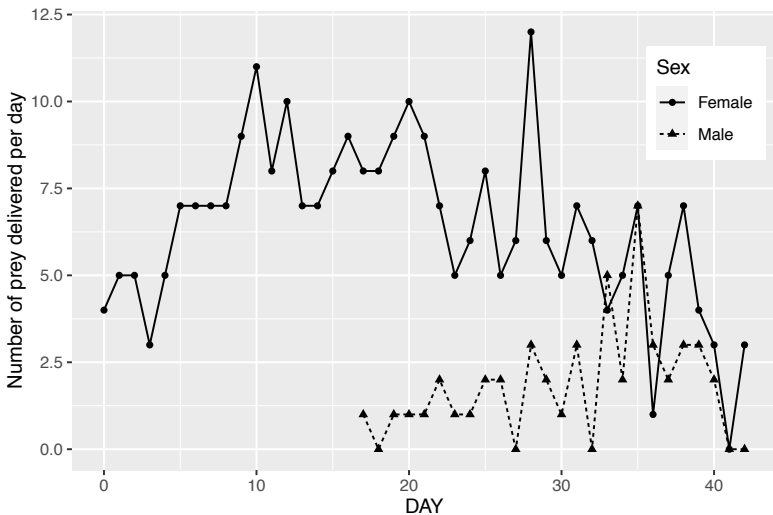


FIGURE 3. Number of prey delivered to a Merlin nest per day, as detected via webcam, by the adult female (circles with solid line) and male (triangles with dashed line) from hatching to day 42.

and increased to 7.7 deliveries per day (range 7–11) for the period from D5 to D25 (from the small downy through feathered nestling stages as defined below), finally reaching 8.4 (range 4–15) deliveries per day from D26 to D38 (the branching/fledgling period). The first feeding usually occurred within one hour of sunrise except on D8, when the first prey item was not brought in until 08:25 after a night of rain. Often whole wings and legs with bone and feathers were given to the chicks. Early in the nestling period the female took large pieces back and ate them herself if the chicks were slow to swallow them. The female typically fed one chick to satiation if it continued to beg strongly, before shifting to feed another chick. During feeding, the female often checked under and around chicks for dropped food.

Male's activity at the nest. The male was present at the nest for only very short periods throughout the entire observation period. There were only two days when the male attempted to brood the nestlings. On D0 the male brooded newly hatched chicks and unhatched eggs three times during the day for periods of up to 3 min. The female was absent all of these times with the male arriving within a minute of the female leaving, but departing abruptly when the female returned with food that presumably had been transferred to the female by the male out of camera range. The male appeared at the nest five other times between D1 and D14, usually after a presumed prey transfer to the female outside the camera's field of view. The male often cleaned his feet at the nest's edge (suggesting a kill and prey transfer) but brooded the nestlings and unhatched egg only one additional time (D8) for 3 min, actively pulling the egg under his body in a fashion similar to that of the female. During this instance of brooding, the male appeared clumsy, spreading his wings and almost falling over, then leaving abruptly when the female returned with prey, almost colliding with her.

When the male appeared at the nest without prey and the female was present, the female confronted the male with a lowered head and spread tail. The male then left immediately. This occurred mostly early in the nestling period. If the male was carrying prey, it was immediately and aggressively taken by the female, which then left the nest for a few minutes, presumably to further prepare the carcass for feeding to the nestlings. The male then often stayed at the nest for a minute or less but left before or as the female returned with the prepared prey.

There was no attempt by the male to feed the young until D17, when he arrived with a whole Horned Lark (*Eremophila alpestris*) while the female was absent. He perched on the nest edge and offered the whole carcass to the chicks, which made no attempt to take it. The male next fed bits from the lark's head to two chicks and then moved into the nest itself, whereupon all the chicks moved away from the male. The male left with the lark carcass but returned after 22 min to feed two chicks for 8 min before leaving once again as the female arrived with prey. The male spent 16 min feeding the chicks again on D19 and 14 min on D20. Starting on D21, prey deliveries by the male were rapidly taken by one of the chicks or by the adult female (if present). Subsequently, the male's time at the nest was limited to only a few seconds per visit.

Brancher/Fledging Period (D26–D42)

During this interval the adults were present at the nest for prey deliveries and feedings only. Direct beak-to-beak feeding of the young by the female decreased within the first few days of this period and ceased by D28, after which the chicks became more aggressive and grabbed prey immediately when delivered by an adult. Thereafter both adults left within seconds of presenting a carcass at the nest. Prey deliveries increased to 8.4 per day (range 4–15) for the period from D26 to D38, then dropped to 3.8 per day (range 0–7) from D39 to D42 as interactions with young at the nest decreased. The number of prey deliveries by the male increased during this period, reaching a high of seven on D35, while those of the female decreased over the same period (Figure 3). We believe that prey deliveries began to be missed during this period as chicks increasingly moved out of the nest and onto adjacent branches, beginning on D26, where they were out of view of the camera. Although we could not quantify deliveries occurring out of view, we presume that the total number of prey deliveries did not actually decrease substantially from D39 to D42.

Behavior and Development of Nestlings

Using criteria based on those defined for the Merlin by Oliphant and Tesaro (1985), we described the nestlings' behavior and development across five stages of the nestling period. This period covers early stages when nestlings are heavily dependent upon the adults for food and protection from the elements (newly hatched and small downy) through greater independence from adults for maintaining body temperature (large downy and feathered nestlings), and finishing with the stage when the chicks require only food from the adults (branching). See representative images in Figure 4.

Newly hatched (D0–D3). Within hours of hatching, young Merlins were able to hold their heads up and beg during feedings; recall that the date D0



FIGURE 4. Development of Merlin chicks monitored by webcam. A, age 5 days; B, age 18 days; C, age 21 days; D, age 26 days.

is standardized for the brood, so this observation reflects individual chicks regardless of which day they actually hatched. Their eyes were completely closed through D2 and they appeared to react mainly to the “tic” calls the female made while feeding. The ability to move increased rapidly and chicks occasionally moved themselves out from under the brooding female by the end of this stage. When left alone, even for short periods, the chicks huddled together, facing each other.

Small downy (D4–D10). The chicks’ eyes were opened completely by D4, and by D5/D6 the chicks appeared to orient themselves to the female by sight when feeding. The chicks actively backed away from the main scrape area to defecate, balancing by spreading their unfeathered wings. They remained awake during long periods of both day and night and began to escape regularly from under the brooding female. Locomotion on their tarsi developed during this period, and on D6 one chick tried to climb up the nest’s edge. By the end of this period, chicks were fairly stable, walking on their tarsi and using their wings to balance. One chick was up on its toes on D10 but very unstable.

By D6 chicks reached for food offered by the female and by D7 rocked up on their tarsi while feeding. The latter behavior was used frequently to reach over other chicks and involved a combination of rising up on tarsi and using other chicks for support. By D8 chicks grabbed food from the beaks of others and pecked at each other during feedings. By D9 chicks pushed and jostled each other for a favorable position during feedings and sometimes grabbed at the carcass being held by the female. Preening behavior was noted for the first time on D6 and became common thereafter. The first wing stretch was noted on D9, and sheaths of emerging primaries supplied with blood could be clearly seen at this time.

Large downy (D11–D18). The chicks rapidly increased in size, as well as gaining balance and coordination during this stage. Flight feathers broke through their sheaths first in the wings and then tail. By D17 the tail and wing feathers extended out far enough to be seen even when the wings were folded, and by D18 primaries (3–4 cm) and tail feathers (1 cm) extended beyond feather sheaths with about 1 cm exposed. The chicks’ posture and movement changed from shuffling on their tarsi to standing and walking upright on their toes, starting by D14 for periods of less than a minute and then transitioning to most of the time by the end of this period. Chicks began to actively seek shade by D12 and spread out when the sun was bright, but they still huddled together when temperatures were lower. Chicks were able to climb up onto the nest’s edge and had sufficient balance to scratch their face while standing on one leg (on D12), and also to stretch their wings and legs. Wing-flapping became common during this period, and preening increased as the juvenile plumage emerged to replace down. Chicks also began to vocalize during this period.

By D14 feeding became more independent of the female. Chicks actively grabbed larger pieces of food with their beaks from the female or from the carcass itself. These pieces were either swallowed whole or held down with their feet and fed from directly. Until at least D17, however, the chicks still relied primarily on the adults to tear pieces from the carcass, although they often moved away from the female to feed themselves when given larger pieces. Casting of pellets was generally missed because of the brevity of this

activity; the only time a chick was actually observed casting a pellet was just before it fed on D17. We noted chicks starting to sleep with their head tucked into their scapular feathers by the end of D13, and the chicks were not attended overnight for the first time on D15.

Feathered nestling (D19–D25). The chicks approached full body size during this period. The flight feathers continued to grow and the body down was rapidly replaced by contour feathers; these changes were accompanied by extensive preening. During this period chicks more often took larger pieces of food from the female, fed themselves, and attempted to eat directly from carcasses held by parents. Whole prey items were forcibly taken from the male, and chicks unsuccessfully attempted to take carcasses from the female. Chicks showed increasing interest in events outside the nest and bobbed their heads as they watched their parents depart from the nest or recognized the approach of a parent. Vocalizing and wing-flapping became more common during this period. On D19 one chick jumped down from the nest edge into the nest cup while flapping its wings, and on D24 one chick moved through a combination of jumping and flying across the nest while flapping its wings, followed on D25 by similar behavior of all chicks.

Branching/fledgling (D26–D32). The chicks reached adult size during this stage, except for completion of flight-feather growth. On D26 they began to leave the nest platform and move out of camera view into the surrounding branches. By this time only wisps of down remained on the head and back of all but the least developed chick. Nestlings first departed the nest by jumping or climbing onto the surrounding branches and moved in and out of nest repeatedly, quickly reaching a point where the nest was often empty during the day although they continued to return to eat, sleep, and to spend the night. On D31 Kozij watched from the ground while two chicks made a flight of ~70 m from the nest tree to an adjacent tree; this timing for unequivocal departure from the nest tree matches the various estimates of fledging in the Merlin (28–32 days; Newton et al. 1978, Becker and Sieg 1985, Oliphant and Tessaro 1985). During the initial days of this period the least developed chick frequently fed first when the female arrived, as it appeared more likely to remain on or nearer the nest platform. Beginning on D26, chicks regularly stole prey from one another, and from the female, engaged in tug-of-wars over prey, and mantled (covered prey with body and spread wings) while eating. By the end of this period, the parents often arrived with prey to an empty nest but were quickly joined by chicks who then fought over the prey item. Two chicks slept away from the nest for the first time on the night of D30, while the two remaining chicks slept in the nest, standing with heads tucked into scapular feathers. All four chicks spent the night away from the nest on D31. We observed five chicks in the nest together for 3 min on D31, the fifth individual presumably being a fledgling from a nearby nest.

Post-fledging (D33–D42). One chick remained in the nest on the night of D32. At 05:00 on D33, the other chicks climbed into the nest from below. Subsequently the nest was empty overnight, but chicks arrived shortly after sunrise on most mornings throughout this period, usually in association with prey deliveries to the nest by adults or chicks arriving with prey items already retrieved from parents. Although the nest was mostly empty during the daytime of this period, through D42 (22 July; Figure 3) the adults con-

tinued delivering prey to the nest, followed quickly by the arrival of one or more chicks. On D33, five chicks were again observed in the nest during the day. On D41, Kozij watched from the ground while three young Merlins flew past the nest tree, showing great control of flight, and later observed seven Merlins chasing each other several hundred meters away from the nest tree.

DISCUSSION

The Merlin's nesting behavior that we observed by webcam, in terms of parental roles, breeding chronology, and chick growth and behavior, broadly matched patterns previously reported on the basis of other approaches. However, by periodic monitoring (as described in the Methods) from nest initiation through incubation and then continuous monitoring from hatching to fledging, our study provides detail far greater than previously possible. Representing only a single nest, our study illustrates a clear division of parental roles that matches the extreme reported for the species: the female responsible for the nest and young, the male providing food (Warkentin et al. 2005). Additionally, our detailed observations facilitate greater understanding of the Merlin's nesting behavior in terms of the level of asynchrony of hatching, how the adult female's allocation of food may help offset competition for food among the young and enhance chicks' survival, a need to revisit the question of when homeothermy becomes established in young Merlins, and the fate of unhatched eggs in the nest.

Our observations of the timing of egg laying, length of incubation period, and extent of asynchrony of hatching largely agree with values reported in the literature. Merlins lay at an interval of 2 days (see reviews by Cramp and Simmons 1980, Palmer 1988), as we observed. Reported values for the onset and duration of incubation vary much more widely. Both Fox (1964) and Rutledge (1985) suggested that full incubation may begin only after the final egg is laid, but observations of captive birds suggest partial incubation (bouts of incubation rather than continuous) before the clutch is complete (Rutledge 1985). Although the female was often on the nest and apparently incubating after the third egg was laid, without temperature monitors in the nest we were unable to ascertain the start of full incubation when heat provided by the female leads to the embryo developing (as defined by Wang and Beissinger 2011). The female's nest attendance suggests incubation phased in gradually, as there was no obvious switch in behavior from limited or no incubation to full incubation that started with either the penultimate or last egg. This gradual increase in incubation activity over time presumably led to the slightly asynchronous hatching over ~36 hours that we observed, rather than a synchronous hatching within 24 hours (terms as defined by Wang and Beissinger 2011). Hatching has been described as synchronous or slightly asynchronous, but there are few precise data for wild Merlins (see overviews by Cramp and Simmons 1980, Palmer 1988). Among raptors more generally, there is an expectation of high intraspecific variability in the onset of incubation and degree of asynchrony of hatching (Bortolotti and Wiebe 1993, Miller et al. 2020). Our observation of Merlin chicks hatching over 3 calendar days (but actually 36–38 hours) matches the patterns in the American Kestrel (*Falco sparverius*; Bortolotti and Wiebe 1993) and also suggests partial incubation

being initiated before the final egg was laid, as documented for the kestrel (Wiebe et al. 1998). The Merlin's incubation period is reported as 28–32 days (Cramp and Simmons 1980, Palmer 1988). Because of our uncertainty around the actual start of incubation we were able only to estimate a 30-day period if incubation began with the laying of the final egg, or 32 days if incubation began with the penultimate egg.

Although observations were intermittent rather than continuous during the incubation period, we detected only a single instance of the male briefly (1 min) incubating the first egg laid. This apparent lack of the male contributing to incubation is in sharp contrast with observations by others. On the basis of a combination of ground-level observations and the flushing of incubating birds at multiple nests per study, male Merlins contribute to incubation (at least during daytime) at levels ranging from 7% to 33% of the time (Newton et al. 1978, Laing 1985, Sodhi et al. 1992, Heavisides et al. 2017). But the male's contribution to incubation could be even higher. Rowan's (1921–1922) observation of a single nest indicated only a slight bias toward the female in terms of time incubating during the day and one instance of the male incubating through an entire night. This range of values may reflect individual behavioral variability among females rather than a need for the female to leave the nest to feed. Even when the female is not incubating for extended periods, data from direct observations suggest that the male still provides most if not all food for the female during incubation (Rowan 1921–1922, Laing 1985, Sodhi et al. 1992) and spends much less time on the nest. Possibly, the pair we observed represents an extreme case of female dominance; the male essentially never incubated and never remained at the nest for more than a few seconds while the female was in attendance. Likewise, when the male arrived with food it was taken quickly by the female. Food transfers seen by ground observation at numerous Merlin nests appeared much more prolonged with less aggression from the female when taking carcasses from the male (Oliphant unpubl. data). We also detected no extensive or frequent “mutual nest displays” as are typical of most large falcons with which we are familiar, such as the Peregrine (*F. peregrinus*; White et al. 2002).

Nest attendance approaching 100% during the first week after hatching is not uncommon among raptors, and is a behavior attributed primarily to the female in most species (Newton 1979). Attendance declines substantially once the nestlings reach thermoregulatory independence (Holthuijzen 1990, Katzenberger et al. 2015, Keeley and Bechard 2017). The species' body size and rate of development modify the chicks' time to homeothermy and the associated drop in the adults' brooding, but brooding varies in response to weather such as rain and abnormally cold or warm temperatures (Watts 2014, Katzenberger et al. 2015). Our observations align with expectations in terms of parental roles during the nestling phase, but the suggestion that Merlins attain homeothermy by D7 (Warkentin et al. 2005) may be too optimistic, given the continued brooding past D7 that we observed. The female remained on the nest for at least 75% of each day through D11, and only thereafter reduced her time at the nest until D17, after which she never brooded the chicks except following rain on D18. The male was observed brooding the chicks for only brief periods on D0 and D8, which concurs with Newton et al. (1986), who found that until D10 male Merlins brood only occasionally.

In terms of food provisioning, our observations are in accord with direct ground observations suggesting that male Merlins provide most of the food during the nestling period, the female's involvement increasing only later (Lawrence 1949) or around fledging (Rowan 1921–1922, Laing 1985, Sodhi et al. 1992; unpubl. data). The increase of male raptors' presence at the nest in the later stages (Warnke et al. 2002, Booms and Fuller 2003, Kross et al. 2012), as well as diminished overall parental presence at the nest, is widespread and attributed to a combination of homeothermy among the chicks, potentially decreased susceptibility to predators, and increased demand for food (Newton 1979). While such factors may help drive these changes, the time the male spent at the nest we observed may have depended more on the simple fact that the female was absent from the vicinity of the nest once she began hunting, leaving opportunity for the male to be more directly involved.

Although we were unable to identify to species all but a few of the prey delivered to the nest, most were headless carcasses of sparrow-sized birds. As a consequence of the adults' selection of such prey (small songbirds constitute the vast majority of the Merlin's diet in this region; Warkentin et al. 2005), the growing chicks' increasing demand for food was met with an increasingly higher average daily rate of prey delivery. Nevertheless, deliveries of prey to the nest seemingly dropped late in the nestling period, presumably a time of greater energetic need for the nearly full-grown chicks. Most likely this reflected the chicks being provisioned away from the view of the webcam rather than an actual decrease. Similarly increased provisioning of nestling raptors is widespread where prey availability is sufficient to meet the chicks' demand, either via increased rates of delivery or the delivery of larger prey (e.g., Watts 2014). At their highest, the rates of prey delivery we observed are slightly lower than Laing's (1985) estimate of 9.6 deliveries per day across the nestling period for Merlin nests in Denali National Park, Alaska. This difference may be attributable to a difference in the availability of larger prey species found around our nest site. Late in the nestling period, the adults delivered several carcasses of birds with long dark tarsi that were probably Common Grackles (*Quiscalus quiscula*), abundant in the area (Kozij unpubl. data) or other species of blackbirds; the male also appeared with one medium-size wader that was probably a yellowlegs (*Tringa* sp.).

The chicks' competition for food became more evident by D9 as they jostled for favorable positions during feeding. Throughout the nestling period, however, when beak-to-beak feeding was common, the female often continued feeding the same chick as long as it begged, paralleling observations of raptors elsewhere (Byholm et al. 2011, but see Fargallo et al 2003). Targeted parental feeding like this may limit competition among siblings through the female's allocation of food resources and enable her to maximize her productivity under circumstances when food is apparently abundant (Szojka et al. 2020).

While our study was based on placing a webcam at a single nest, these observations were useful in confirming many aspects of Merlin behavior during the nestling phase of the annual cycle that had been identified from ground-based and nest-visit studies. Until nearly midway through this nestling phase, the female was dominant in her role of providing care for the young at the nest. The male tended the young for very brief periods when the female was

absent, but otherwise appeared on camera only to deliver food to the nest. The webcam did give us a much more detailed view of the constant competition for food among the chicks but also the apparent efforts of the adult female to ensure that each chick received sufficient food. Given the camera's limited field of view, either additional cameras or ground observers would have greatly aided in documenting the chicks' behavior as they moved away from the nest itself and into the surrounding branches during the later stages of the nestling period. That said, the capacity for citizen science by webcam is enormous and provides a great way to introduce the broader public to the fascination of being able to watch birds up close.

ACKNOWLEDGMENTS

We thank the nest watchers who helped to collect these data by joining us online to do science from our desks during the pandemic, particularly Christy Mann. We thank Joe Eisaguirre, Bryce Robinson, and Dan Ruthrauff for their editorial contributions to an earlier draft.

LITERATURE CITED

- Becker, D. M., and Sieg, C. H. 1985. Breeding chronology and reproductive success of Richardson's Merlins in southeastern Montana. *Raptor Res.* 19:52–55.
- Booms, T. L., and Fuller, M. R. 2003. Gyrfalcon feeding behavior during the nestling period in central west Greenland. *Arctic* 56:341–348; <https://doi.org/10.14430/arctic631>.
- Bortolotti, G. R., and Wiebe, K. L. 1993. Incubation behaviour and hatching patterns in the American Kestrel *Falco sparverius*. *Ornis Scandinavica* 24:41–47; <https://doi.org/10.2307/3676408>.
- Byholm, P., Rousi, H., and Sole, I. 2011. Parental care in nesting hawks: Breeding experience and food availability influence the outcome. *Behav. Ecol.* 22:609–615; doi.org/10.1093/beheco/arr019.
- Cramp, S., and Simmons, K. E. L. 1980. *The Birds of the Western Palearctic*, vol. 2. Oxford Univ. Press, Oxford, England.
- Delaney, D. K., Grubb, T. G., and Beier, P. 1999. Activity patterns of nesting Mexican Spotted Owls. *Condor* 101:42–49; <https://doi.org/10.2307/1370444>.
- Fargallo, J. A., Laaksonen, T., Korpimäki, E., Pöyri, V., Griffith, S. C., and Valkama, J. 2003. Size-mediated dominance and begging behaviour in Eurasian Kestrel broods. *Evol. Ecol. Res.* 5:549–558; <https://doi.org/10.1046/j.1461-0248.2002.00290.x>.
- Feldsine, J. W., and Oliphant, L. W. 1985. Breeding behavior of the Merlin: The courtship period. *Raptor Res.* 19:60–67.
- Fox, G. A. 1964. Notes on the western race of the Pigeon Hawk. *Blue Jay* 22:140–147; <https://doi.org/10.29173/bluejay2600>.
- Heavisides, A., Barker, A., and Poxton, I. 2017. Population and breeding biology of Merlins in the Lammermuir Hills. *Br. Birds* 110:138–154.
- Henderson, M. T., Booms, T. L., Robinson, B. W., Johnson, D. L., and Anderson, D. L. 2021. Direct and indirect effects of nesting site characteristics for a cliff-nesting raptor in western Alaska. *J. Raptor Res.* 55:17–32; <https://doi.org/10.3356/0892-1016-55.1.17>.
- Holthuijzen, A. M. A. 1990. Prey delivery, caching, and retrieval rates in nesting Prairie Falcons. *Condor* 92:475–484; <https://doi.org/10.2307/1368244>.
- Katzenberger, J., Tate, G., Koeslag, A., and Amar, A. 2015. Black Sparrowhawk brooding behaviour in relation to chick age and weather variation in the re-

- cently colonised Cape Peninsula, South Africa. *J. Ornithol.* 156:903–913; doi.org/10.1007/s10336-015-1199-0.
- Keeley, W. H., and Bechard, M. J. 2017. Nesting behavior, provisioning rates, and parental roles of Ferruginous Hawks in New Mexico. *J. Raptor Res.* 51:397–408; doi.org/10.3356/JRR-16-85.1.
- Kozij, K. 2003. Urban-nesting Merlins and Cooper's Hawks in Weyburn, SK. *Blue Jay* 61:33–38; doi.org/10.29173/bluejay5832
- Kross, S. M., Tylianakis, J. M., and Nelson, X. J. 2012. Translocation of threatened New Zealand Falcons to vineyards increases nest attendance, brooding and feeding rates. *PLoS One* 7(6): e38679; doi.org/10.1371/journal.pone.0038679.
- Lack, D. 1968. *Ecological Adaptations for Breeding in Birds*. Methuen, London.
- Laing, K. 1985. Food habits and breeding biology of Merlins in Denali National Park, Alaska. *Raptor Res.* 19:42–51.
- Lawrence, L. de K. 1949. Notes on nesting Pigeon Hawks on Pimisi Bay, Ontario. *Wilson Bull.* 61:15–25.
- McCullough, J. M., and Conway, C. J. 2017. Breeding behavior of Northern Saw-whet Owls in Oregon. *Northwest Sci.* 91: 222–227; doi.org/10.3955/046.091.0211.
- Miller S. J., Dykstra, C. R., Hays, J. L., and Simon, M. M. 2020. Partial incubation and hatching asynchrony in the Red-shouldered Hawk (*Buteo lineatus*). *J. Raptor Res.* 54:364–375; doi.org/10.3356/0892-1016-54.4.364.
- Newton, I. 1979. *Population Ecology of Raptors*. T. & A. D. Poyser, Berkhamsted, England.
- Newton, I., Meek, E. R., and Little, B. 1978. Breeding ecology of the Merlin in Northumberland. *Br. Birds* 71:376–398.
- Newton, I., Meek, E. R., and Little, B. 1986. Population and breeding of Northumbrian Merlins. *Br. Birds* 79:155–170.
- Oliphant, L. W., and Tessaro, S. V. 1985. Growth rates and food consumption of hand-raised Merlins. *Raptor Res.* 19:79–84.
- Palmer, A. G., Nordmeyer, D. L., and Roby, D. D. 2001. Factors influencing nest attendance and time-activity budgets of Peregrine Falcons in interior Alaska. *Arctic* 54:105–114; https://doi.org/10.14430/arctic769.
- Palmer, R. S. (ed). 1988. *Handbook of North American Birds*, vol. 5. Yale Univ. Press, New Haven, CT.
- Reif, V., and Tornberg, R. 2006. Using time-lapse digital video recording for a nesting study of birds of prey. *Eur. J. Wildlife Res.* 52:251–258; doi.org/10.1007/s10344-006-0039-1.
- Rowan, W. 1921–1922. Observations on the breeding habits of the Merlin. *Br. Birds* 15:121–129, 194–202, 222–231, 246–253.
- Rutledge, W. 1985. Captive breeding of the European Merlin (*Falco columbarius aesalon*). *Raptor Res.* 19:68–78.
- Shorthouse, J. D. 2010. Ecoregions of Canada's prairie grasslands, in *Arthropods of Canadian Grasslands: Ecology and Interactions in Grassland Habitats* (J. D. Shorthouse and K. D. Floate, eds), pp. 53–81. *Biol. Surv. Can.*, Ottawa; doi.org/10.3752/9780968932148.ch3.
- Sodhi, N. S., James, P. C., Warkentin, I. G., and Oliphant, L. W. 1992. Breeding ecology of urban Merlins (*Falco columbarius*). *Can. J. Zool.* 70:1477–1483; https://doi.org/10.1139/z92-204.
- Sonerud, G. A., Steen, R., Selås, V., Aanonsen, O. M., Aasen, G.-H., Fagerland, K. L., Fosså, A., Kristiansen, L., Løw, L. M., Rønning, M. E., Skouen, S. K., Asakskogen, E., Johansen, H. M., Johnsen, J. T., Karlsen, L. I., Nyhus, G. C., Røed, L. T., Skar, K., Sveen, B.-A. Tveiten, R., and Slagsvold, T. 2014. Evolution of parental roles in provisioning birds: Diet determines role asymmetry in raptors. *Behav. Ecol.* 25:762–772; doi.org/10.1093/beheco/aru053.
- Steen, R., Sonerud, G. A., and Slagsvold, T. 2012. Parents adjust feeding effort in

- relation to nestling age in the Eurasian Kestrel (*Falco tinnunculus*). *J. Ornithol.* 153:1087–1099; doi.org/10.1007/s10336-012-0838-y.
- Szojka, M. C., Bayne, E. M., Wellicome, T. I., Nordell, C. J., and Ng, J. W. 2020. The role of sibling competition and parental provisioning on food distribution among Ferruginous Hawk nestlings. *J. Raptor Res.* 54:376–387; doi.org/10.3356/0892-1016-54.4.376.
- Temple, S. A. 1972. A portable time-lapse camera for recording wildlife activity. *J. Wildlife Mgmt.* 36:944–947; https://doi.org/10.2307/3799452.
- Wang, J. M., and Beissinger, S. R. 2011. Partial incubation in birds: Its occurrence, function, and quantification. *Auk* 128:454–466; doi.org/10.1525/auk.2011.10208.
- Warkentin, I. G., Sodhi, N. S., Espie, R. H. M., Poole, A. F., Oliphant, L. W., and James, P. C. 2005. Merlin (*Falco columbarius*), version 2.0, in *The Birds of North America* (A. Poole, ed.), no. 44. Cornell Lab Ornithol., Ithaca, NY; doi.org/10.2173/bow.merlin.01.
- Warnke, D. K., Andersen, D. E., Dykstra, C. R., Meyer, M. W., and Karasov, W. H. 2002. Provisioning rates and time budgets of adult and nestling Bald Eagles at inland Wisconsin nests. *J. Raptor Res.* 36:121–127.
- Watts, S. H. 2014. A study of nesting Sparrowhawks *Accipiter nisus* using video analysis. *Bird Study* 61:428–437; doi.org/10.1080/00063657.2014.940838.
- White, C. M., Clum, N. J., Cade, T. J., and Hunt, W. G. 2002. Peregrine Falcon (*Falco peregrinus*), in *The Birds of North America* (A. Poole and F. Gill, eds.), no. 660. Birds N. Am., Inc., Philadelphia; https://doi.org/10.2173/bow.perfal.01.
- Wiebe, K. L., Wiehn, J., and Korpimäki, E. 1998. The onset of incubation in birds: Can females control hatching patterns? *Anim. Behav.* 55:1043–1052; https://doi.org/10.1006/anbe.1997.0660.

Accepted 6 October 2021

Associate editor: Daniel R. Ruthrauff