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Polygyny in Canada Geese: An Unusual Example of Nest Sharing

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ABSTRACT.—We observed an apparent incident of polygynous behavior in Giant Canada Geese (*Branta canadensis maxima*). Two females were paired with the same male and concurrently incubated side by side within the same nest tub. Reciprocal changes in the number of eggs within each bowl during incubation indicated that eggs were shifted between nest bowls in both years. This behavior was observed at the same location in two successive years. Goslings hatched from both nests each year. Polygynous behavior in typically monogamous Canada Geese has rarely been observed, and nest sharing has not been previously documented. Received 19 June 2000, accepted 2 February 2001.

All 11 subspecies of Canada Geese (*Branta canadensis*) are believed to be monogamous (Bellrose 1980). Twenty-one incidences of polygyny have been reported, including three cases involving pinioned captive birds (Kosack 1950) and 18 cases in a sedentary flock of Giant Canada Geese (*Branta canadensis maxima*; Brakhage 1965). All previous cases involved multiple females that paired with a single male, but nested separately. Here we report observations of nest sharing, an unusual and previously unreported variation of the nesting behavior of geese involved in a polygynous relationship.

In a study area in central Missouri, we observed two instances in which tub-nesting female Giant Canada Geese shared the same mate and tub. These observations were made at the same nest tub during successive breeding seasons in 1995 and 1996. Although po-

lygyny was not confirmed by observation of copulation, defense of both females by the male while they were away from the nest, mutual participation in triumph ceremonies by all three individuals, and absence of other unpaired individuals at the site strongly suggest polygyny. The triumph ceremony is a behavioral display of the *Anserinae* that is performed by mated pairs or all family members after spatial or temporal separation, prior to vigorous aggressive encounters, and after such encounters by the victors (Baldassarre and Bolen 1994).

We observed, as did Brakhage (1965), a hierarchy between females. The dominant female often pecked the subordinate female. This behavior left the second female's mantle and back devoid of feathers, providing a means of distinguishing the two individuals.

In 1995, the nest tub (a No. 3 galvanized wash tub, 62 cm × 28 cm × 54 cm) contained two distinct nest bowls approximately 1 cm apart and a total of 16 eggs. Both females carried out incubation side by side on the nest until their clutches hatched. Eight goslings were observed leaving the nest tub. Two pipped eggs containing dead goslings and two infertile eggs remained. Four eggs were broken during incubation.

In 1996, the nest tub again contained two distinct nest bowls approximately 1 cm apart and a total of 14 eggs. Both females carried out incubation side by side on the nest until their clutches hatched. Following hatch, the tub contained six membranes, two infertile eggs and six eggs that apparently had been broken during incubation.

Reciprocal changes in the number of eggs within each bowl during incubation indicated that eggs were shifted between nest bowls in both years. Although the motivation for egg shifting is unknown, the functional result was a joint nest in which incubation of eggs produced by both females was shared. Distribution of hatched eggs between the two nests

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could not be determined in either year as nest bowls were indistinguishable after hatching.

We observed the trio tending the brood on the nest pond for two days following hatching in 1995, but the adults and goslings were not observed following hatching in 1996. Because the birds were unmarked and nearby brood rearing areas contained numerous family groups and creches, we were unable to definitively relocate the trio after they left the nest pond in either year. Furthermore, due to the absence of leg or neck bands on this group, age, relation, and previous nesting histories are unknown.

Nest sharing has been defined as two females sharing a nest, incubating their eggs together, and (perhaps) sharing care of the young (Terres 1982, Fournier and Hines 1996). This is a relatively uncommon phenomenon and is particularly unusual among waterfowl (Terres 1982). Females occupied separate nests within the same nesting territory in all previous studies reporting polygynous mating. To our knowledge, two female geese nesting and incubating within the same nest tub concurrently has not been documented previously. Although this behavior is rare, it is notable because it demonstrates the degree of flexibility that can occur in the social system of a highly territorial species.

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Postnatal Development of the Violet Sabrewing in Costa Rica

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ABSTRACT.—I observed the incubation and nestling periods of five nests of the Violet Sabrewing (*Campylopterus hemileucurus*) in Costa Rica. Each nest was built above running water. Mean incubation period was 20 d and only the female incubated. Mean nestling period lasted 23 d. Nestlings reached and sur-

passed adult mass before fledging (132% of adult size in males and 130% in females), although wing, tail, and culmen length did not reach adult size until after fledging. Because the Violet Sabrewing is highly sexually dimorphic in size and plumage color, I compared the postnatal development of five females and two males. Males were heavier than females and grew more slowly, consistent with generally slower growth rates in larger birds. The $T_{(10-90)}$ period was 15.3 d for the fastest growing male and 13.8 d for the fastest growing female. *Received 26 June 2000, accepted 7 February 2001.*

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TABLE 1. Measurements of adult Violet Sabrewing (*Campylopterus hemileucurus*) specimens collected in Costa Rica and deposited in the Western Foundation Museum of Vertebrate Zoology. Values are means \pm SD. For all *t*-tests *df* = 16 and *P* < 0.001.

Variable	Males (<i>n</i> = 8)	Females (<i>n</i> = 10)	<i>t</i>
Mass (g)	11.4 \pm 0.85	9.2 \pm 0.85	5.99
Flattened wing length (mm)	82.6 \pm 1.09	76.1 \pm 1.00	13.09
Tail length (mm)	58.0 \pm 1.51	52.4 \pm 2.22	6.07
Exposed culmen length (mm)	29.2 \pm 1.06	32.2 \pm 1.60	4.57

The Violet Sabrewing (*Campylopterus hemileucurus*) is one of the largest hummingbirds inhabiting the Middle American region. It is a resident species in the highlands from southern Veracruz (southeast Mexico) south to Herrera and Los Santos (western Panama; American Ornithologists' Union 1998). Most hummingbirds are sexually dichromatic and the large majority are sexually dimorphic in size (del Hoyo et al. 1999). The Violet Sabrewing is highly sexually dimorphic both in size and plumage color. The male has a dark violet head, underparts, and upper back, while the female has green upperparts, gray underparts, and a violet gorget. In both sexes the distal half of the three outer rectrices is white (Stiles and Skutch 1989).

The only previous paper related to the breeding biology of this species (Skutch 1967) was based primarily on observations of behavior at one nest. There is no information available on the postnatal development in more than 90% of the known species of hummingbirds (summary in Starck and Ricklefs 1998).

In other groups of birds in which many species are sexually dimorphic in size (e.g., Falconiformes and Procellariiformes) there is also a corresponding difference in growth rates, with the larger gender growing slower (Newton 1979, Warham 1990), consistent with the prediction that larger species grow more slowly (Case 1978; Ricklefs 1979, 1983). The goal of this study was to observe the postnatal development of the Violet Sabrewing and to determine if the growth rates differed between the sexes in this morphometrically dimorphic species of hummingbird.

METHODS

Data were gathered in Costa Rica in the Rio Tiribí area, prov. San José, at 9° 57' N. The site was described in detail by Marín and Stiles (1992). We gath-

ered data from May through August 1996 and 1997. Nests were observed during incubation and nesting periods at 1- to 5-d intervals. Body mass was determined with a spring balance to 0.1 g. I measured wing length (flattened) and tail length using a stopped wing ruler to 0.5 mm. Exposed culmen length was measured to the nearest 0.1 mm with a dial caliper, following techniques described in Baldwin et al. (1931). When two nestlings were present at one nest one of them was banded with a thread on one leg for individual recognition. Because of daily changes in growth, nestlings were measured only in the morning between 08:00 and 11:00.

The nomenclature of egg shape follows Palmer (1962). Egg measurements were from museum specimens (*n* = 14) deposited at the Western Foundation of Vertebrate Zoology (WFVZ) and our study area (*n* = 8). Eggs were measured to the nearest 0.1 mm with a digital caliper. Mean egg mass was calculated from the museum specimens, using the formula ($M = k \times LB^2$; Hoyt 1979), where L = length, B = breadth, and *k* was calculated by regression using fresh egg mass (*n* = 8) from field measurements.

Differences in growth rates between male and female nestlings were assessed by comparing the maximum mass and wing length increase per unit time. The increase in body mass (g/day) was compared during the period of fastest growth, from 10–90% of the maximum mass (the $T_{(10-90)}$ period; Case 1978). Likewise, I compared wing length growth (mm/day) during the fastest growth period (ages 9–21 d; feathers emerged at day 9). Adult measurements and body mass information were taken from museum specimens (WFVZ) collected in and near the study area.

RESULTS AND DISCUSSION

Adult male sabrewings were significantly larger than adult females with respect to body mass, wing length, tail length, and culmen length (Table 1).

Breeding seasonality.—While nests with eggs were found from May through August, the nesting season may last until the end of the rainy season in November. Although I did not individually mark the females, the Sabrewing apparently has two or more broods

TABLE 2. Measurements of eggs of the Violet Sabrewing (*Campylopterus hemileucurus*) from Costa Rica. Data from fresh eggs ($n = 8$) and specimens deposited in the Western Foundation Museum of vertebrate Zoology ($n = 14$) were pooled. Egg mass for museum specimens was estimated by $M = k \times LB^2$ where k was derived from fresh eggs (see Methods).

Variable	Mean	SD	Range
Length (mm)	16.7	0.67	15.7–17.9
Width (mm)	11.3	0.23	10.8–11.6
Mass (g)	1.2	0.09	1.0–1.3

per season because second or third nests were built very close to or on top of the old nests.

Nest, eggs, and incubation.—Skutch (1967) and Stiles and Skutch (1989) described the nest as a bulky, well-built cup. The 16 nests I found were built with green moss and were lined with a few very fine green plant fibers. A few nests had some very fine brownish plant matter, probably fern scales. The diameter of nest cups ($n = 11$) varied less than the depth ($40.4 \text{ mm} \pm 1.19 \text{ SD}$ vs $30.5 \text{ mm} \pm 4.2 \text{ SD}$, respectively). All nests were built 1–5 m above water (mean = 2.3 ± 1.08 , $n = 16$).

Each active nest ($n = 5$) contained two large, dull white, subelliptical eggs. Egg measurements are given in Table 2. Individual egg mass was 13% of the female mass. Hatching success was 70% ($n = 10$ eggs); two eggs were addled and one egg failed to hatch. All seven eggs that hatched fledged young. Mean incubation period for four nests was 20 d (range = 19–22). On 51 visits to active nests only the female was observed incubating and raising the young. On two occasions I observed a male near a nest, but saw no interaction with the young or the female.

Nestling appearance and plumage.—I observed the development from hatching through fledging of seven nestlings from five nests. Hatching of the two young was very synchronous, less than 12 h. At hatching, the skin was pinkish on the ventral side and tinged gray dorsally; there were a few light brown down feathers on the back. The dorsal skin became blackish after 2–3 d. The base of the culmen was yellowish-gray, the distal part gray, and the gape yellowish. The feet were pinkish and claws gray. About 1–3 h after hatching the female fed the nestlings with flu-

id and black spiders with yellow abdomens that were clearly visible in the nestlings' crops. This combination of fluid and one type of spider was consistent throughout the nestling cycle. By 4–8 d the eyes were about 1/3 open, the dorsal skin was nearly black, and pin feathers began to emerge on the sides and back. In both sexes the tail began to emerge at about day 10 and the sheaths opened at about 15–16 d. Primaries began to break their sheaths at about 13–14 d and by 12–15 d all body feathers were breaking sheaths. The mandible became blackish, the maxilla was yellowish, and the gape was still yellowish. By day 12–15 nestlings were very active and noisy when handled.

At 16–19 d, body feathers were green and the tips of the feathers on the head, nape, and back were finely rufous-edged. The white postocular spot was clearly visible and plumage dimorphism was evident; ventral feathers on males were dark gray to blackish, whereas on females they were pale gray. In males violet feathers emerged first on the gorget and nape area. The brownish down feathers were still present on the dorsum. At 20–22 d a few pin feathers remained on the head, but the overall plumage was well defined, with only very few down feathers still present on the back. Nestlings fledged in the morning at 22–24 d (mean = 23, $n = 5$). One nest contained a male and a female chick, one contained a single male, one contained two females, and two contained single females.

Nestling morphometrics.—Nestling mass at hatching was $1.17 \pm 0.03 \text{ g}$ for two males and $1.05 \pm 0.21 \text{ g}$ for two females, representing 10.3% and 11.3% of adult mass, respectively (Fig. 1A). Overall adult mass was reached on about day 11 in females and day 12 in males. Maximum body mass was 15.1 g (132% of adult size) for males and 12 g (129% of adult size) for females. Males reached their maximum mass by day 17–18 and females by day 18–19.

The time from 10–90% of the maximum mass (the $T_{(10-90)}$ period) was 15.3 d for the fastest growing male and 13.8 d for the fastest growing female. Overall the males grew a mean of 41% slower than females during the $T_{(10-90)}$ period (0.80 vs 1.35 g/d).

Wings of males and females grew at similar rates between 9–21 d, 2.5 and 2.3 mm/d, re-

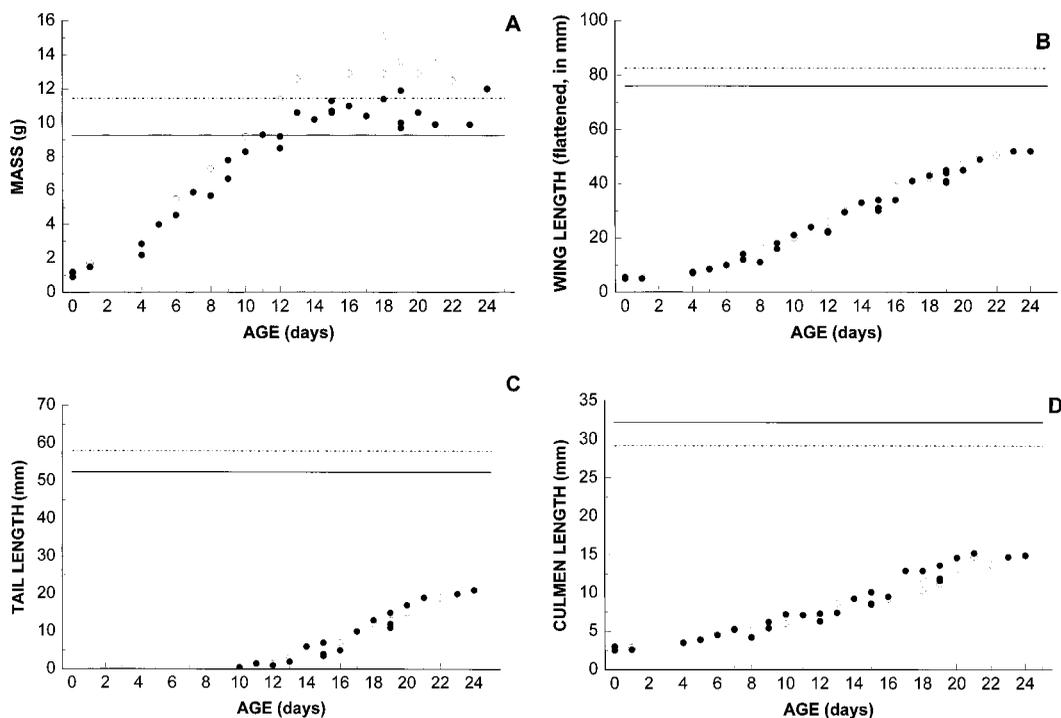


FIG. 1. Growth of nestling Violet Sabrewing (*Campylopterus hemileucurus*) in Costa Rica, 1996–1997. Open circles are two males from two broods and closed circles are five females from four broods. Horizontal lines are mean adult size (dashed for male, solid for female; see Table 1). (A) Mass, (B) flattened wing length, (C) tail length, and (D) culmen length. Fledging occurred between day 22 and 24.

spectively; females fledged when their wing length was about 68% of adult size and males fledged at about 61% of adult wing length (Fig. 1B). Tails grew steadily, with females fledging when the tail was about 40% of adult length and males fledging at about 35% of adult length (Fig. 1C). Females left the nest when their culmens were about 47% of adult size, and males left at about 50% of adult size (Fig. 1D).

The large maximum mass of Violet Sabrewing nestlings is reminiscent of aerial feeding birds and procellariiform seabirds whose nestling mass exceeds adult mass because of subcutaneous fat deposition. This strategy was labeled by O'Connor (1978) as a resource storage strategy for birds whose food supply is patchy and ephemeral. In the Violet Sabrewing there were no obvious subcutaneous fat depositions, but their large mass might be explained by the large storage of fluid and spiders in the crop, which was very

conspicuous from day 1 until fledging. Large nestling size has also been observed in other hummingbirds (Johnsgard 1983). The Blue-throated Hummingbird (*Lampornis clemenciae*) is also sexually dimorphic in size, and nestlings have both a large crop and a maximum mass reaching 25–35% above adult size (Wagner 1945, 1951).

Foster (1974) suggested that the rainy season has a two-sided effect on food availability. Food abundance peaks during this time, but the heavy rains obstruct the birds' abilities to obtain nectar and spiders. Thus, the nestling's large crop might serve for energy storage during bad weather conditions. Many species of tropical hummingbirds breed during the rainy season and periods of rain might have considerable effects on nestling growth (Wagner 1945, 1951). These factors suggest that a large crop and a rapid mass increase would be most pronounced in hummingbirds that nest in the most environmentally variable areas.

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Goal-directed Use of Objects by American Crows

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ABSTRACT.—I report the intentional use of objects by American Crows (*Corvus brachyrhynchos*) in the contexts of foraging, nestling defense and play. Received 2 June 2000, accepted 17 January 2001.

Several members of the genus *Corvus* have been documented to use objects to attain im-

mediate goals. Fish Crows (*Corvus ossifragus*) and Common Ravens (*C. corax*) dropped dried grass on incubating gulls, apparently in attempts to flush them from their nests (Montevocchi 1978). Hooded Crows (*C. corone cornix*) and Common Ravens dropped objects (twigs and rocks, respectively; Rolando and Zunino 1992, Janes 1976) on approaching humans, potential threats to vulnerable offspring. Heinrich (1988) proffered displacement be-

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havior directed toward the substrate and the incidental dislodging of material as a possible explanation for Janes' (1976) observations, yet the growing body of literature on the seemingly intentional use of objects by crows and ravens begs more goal-directed explanations.

Particularly compelling are cases of a Rook (*C. frugilegus*) selectively plugging a laboratory drainage hole so as to create a pool of water (Reid 1982), a Fan-tailed Raven (*C. rhipidurus*) using stones in an attempt to break open an "egg" (a ping-pong ball; Andersson 1989), a House Crow (*C. splendens*) "fishing" for ants with leaves (Rajan and Balasubramanian 1989), and an American Crow dropping nuts onto a road and waiting for cars to crush them (Grobeck and Pietsch 1978). Cristol et al. (1997) disputed the intentionality of the latter behavior, but on at least eight occasions I observed Western American Crows (*C. brachyrhynchos hesperis*) in Encino, California, land on wires above a road, drop pecans onto the pavement, and not fly down to inspect or retrieve them until a car had passed. Hunt (1996, 2000) described not only tool use, but tool manufacture by New Caledonian Crows (*C. moneduloides*). I recently described the modification of an object and its use as a tool by an American Crow (Caffrey 2000). Here I report additional examples of the intentional use of objects by American Crows.

As part of a field study on social organization and cooperative breeding in a population of Eastern American Crows (*C. b. brachyrhynchos*) in Stillwater, Oklahoma, nestlings were marked approximately 25 d post-hatching. On 27 April 2000, at approximately 15:30, an assistant began the ascent to a nest near the top of an 18-m pine tree. The breeding pair began issuing loud alarm calls and swooping to within 3 m of the tree climber. As the climber approached the nest, the pair landed approximately 2 m from him and continued to vocalize loudly. The female broke off a pine cone, flew just above the tree, and dropped it on the climber's head. She repeated this three times, hitting him twice more.

American Crows also drop objects with intent in the context of play. On several occa-

sions in Encino, California, I saw an individual carry a stick aloft in its bill or with its feet, drop it, and dive down to snatch it out of the air with its bill or feet. Similar to the observation described above, one day in Encino, a male (12 months postfledging) was foraging with his father underneath a flowering magnolia (*Magnolia* sp.) tree. His sister, a broodmate, flew in and landed in the tree above them, and inadvertently dislodged a flower petal. The petal fell next to the face of her brother, whose head was down. Apparently startled, he jumped backwards. He looked up at his sister and then resumed foraging. His sister looked down at him, turned and inched about 0.6 m along the branch to a flower, plucked off a petal, and inched back until over his head. She leaned forward and dropped the petal, which landed right next to him. Apparently startled again, he jumped backwards, looked up at her looking down at him, and walked out of her range.

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