Adaption of the 'parallel' reproductive strategy may allow males to conserve energy and maintain nutritional condition. Degen et al. (1992) demonstrated that male Northern Shrikes were able to maintain the lowest reported energy costs for adult birds feeding altricial young, and Yosef and Pinshow (1989) showed that males create large caches prior to the breeding season. The cached prey augment the fresh prey and help reduce energetic costs. In this manner, males are never in a situation wherein they feed more than one brood at a time. Although the total investment of males during various nesting stages remains unknown, this result is of importance because Loggerhead Shrikes are also capable of changing strategies, but the energetic consequences remain to be studied.

Loggerhead Shrikes display flexibility in their capability to live off the more abundant prey species during different seasons of the year. They may also enhance their fitness by choosing between alternate reproductive strategies dependent on the abundance of food resources in caches and in the territory.

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LITERATURE CITED

DEGEN, A. A., B. PINSHOW, R. YOSEF, M. KAM, AND K. A. NAGY. 1982. Energetics in Northern Shrikes: growth of nestlings and field metabolic rate of adults. Ecology (in press).

VERNER, J. AND M. F. WILSON. 1969. Mating systems, sexual dimorphism, and the role of male North American passerine birds in the nesting cycle. Ornithol. Monogr. No. 9.

YOSEF, R., W. A. MITCHELL, AND B. PINSHOW. 1991. The proximate costs and benefits of polygyny to male Northern Shrikes. Wilson Bull. 103:146–149.

——— AND B. PINSHOW. 1988. Polygyny in the Northern Shrike, *Lanius excubitor,* in Israel. Auk 105:581–582.

——— AND ———. 1989. Cache size influences female mate choice and reproductive success in the Northern Shrike, *Lanius excubitor.* Auk 106:418–421.

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The waving display and other nest site anti-predator behavior of the Black-capped Chickadee.—Adult Black-capped Chickadees (*Parus atricapillus*) and other *Parus* spp. show conspicuous postures and movements directed toward potential predators at the nest site (Odum 1941, Dixon 1949, Hinde 1952, Laskey 1957, Betts 1958, McLaren 1976, Long 1982). Descriptions of these displays, called "injury-feigning" (Pettingill 1937, Odum 1941, McLaren 1976) and "distraction" (Hinde 1952, Laskey 1957, Long 1982, Smith 1991) displays, often are incomplete and have not been defined consistently in the literature. Some descriptions are inconsistent among different authors (Long 1982), suggesting that the display is either highly variable or that more than one display is involved. Furthermore, the name "distraction" for the display implies a function for which there is currently no evidence and for

which alternative functions exist. This paper re-examines anti-predator behavior using video recordings and slow-motion analysis with the objective of redescribing the behavioral components in greater detail. We suggest the name "waving" for this primarily visual display to depict the noticeably slow movements of the body and wings. In addition, we presented study skins of potential predators to chickadees at the nest site to determine which predators elicit specific behaviors.

Methods.—Observations were made in June 1990 at Picnic Point on the campus of the Univ. of Wisconsin–Madison. Four adult Black-capped Chickadees, two mated pairs, were observed displaying near their nests in holes excavated about 1 m above ground in rotting snags. The nestlings were 7–10 days of age. Study skins of an eastern chipmunk (*Tamias striatus*), gray squirrel (*Sciurus carolinensis*), Blue Jay (*Cyanocitta cristata*), Eastern Screech-Owl (*Otus asio*), and a House Wren (*Troglodytes aedon*), were presented to two other mated pairs of chickadees during five days from 5–13 June 1991 when the nestlings were 8–16 days of age. Both pairs were nesting in boxes about 1 m above ground at Picnic Point and the nearby residential area of Shorewood Hills. Each predator was presented one at a time in varied order at two distances from the nestboxes; on the ground 1–3 m from the nestbox and on a branch $\leq$½ m or on top of the nestbox. One pair was tested on three days, and the other pair was tested on four days with one to three different predators being presented on a given day. The observers stood 5–10 m from the nest to record the reactions of the birds. Individuals could be identified by unique color-band combinations. The birds' reactions were recorded with a VHS RCA CC520 Pro Edit Video Camcorder (scanning specifications = 525 lines/60 fields/30 frames per sec). Recordings were made on a Polaroid Supercolor Plus 246 m video cassette tape with the camcorder set on super long play. Some of the trials were recorded with a Sony Handycam CCD-F77. The recordings were viewed on a Sony Multichannel TV Sound KV-2084R. Screen pictures on the TV were captured with freeze-frame control and sketches of the birds' postures were traced from these.

Results.—Different predators elicited different behavioral combinations. Using terminology of previous authors whenever appropriate (see Hinde 1952, Stokes 1962a, Smith 1972), these are as follows. (1) Head forward. The head is lowered to align with the longitudinal axis of the body and the neck is extended anteriorly. The bill is pointed in the direction of the predator. When the predator is below the bird, the bird may tip down anteriorly, such that its head is lower than its tail. (2) Wings raised. The wings are rotated outward so that the leading edge of the wing is lifted away from the body. The wing tips may separate from the tail to a varying degree, but usually not more than 45° laterally from the longitudinal axis. The wing tips are sometimes held below the level of the tail and sometimes above. (3) Body wave (Fig. 1C). The bill and neck are extended in the head forward posture (above) and the head is moved slowly from side to side at a rate of about 1 cycle every 5 sec, or 0.2 cycles/sec, for a variable length of time. The side to side movement usually includes the body as it aligns with the head, and sometimes the tail. The slow movement and stiffened appearance of the neck and head during body waving contrasts with the scanning head movements of a bird in a relaxed perch position. The side-to-side movement may also resemble the motion of a pendulum, with the head held high at either end of the arc and dipping down and then back up again during the course of the swing. (4) Wing wave (Fig. 1A, B). One or both wings are elevated above the longitudinal axis so that the inner linings are exposed to view. The raised wing is rotated forward, down, and back up in a rowing motion at a rate ranging from 1–5 cycles/sec ($\bar{x}$ = 3 cycles/sec). Higher intensity wing waving where the wings are more fully extended occurs at slower rates than less intense waving. The circular motion of the wings is repeated a variable number of times. This movement results in the flashing of the white inner linings of the wing. (5) Waving display. Behavior involving wing waving or body waving or both. (6) Body flick. In one

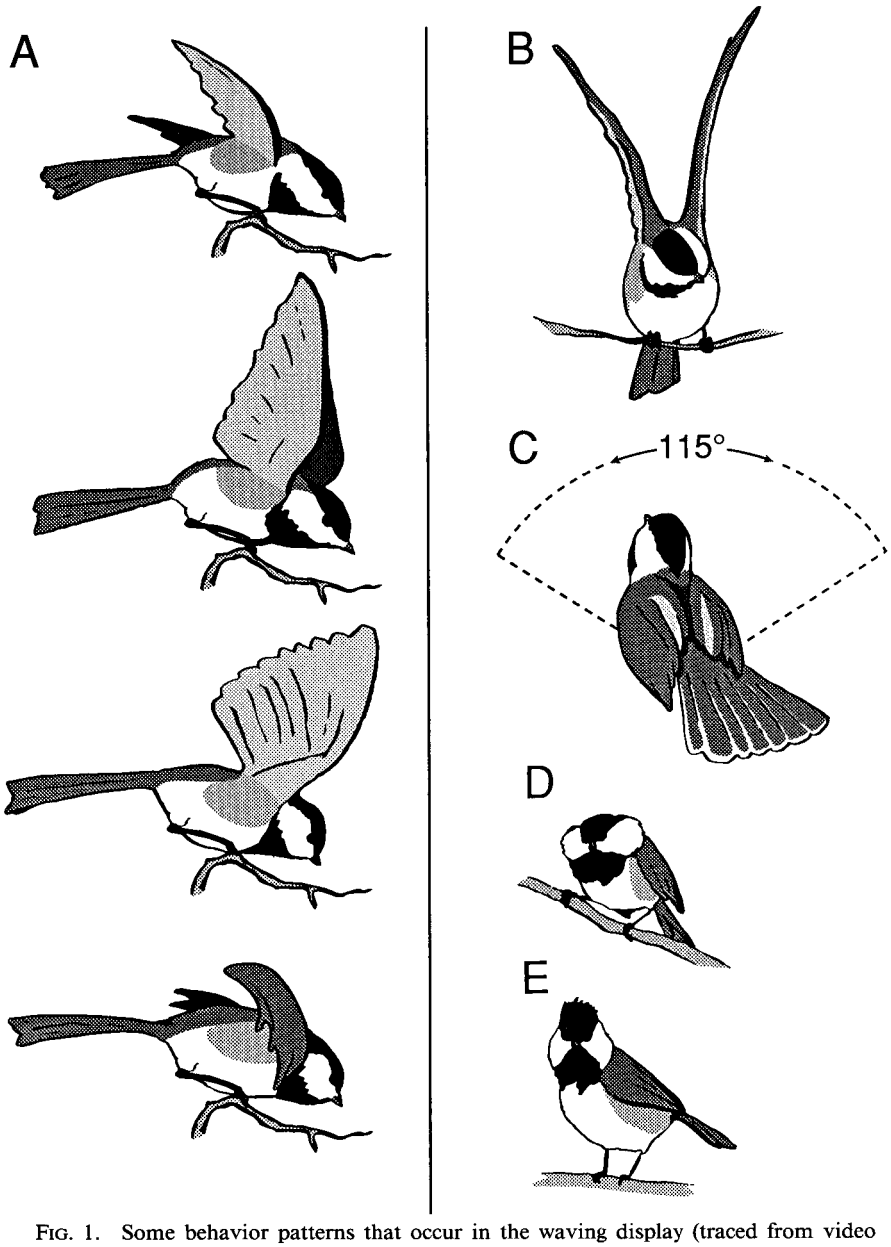

FIG. 1. Some behavior patterns that occur in the waving display (traced from video recordings displayed on a screen). A. Sequence of movements showing wing waving. B. Anterior view of the upward extension of the wings during wing waving. C. Body waving, showing the angle of side to side movement. D. Wide face, produced by raising feathers on the cheeks and sides of the neck combined with depression of feathers on the crown. E. Long face, produced by raising feathers on the crown, combined with normal or depressed feathers on the cheeks.

case while a bird was perched above a stuffed wren, it thrust its body vertically downward with its bill pointing at the wren, then raised its body back to normal perch position in a single motion lasting about 0.3 sec. The act was repeated two more times over the course of a min. (7) Feather postures. Various degrees and patterns of feather erection or depression give further expression to the above behavior patterns. In some cases the feathers on the cheek (cheek ruffle), sides of the neck, and nape (nape crest) were raised and the feathers on the crown were flat (crown sleek), giving a wide appearance to the face (Fig. 1D). The wide face sharply contrasted with the long face, which was produced by raised feathers on the crown (crown ruffle) and flattened or normal feathers on the cheek (Fig. 1E). Both long and wide faces were observed during head forward, wing wave, and body wave. In one waving display, a male had feathers erected throughout the torso (body ruffle) and on the crown. (8) Wing flick. The wing is quickly raised and brought back to rest in a single motion of about 0.07 sec in duration. (9) Tail flick. The tail is either quickly moved up and down or vibrated for about 0.07 sec such that the tail appears as a blur during slow motion playbacks. (10) Wing quiver. The tips of the wings are extended laterally and retracted again in a rapid motion of about 15 cycles/sec. The movement is repeated continuously for a variable amount of time, ranging from only a few cycles to several min of quivering. Wing quivering was frequently observed during bouts of antipredator display behavior, but it may not have been a reaction to the predator (see below). (11) Dive. The bird flies directly at the predator but does not make contact with it. (12) Attack. The bird flies directly at the predator and makes contact with it. (13) Open beak. The beak is held open. (14) Miscellaneous. Other forms of behavior given in the presence of potential predators included spreading of the feathers in the tail (tail fan) and extension of the legs. During wing waving, the bird frequently moved along the branch or to lower perches with a slow hopping motion that nearly resembled walking (only one foot left the perch at a time, but at some point both feet were off the perch). The birds were usually quiet during wing and body waves, but produced "hisses" on two occasions while lunging forward in the direction of the predator. Hissing occurred more frequently during dives and attacks.

Reactions to the study skins that occurred at least once are given in Table 1 for the different predator contexts. Some acts were more specific, occurring in the presence of some predators but not others. For example, wing waves and body waves occurred only during the presentations of the chipmunk and squirrel, whereas other acts, such as crown sleeks and nape crests occurred in all contexts. The combination of acts was highly variable, but a few generalizations follow. Tail fans occurred with wing waves, body waves, and attacks; hissing occurred with wing waves, dives, and attacks; crown ruffles occurred during wing waves, body waves, and with chick-a-dee calls; and wing and tail flicks occurred during bouts of chick-a-dee calling and sometimes preceded attacks and dives.

Two components, wing quivering and open beak, were probably not reactions to predators. Wing quivering occurred in all contexts, but in five of the six cases, the female wing quivered just as either she or her mate or both birds arrived together at the nest site or emerged from the box. In the sixth case where the female wing quivered, the position of her mate was not recorded. Around the nest site, wing quivering is given in the presence of the mate and is used to coordinate nestling care (Lambrechts et al., in press). Open beak was given by a female when her mate, who was in the head forward posture, was perched less than 0.5 m from her. While the female's beak was open, her head was turned away from the predator and toward her mate. The male then also opened his beak.

Although different predator contexts shared display components, the frequency of occurrence of these components varied widely (Fig. 2). Chick-a-dee calls occurred in most contexts, but, whereas it was the only one of five acts given in the presence of the jay or owl, it was

TABLE 1
DISPLAY COMPONENTS GIVEN TO DIFFERENT PREDATOR MODELS

Components	Eastern chipmunk	Gray squirrel	House Wren	Blue Jay	Screech-Owl
Wing wave	X	X			
Body wave	X	X			
Head forward			X		
Crown ruffle	X	X		X	X
Crown sleek	X	X	X	X	X
Nape crest	X	X	X	X	X
Cheek ruffle	X		X		
Cheek sleek	X	X			
Tail fan	X	X			
Dive	X	X	X		
Attack	X	X	X		
Hiss	X	X			
Chick-a-dee call	X	X	X	X	X
Wing flick	X	X		X	
Tail flick				X	
Body flick			X		
Hop	X	X			
Leg extension	X				
Wing quiver[a]	X		X	X	X
Open beak[a]		X			

[a] Probably not reactions to predators (see text).

rarely given in the presence of the chipmunk or squirrel. Dives and attacks occurred only with the chipmunk, squirrel, and wren predators, and the waving display occurred only with the chipmunk and squirrel predators. Although the experimental sample sizes were smaller, the results were similar when the predator was presented at greater than 1 m distance from the nest, with the exception that dives, attacks, and hisses dropped out. The frequency with which the other displays were given, however, tended to decrease with the greater distance.

The reaction to the owl and jay, i.e., chick-a-dee calling, wing and tail flicking, and frequent perch changes, contrasted so sharply with the reaction given to the chipmunk, i.e., the quiet waving display and/or hissing and attacks, that we decided to further test the differences in responses by switching the chipmunk model with the owl or jay, and vice versa, in front of the chickadees. Although these tests were performed only three times, the changes in responses occurred completely and immediately within a few seconds of the switch. Hence, the qualitative differences in reactions given to the different predators held true whether we presented the predators on different days or one consecutively after the other.

In addition, in 1990 chickadees were observed displaying to live chipmunks on ten occasions, both alone and near their mates. In eight of the ten occasions the displayers were oriented toward an eastern chipmunk on the ground within 2 m of the nesthole stump. Although chipmunks were not noted in the other two occasions, their presence may have been obscured by thick ground cover. The chipmunks gave no apparent reaction to the birds' displays, but merely passed by the nesthole stumps while foraging. The displays

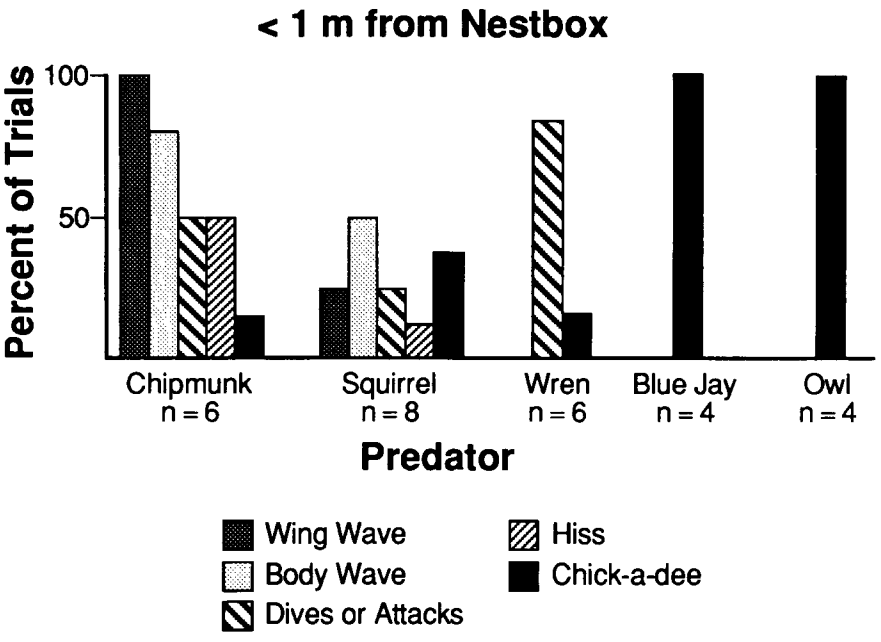

FIG. 2. The frequency of occurrence of five behavior patterns of chickadees when different types of predators were presented at a distance of less than 1 m or in contact with the nestbox.

included any number and variety of postures and movements, including wing waves, body waves, tail fans, crown sleeks, nape crests, leg extensions, hopping along the perch toward the chipmunk, and hisses.

In 1991 we made six observations of reactions to live Blue Jays, one to a live cat (*Felis domestica*), and one to a live raccoon (*Procyon lotor*) within 20 m of the nest. In each case the chickadees responded with chick-a-dee calls. On several occasions one bird assumed the head forward posture and dived at a human opening the nest box.

Discussion.—We used the same names for behavior patterns described in other studies for Black-capped Chickadees or other *Parus* spp. whenever it appeared that the behavior in each species was the same or homologous. For example, chickadees frequently raised their wings during the body wave in a manner that resembled the wings raised act described and photographed during agonistic encounters of the Great Tit (*P. major*; Hinde 1952, Fisher and Hinde 1949). Although Hinde (1952) stated that the wings may be raised above the level of the back, there was no mention of wing movement in the wings raised act as observed in this study. Hence, it seems appropriate to distinguish between wings raised and wing waving. In some cases, more than one name has been used to describe the same display. For example, "open beak" (Stokes 1962a) has also been called "gape" (Smith 1972, Smith 1991). We chose to go with "open beak" to distinguish it from the gaping action given by nestlings, fledglings, and sometimes females, which involves a wider opening of the mouth while calling for or receiving food.

The purpose or usefulness of the waving display at the nest site is not entirely clear. Previous observers described the display or similar components of the display as being either injury-feigning, distraction, or threat displays. Odum (1941) described an "injury-feigning"

display by a Black-capped Chickadee pair directed toward himself after capturing one of the newly fledged young. In both parents the wings were outstretched and slowly flapped over the back, and the head was held straight out and moved side to side. The display appeared to be elicited only by the cry of the young or when the cry of the young was imitated. Although the waving display we observed shares components with the "injury-feigning" display described by Odum (1941), our birds did not appear to be injured and there was no attempt to lead the predator away from the nest hole. In all of the 1990 observations where distance was noted, the chipmunks were 1–2 m from the nest, and the nesthole was frequently between the chipmunk and the bird that displayed. The birds usually remained stationary or shifted short distances along the perch or to nearby perches. Nevertheless, the slow waving motion may serve to attract and focus the attention of the predator on the displayer, thereby decreasing the chance that the predator will find the nest. Alternatively, the waving display may represent intention movements to convey aggressive tendencies or movements to make the bird appear larger or more menacing. At least some of the same components of the waving display are used in agonistic situations. In both Great and Blue tits (*P. caeruleus*), wings raised and head forward postures accompanied by raised feathers of the cheek and crown, open beak, body waving, and tail fanning occurred when a bird at the feeder was approached too closely by another bird (Hinde 1952). In Blue, Great, and Marsh tits, these behavior patterns correlated with the tendencies of birds to attack, escape, or stay (Stokes 1962a, b). Behavior resembling wings raised and head forward postures also occurs in agonistic interactions of the Carolina Chickadee (*P. carolinensis*; Brewer 1961) and Tufted Titmouse (*P. bicolor*; Wallace 1967). The threat display hypothesis may explain why the female we observed reacted to her mate by opening her beak when he displayed toward the predator model in the head forward posture near her. However, not all components of the waving display have been noted in agonistic interactions. Specifically, the waving motion of the wings has been described only in predator encounters.

Of particular importance are the different reactions chickadees have to different types of predators. In this study, only sciurids elicited wing waving, wrens and sciurids both evoked body waving and attacks or dives, and owls and Blue Jays elicited chick-a-dee calls. Long (1982) noted that a "distraction" display was given to study skins of various sciurids as well as to the House Wren and a live snake. However, Long did not distinguish between the various components of the display given in different predator contexts, thereby making comparisons with our results difficult.

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LITERATURE CITED

BETTS, M. M. 1958. The behaviour of adult tits toward other birds and mammals near the nest. Brit. Birds 51:426–427.

BREWER, R. 1961. Comparative notes on the life history of the Carolina Chickadee. Wilson Bull. 73:348–373.

DIXON, K. L. 1949. Behavior of the Plain Titmouse. Auk 58:110–136.

FISHER, J. AND R. A. HINDE. 1949. The opening of milk bottles by birds. Brit. Birds 42: 347–357.

HINDE, R. A. 1952. The behaviour of the Great Tit (*Parus major*) and some other related species. Behav. Suppl. 2:1–201.

LAMBRECHTS, M. M., J. R. CLEMMONS, AND J. P. HAILMAN. Wing quivering of Black-capped Chickadees with nestlings: invitation or appeasement? Anim. Behav. (in press).

LASKEY, A. R. 1957. Some Tufted Titmouse life history. Bird-Banding 28:135–145.
LONG, C. A. 1982. Comparison of the nest-site distraction displays of Black-capped Chickadee and White-breasted Nuthatch. Wilson Bull. 94:216–218.
MCLAREN, M. A. 1976. Vocalizations of the Boreal Chickadee. Auk 93:451–463.
ODUM, E. P. 1941. Annual cycle of the Black-capped Chickadee. 2. Auk 58:518–535.
PETTINGILL, E. R. 1937. Grand Manan's Acadian Chickadees. Bird Lore 39:277–282.
SMITH, S. M. 1991. The Black-capped Chickadee: behavioral ecology and natural history. Cornell Univ. Press, Ithaca, New York.
SMITH, S. T. 1972. Communication and other social behavior in *Parus carolinensis*. Nuttall Ornith. Club 11.
STOKES, A. W. 1962a. Agonistic behaviour among Blue Tits at a winter feeding station. Behaviour 19:118–138.
———. 1962b. The comparative ethology of Great, Blue, Marsh, and Coal tits at a winter feeding station. Behav. 19:208–218.
WALLACE, G. O. 1967. An aggressive display by a Tufted Titmouse. Wilson Bull. 79:118.

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Peculiar behavior of a subadult female Tree Swallow.—I observed peculiar behaviors displayed by a dull-brown subadult (SY; Hussell 1983) female member of a trio of nesting Tree Swallows (*Tachycineta bicolor*) at the Creston Valley Wildlife Management Area, southeastern B.C. (49°05′N, 116°35′W), during May–June 1991. The range of behaviors exhibited by the SY female included typical parental breeding behavior, apparent "helping" behavior when the SY female tended only the offspring of the other female, and non-breeding (i.e., nest attendant) behavior when the SY female repeatedly took food from both the male and other female (cf Lombardo 1986, 1987a, b). The observations suggest that mistaken "helping" behavior may occur frequently in Tree Swallow trios (cf Quinney 1983) and that behavior in adult Tree Swallows during the breeding season has evolved considerable plasticity, perhaps in response to the unpredictable availability of nest-sites.

The trio of birds included an unbanded male, an after-second-year (ASY) female, and the SY female. The ASY and SY females were captured, banded, and painted on 30 May and 7 June, respectively, but the marked differences in plumage color enabled me to distinguish each bird prior to banding. The ASY female completed a clutch of five eggs on 23 May. The SY female was observed circling the box on 26 May while the ASY female was incubating, and she was also present when I banded the ASY female. On 2 June, I discovered eight eggs in the nest cup. Evidently, the SY female began laying on 31 May and she completed her clutch on 4 June when there were ten eggs in the nest cup. I marked the new eggs with a non-toxic permanent marker beginning 2 June. On 5 June one of the eggs of the ASY female began pipping, and by 7 June there were five nestlings belonging to the ASY female and five eggs belonging to the SY female.

Three 1-h watches were conducted (08:00–11:30 MST) at the nest on 7, 10, and 14 June, corresponding to nestling-days (ND) 2, 5, and 9. Watches were conducted from 45 m using 7 × 50 binoculars and a 15× spotting scope. After the first watch I captured the SY female while she lay on the ASY female, which was brooding the nestlings. The SY female was