OBSERVATIONS ON THE INCUBATION BEHAVIOR OF A COMMON NIGHTHAWK

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Although the Common Nighthawk (*Chordeiles minor*) has been studied extensively, certain phases of its breeding biology have been considered only superficially. Among these are the incubation movements of the female, the manner in which eggs are moved, and certain activities of the male. An opportunity to investigate this behavior presented itself when a Nighthawk nested on the graveled roof of the Wildlife Building of the University of Missouri in 1957. I am indebted to Thomas S. Baskett, William J. Hamilton III, Frank McKinney, and Margaret M. Nice for assistance with the manuscript.

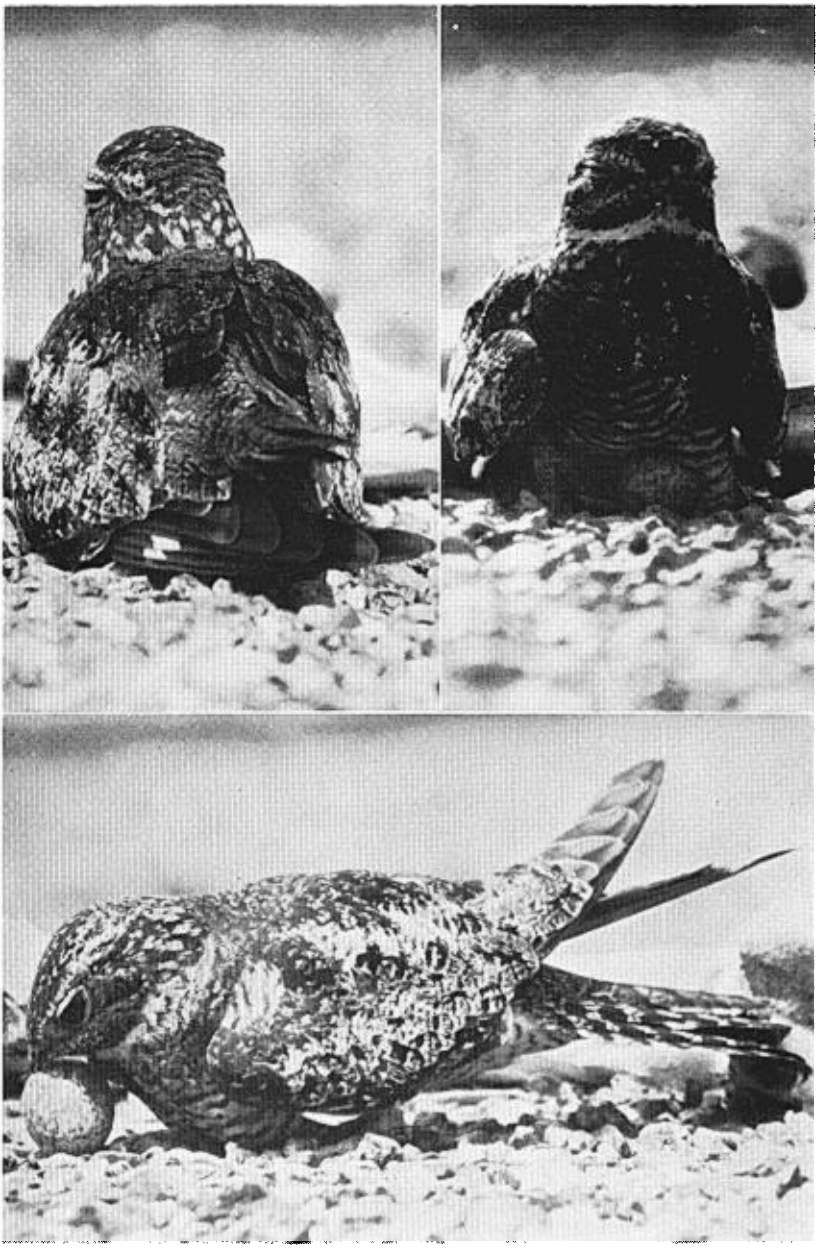
Orientation to the Sun

The incubation movements of the European Nightjar (*Caprimulgus europaeus*) have been studied in detail in a captive bird by Heinroth (1909). Lack (1932) states that Heinroth (1928: 279) reported both the Nightjar and the Sand Grouse (*Pterocles* spp.) usually facing the sun during incubation. Shadow thus was reduced to a minimum and the effectiveness of the bird's camouflaging plumage maintained. Lack (1932), however, found that less than half the female Nightjars he observed faced the sun. Few workers in North America seem to have considered orientation behavior in the Nighthawk; but Gross (1940: 214) observed that a Nighthawk he watched "usually faced the sunrise in the morning and the sunset in the evening."

In the present study, this orientation was measured more precisely by means of a sun dial constructed by mounting a vertical rod in the center of a board marked with a circle scaled in 10° intervals. This was placed near the roof door from which observations were made. Most observations were made at hourly intervals. The direction of the sunlight was determined by the shadow of the rod of the sun dial and the position of the bird's axis was estimated in degrees by reference to the dial.

These observations are summarized for one complete day in Figure 1. Remarkably precise agreement is shown between the bird's position and the angle of the sun. The bird maintained the sun at her back throughout the day.

At only one observation was a conspicuous disagreement noted between the bird's long axis and the angle of the sun. This occurred at 9 a.m. during a partly cloudy period. By 10 a.m., when the temperature at roof level reached approximately 110° F (43° C), the bird had not only moved



Common Nighthawk. (A. *Left*) Showing position of wings and ruffling of head and back feathers. (B. *Right*) Shading first egg of second clutch. (C. *Below*) Poking displaced egg under her. Photos. by M. W. Weller.

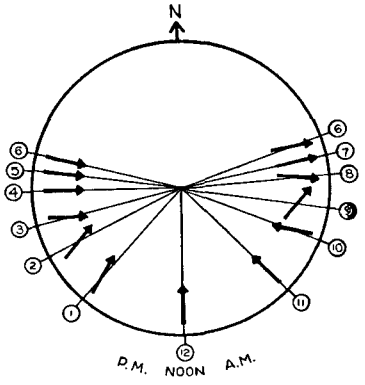


FIGURE 1. Orientation of an incubating Nighthawk to the sun. The position of the bird is shown by the arrow. Time of day and position of the sun are shown by the small circles. Clear circles indicate bright sun; half-black circles indicate partly cloudy conditions.

to a new position in line with the sun, but had reversed so that its head faced away from the sun's rays. A similar pattern is shown by several observations on another bright day (Figure 2). On this day, the bird was forced to leave its nest on two occasions: At 11 a.m. the bird was sitting with the sun at her back. After being flushed, she returned facing the sun but still well oriented to its rays. At 2 p.m., she was flushed again and on her return, oriented perfectly and in the same position as before leaving the nest. In the latter situation, she could easily see the observer and still have the sun at her back, while in the morning she apparently turned to watch the investigator. She maintained a position with the sun at her back throughout the remainder of the day.

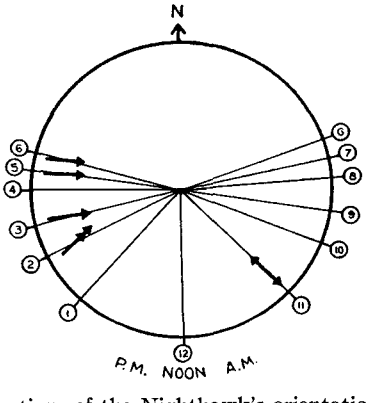


FIGURE 2. Seven observations of the Nighthawk's orientation to the sun on another bright day.

The observations described above were made during the first week in June. During the incubation of the second clutch during the first week in July, it was noted that orientation to the sun was poor between 11 a.m. and 2 p.m. This was probably due to the fact that the sun was more nearly overhead than during early June and its rays were less directional. Either the bird could not recognize or did not respond to such slight differences in sun position. Moreover, these differences would be insignificant as far as shadow is concerned. The lack of orientation during this period may explain in part why this phenomenon has not been widely recognized.

Observations for an overcast day, when the position of the sun was not apparent to the observer, are shown in Figure 3. It is apparent that

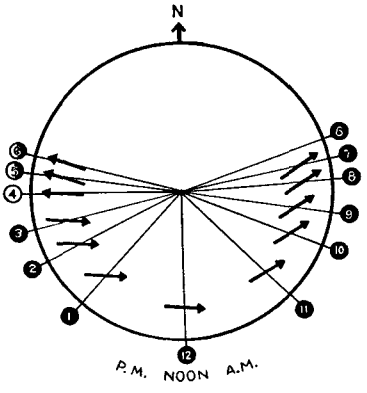


FIGURE 3. Positions of the Nighthawk in relation to the theoretical position of the sun on an overcast day.

no orientation to the sun occurred on that day until between 3 p.m. and 4 p.m., when the sky partly cleared. At that time the bird reversed its position and faced into the sun. The bird had moved again by 5 p.m., and remained there the rest of the day. Although observations were made only every hour, the bird apparently remained in the same position for as long as four hours when the sun was not shining. On the bright days, no position was held for much more than an hour. There was some indication that the bird sat at right angles to the sun on hazy days, perhaps to aid in heat absorption. When the sun appeared on cool, cloudy, days, the bird faced it rather than turning away from it.

Without question, the bird responded to the sun on clear days but did not orient when the sun was hidden by clouds. Then, artificial shade was provided. The bird was kept in the shade from 8 a.m. until 12 noon; the result of this shade on movements is shown in Figure 4. Although

minor movements occurred, her orientation was definitely impaired by the shade. Thus Lack's observation (1932) that not all Nightjars oriented to the sun was probably a result of the presence of shade.

Conceivably, orientation to the sun would not only aid in protection from aerial predators but would cause an even distribution of heat over the body and might reduce the body area exposed to the sun. Thus heat, as well as light, could act as a stimulus for orientation. On the day shade tests were conducted, temperatures at roof level ranged from 92° F (33° C) at 8 a.m. to 126° F (52° C) at 12 noon. In spite of the fact that the heat under the shade was nearly as great as in the open sun, no orientation occurred. However, the effect of this shade on body tem-

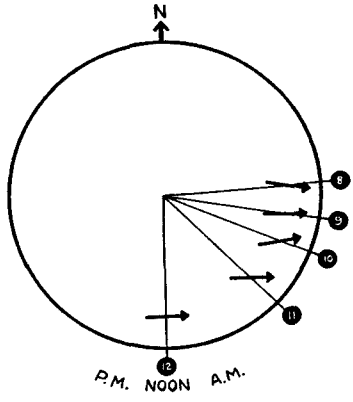


FIGURE 4. Position of the Nighthawk in relation to the sun when the bird was artificially shaded.

perature was unknown. Thus, light seemed of greater importance in orientation than heat.

Then, partial shading tests were conducted in an effort to determine the body area most influenced by the sun. First, the Nighthawk's head was exposed while her body was shaded. She immediately began panting, indicating a greater body heat, and within two minutes had moved nearly 60° from a position at a right angle to the sun to within 30° of the axis of the sun's rays. She remained in this position for 35 minutes and then the shade was moved to cover her head. She did not move for an hour and twenty minutes. When she finally moved, it was probably due to the hatching of one of the young rather than to the position of the sun. She took a position within 30° of the sun's axis but with her head still shaded. Shortly afterwards, her head was uncovered and her body shaded. She immediately moved to a new position, also within 30° of the sun's angle but reversed, and with her head in the shade! Shading exper-

iments were then discontinued. Apparently, the head was of more importance than the body in inducing orientation.

After the young hatched, the female moved them around on the roof to utilize shade available from pipes and other structures on the roof. There was some evidence that the young oriented to the sun when only seven and eight days of age, but because they spent most of their time in the shade, their ability to orient to the light could not be accurately determined. The female oriented to the sun in spite of the fact that she provided less shade for the young.

It would seem that sun orientation in the Nighthawk may well have resulted from the tendency of a nocturnal bird to avoid glaring light. However, more detailed information is necessary on the Nightjar, and

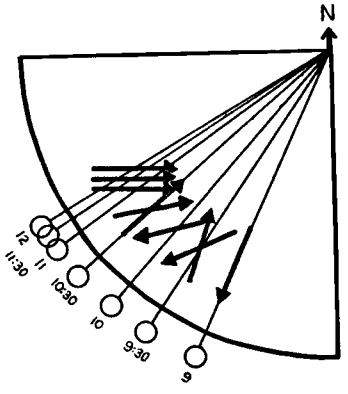


FIGURE 5. Position of the Nighthawk in relation to the position of the moon.

especially on diurnal birds which nest in the open, such as the Sand Grouse.

Shortly after sunset each evening, the female left the eggs or young for a short feeding flight, staying away 20 minutes on one night and 17 minutes on another. When she returned, her orientation was not toward the glow of the western sky. The presence of the moon, and its probable importance in the reproductive cycle (Wynne-Edwards, 1930), suggested a possible orientation to that light source. Such orientation would reduce shadows as does orientation to the sun. Observations were made of the bird's position in relation to the moon on two nights. These observations were of short duration due to cloudy conditions and the influence of the more mobile young under the Nighthawk. The data are summarized in Figure 5 and show no very strong orientation to the moon. Efforts to orientate the female with a strong flashlight failed.

COOLING MECHANISMS

Because heat is dissipated by panting (Cowles and Dawson, 1951), shading of the mouth region by orienting away from the sun may aid in cooling. Orientation to the sun also may aid in cooling the Nighthawk by reducing the amount of surface exposed to the sun. When the female was in the open sun, and facing away from it, panting started when roof temperatures reached 95° F (35° C).

An additional cooling mechanism was the ruffling of the back and head feathers (Plate 5A) which created shaded air spaces (see Morris, 1956). This started in the open sun when roof temperatures were between 103° F (39° C) and 112° F (44° C), depending on the amount of the breeze. At the same time, the primaries were often lowered below the tail, forming a shading canopy (Plate 5A).

The female's cooling devices permit her to survive in spite of temperatures of up to 142° F (61° C), as recorded once during this study. Moreover, the female seems to be in a lethargic state most of the day. For about 15 minutes prior to leaving the nest in the evening, she goes through a "waking" period. She opens her eyes wide frequently, moves her lower mandible, gapes once, watches the activities of the male and other birds flying by, and then leaves (with or without the presence of the

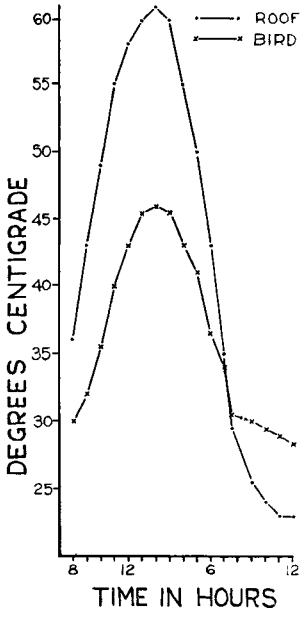


FIGURE 6. Temperature of the nest site when covered by the bird compared with the temperature of the open roof from 8 A.M. until Midnight.

male). Her influence on the cooling of eggs during the summer heat is probably of greater importance than heating them during cool periods. To measure grossly the influence of the hen's body on the temperature of the area under the eggs, a thermometer was placed upside-down, through the roof, with the bulb just under the eggs. Another thermometer was placed in the roof in a like manner but with the bulb of the thermometer exposed to the sun. The results of one day's records (8 a.m. to midnight) are shown in Figure 6. During the heat of the day, the presence of the bird lowered the temperature of the nest site as much as 15° C. The opposite was true at night, when the presence of the female increased the nest temperature by five to six degrees Centigrade. The rapid decline in temperature of the nest from five until nine p.m. was due to the fact that the female had moved the eggs slightly and was not directly on the thermometer.

MOVEMENT OF EGGS AND YOUNG

Another problem of interest raised by several investigators is how eggs are moved by the Nighthawk. It is commonly believed that members of the Caprimulgidae move eggs in their mouths when the nest is disturbed (Armstrong, 1947: 35). However, there seem to be no authentic records of such movements. Sutton and Spencer (1949) noted that the eggs of a Nighthawk were moved 28 inches when the old nest site was flooded but the method of movement was unknown. Gross (1940: 213) stated that two clutches of eggs were moved five and six feet by the females, but this movement was attributed to the female's habit of poking eggs under her when she approached them. Because she usually approached from the same direction, the movement of eggs occurred in a rather straight line and left a trail in the gravel. Warren (1890: 181) recorded the movement of a Nighthawk's eggs a distance of 200 yards and implied that the Nighthawk carried them in her mouth. However, he did not see this act and did not say how he identified the eggs of that particular individual. Audubon (1831: 275–276) said that both eggs and young are moved in this fashion by the Chuck-will's-widow (*Caprimulgus carolinensis*). He also commented that:

> "... The Negroes, some of whom pay a good deal of attention to the habits of birds and quadrupeds, assured me that these birds push the eggs or young with their bill along the ground. Some farmers without troubling themselves much about the matter, imagined the transportation to be performed under the wings of the old bird."

Rysgaard (1944) and Kilham (1957) observed a Chuck-will's-widow and a Whip-poor-will (*Caprimulgus vociferus*), respectively, carrying eggs

by use of their feet. The former case was clearly accidental but the nature of the latter is uncertain.

In the present study, one of the two eggs was displaced from the nest site to determine how eggs were transported as well as to study incubation movements. When the egg was moved one inch from the original nest site, the female first straddled the egg in the original site and poked the displaced egg under her with the lower mandible (Plate 5C), a movement characteristic of many birds (Poulsen, 1953). After the egg was displaced four inches, the bird again returned to the nest site and covered the remaining egg. Then she rose slightly, and walked a few inches toward the displaced egg, apparently pushing the other egg in front of her feet, until she could reach the displaced egg. This she immediately poked under her. Next, the egg was displaced 12 inches, far beyond where she could poke an egg into the nest site. She took a position between the two eggs, and after a period of hesitation, went back to the original nest site. After a few seconds, she left the egg in the nest, moved toward the second egg, and poked it under her as if to brood. Simultaneously, she turned toward the nest. She then walked slowly toward the first egg, apparently rolling the displaced egg in front of her feet. However, the egg was partly hidden by the breast feathers. The egg was moved about seven inches in this fashion and then the female moved off the egg and toward the egg at the nest site, which she poked under her. Then she turned and poked under her the egg which she had rolled. Finally, she covered both eggs, and the nest was moved only two or three inches toward the displaced egg.

When the female incubated her second clutch, experiments with moving an egg were again tried. When the egg was moved 12 inches, the female returned to her nest, remained two minutes, and then moved to the displaced egg. She poked the egg under her and moved sideways for a distance of eight inches, rolling, at times holding, the egg with her flank and breast feathers. Then she returned to her nest and poked in the retrieved egg.

When the egg was moved three feet from her, she did not attempt to retrieve it. Gross (1940: 213) and Parks (1947) also noted a stronger attraction to the nest site than to eggs displaced several feet from the nest. After 45 minutes, the egg was moved within 12 inches of her. She immediately retrieved it, holding it mainly by means of her breast feathers and her legs.

The manner in which the young were moved was observed early one morning when one young had hatched and was less than one day old. At 7:30 a.m., the adult was found incubating her young within three feet of the roof door in the shade, about 10 feet from the remaining egg at the

nest site. After being flushed by the investigator, she walked to the remaining egg, sat on it, and in a few seconds returned to the young and brooded it within three feet of the observer's head. Then she left the young, and moved toward the nest, giving a low nasal "kurr" or "kra" call at a rate of about one per second. The young followed her, resting periodically, until they reached the nest site.

OTHER INCUBATION BEHAVIOR

During the 45 minutes when only one egg was present in the nest, several movements were observed which were not seen during normal incubation of two eggs. When returning to the single egg, she poked it under one side of her brood patch. Then she poked toward the other side of her breast feathers as if she noted the absence of the second egg. She rotated on the nest, often completely disoriented to the sun, and poked "falsely" at the missing egg. Occasionally she pecked at a piece of gravel instead of completing the poke. Once she left the nest in a direction opposite to the displaced egg but returned immediately. It appeared impossible for her to incubate comfortably on one egg, and possibly this fact alone causes her to shade her first egg but not to incubate it until the second is laid (Plate 5B).

Once, after the female was chased off the nest three times in two hours, she hesitated to return. She stopped a foot from the nest and preened both her breast and her scapulars before she incubated the eggs. This was not observed on any other occasion and may well have been a displacement activity.

Another activity, which was probably a displacement movement, occurred on the first evening that incubation of the second clutch started. The second egg had been added at 10:30–11:30 a.m. after an interval of at least one full day. The female started incubation immediately and that evening left the nest about 15 minutes later than in the two previous nights when she was not incubating. The male landed by her, and called a low nasal "nar-r, nar-r" and the hen responded with a gutteral "kra-a" but did not leave the nest. Soon, she preened under her left scapulars 14 times in rapid succession. This action, which was not witnessed under any other circumstances, may have represented precopulatory behavior. (Copulation during the incubation period has not been reported for the Nighthawk, but was observed in the Nightjar by Lack, 1932.) Following this activity, the male left but the female did not follow until five minutes later. After 32 minutes, she returned to the eggs and remained there. On the previous two evenings, before completion of the clutch, she did not remain near the eggs at night.

No other incubation movements were observed; all nest building

motions being absent or at least not stimulated under the observed conditions.

BEHAVIOR OF THE MALE

Numerous investigators have observed that the male Nighthawk usually roosts a short distance from the female in a tree or on a building. Calling by the male on leaving the roost in the evening indicated that his roost was in a tree within 25 yards of the nest. This calling seemed to arouse other males in the area. Territoriality of the male Nightjar has been described by Lack (1932). In the present study no observations were made during the period of pair formation and establishment of territory, but the territory of the male Nighthawk seemed well defined and clearly outlined by his flight pattern during the hen's period of incubation. He repeatedly utilized the same area in his feeding flights and returned to "boom" near the female on the nest. Another male frequented an adjacent area, and some chasing occurred when either male strayed into the other's territory. One active chase was noted when the adjacent male dived to the nest-site as the owner visited his female.

During the period between the first and second clutches, which presumably was fairly well timed with activities of other females in the area, a larger number of Nighthawks were seen in the territory. Often pairs or triples were observed in chases when both the members of the territorial pair were accounted for. When such birds passed close to the male, he often joined the chase but his actions were never clearly observed. When other birds were high in the sky or at the edge of his territory, the male seemed uninterested.

"Booming" of the male was usually, but not always, restricted to the area of the nest. On two occasions, the number of dives made by the male from the time he left his roost to the time he visited the female was counted. On one evening he performed 32 dives in 40 minutes, and on another, 39 dives in 34 minutes, averaging one dive per minute for the two nights. Shallow dives were often performed away from the nest-site and in some cases, seemed more common at the imaginary boundary of the territory. When the young was able to fly, the male was observed on several occasions to dive at it.

While "booming" may be chiefly aggressive behavior, and occasionally seemed to be directed at intruders in view of the male, a more intense display was witnessed when the investigator was examining the eggs during the female's "off" period. The male approached the building and circled within 20 feet of the investigator, flying with a "wing-clapping" stroke and calling intensely and rapidly: "cho-ic" or "che-wip". The male landed on a nearby roof and made the same call in a milder tone,

until the investigator left. The male flew from the roof with the "cho-ic" call, which soon changed to the usual "peent" call.

Although it has been stated occasionally that the male *Chordeiles minor* assists in incubation, workers who have made detailed observations have not witnessed this (Bowles, 1921; Gross, 1940; Tomkins, 1942; Rust, 1947; Sutton and Spencer, 1949; and Dexter, 1952). In the present case, the male visited the female in late evening. On alighting, he called with a nasal "narr"; the female responded with a rasping "kra-a", or "kra-p." The female immediately took flight and the male soon followed her and did not attempt incubation. This was possibly the result of the investigator's presence, but the male showed few signs of broodiness. The male was seen to feed the young when they were less than a day old, and the surviving young after it fledged. After the first egg of the second clutch was laid, the male fed the young much more often than did the female. The female tolerated the young on the nest with her and was never seen to chase it, but her tendency not to feed the juvenile undoubtedly prevents the latter from molesting the female by "begging" for food while she is incubating. In feeding, the male seemed to "tease" the young by landing and quickly taking flight. When the male flew near the roof on which the juvenile was perched, the latter became very excited, peeped, raised its wings, and ran toward the passing male. The bird did not react to the female in this way, although it sometimes peeped and pecked at her bill. The call of the male seemed most important as a signal to the young of the male's approach. When the young Nighthawk was 28–29 days old, it often chased the male. Also at this age, while perched on the roof awaiting the male, the juvenile flew up and captured insects. These flights became longer as the young matured.

SUMMARY

A study of the incubation behavior of the female Nighthawk was conducted on an exposed nest located on a roof. It was found that on clear days the female oriented her body along the axis of the sun's rays with her head away from the sun. On cloudy days, or when artificially shaded, she did not orient. Her head was more sensitive to the sun than her body and was of greatest importance in maintaining orientation.

Cooling devices of the Nighthawk include panting, facing away from the sun, and fluffing the feathers. The presence of the female cooled the eggs as much as 15° C on a warm day and warmed them as much as six degrees at night.

Movement of eggs and young by the Nighthawk was observed. Movement of eggs was accomplished by means of the bill, feet, and breast

feathers, while young were capable of self-locomotion in response to the female's call during their first day after hatching.

The male assumed responsibility for feeding the young of the first brood while the female incubated the second clutch. Behavior and the early flights of the juvenile are described.

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