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EGG-TURNING BEHAVIOR AND NEST ATTENTIVENESS OF THE ENDANGERED HAWAIIAN GOOSE ON KAUAI

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ABSTRACT: We used infrared video cameras to obtain the first quantitative measurements of the frequency and details of egg-turning behavior in wild Hawaiian Geese or Nene (*Branta sandvicensis*). We recorded a total of 240 hr of video, of which 53.8% was at night, over 7 days at two nests in Kilauea Point National Wildlife Refuge, Kauai, Hawaii. The mean of the two females' daytime egg-turning frequency (1.15 turns/hr) was similar to the value reported for other waterfowl and identical with that of the Canada Goose (*Branta canadensis*), from which the Nene is thought to be derived. One female turned her eggs less frequently at night, a pattern typical of waterfowl, whereas the other did not. The total number of bouts of egg turning per 24 hr averaged 25.7 for one female and 22.7 for the other. Waterfowl almost always turn their eggs by rotating them solely about the long axis, yet one of these Nene rotated one egg (occasionally two) 180° about the short axis during 21% of egg-turning bouts. We observed a combined total of 65 incubation recesses by the two females, of which 16.8% occurred at night. One of the birds took longer recesses and spent substantially more time away from the nest than the other. As on other Hawaiian islands, the Nene on Kauai tended to take recesses more frequently near dawn and dusk. The two females' nest attentiveness differed during the daytime but not when averaged over 24 hr.

The Hawaiian Goose or Nene (*Branta sandvicensis*), Hawaii's only extant endemic goose, is among the most threatened of waterfowl. It was declared endangered by the U.S. Fish and Wildlife Service in 1967. It currently inhabits the islands of Kauai, Maui, Hawaii, and Molokai but is most abundant on Kauai, the only island lacking the introduced Indian Mongoose (*Herpestes auropunctatus*), a significant predator on adults, goslings, and especially eggs of the Nene (Black and Banko 1994). Despite the Nene's being most numerous on Kauai, our knowledge of its biology derives largely from studies of wild populations on the islands of Hawaii and Maui (Banko 1988, Black et al. 1994, Banko et al. 1999). In this study on Kauai, we examine two aspects of incubation behavior—egg turning and nest attentiveness—in two wild Nene that were habituated to people and draw comparisons with previous studies of the Nene and of the Canada Goose (*Branta canadensis*), from which the Nene is thought to be derived (Banko et al. 1999). For all but a few species of birds, such as the megapodes, turning the eggs during incubation is essential for optimal hatching. To our knowledge, no information exists on the egg-turning behavior of the Nene.

On Hawaii and Maui, Nene inhabit grassy shrublands and sparsely vegetated lava flows (Banko et al. 1999). On Kauai, they inhabit mainly lowland pastures and other modified habitats. On Hawaii and Maui breeding productivity is low because diets are limited by insufficient protein and because introduced mammals destroy many nests (Banko et al. 1999). Productivity is higher on Kauai where nutritious food is readily available in managed grasslands and where predators are fewer (Black and Banko 1994). These differences in the islands' habitat might affect nest attentiveness if on the islands of Hawaii and Maui Nene have to take more frequent or longer incubation recesses to eat sufficient food. We evaluated this possibility by quantifying nest attentiveness and incubation recesses of the Nene on Kauai and comparing our data with those from Hawaii and Maui.

METHODS

We monitored the incubation behavior of two female Nene at Kilauea Point National Wildlife Refuge, Kilauea, Kauai, from 26 December 2007 through 3 January 2008. Both females and their mates were hatched in the wild at the refuge. Nene 1 was tending her first nest of the 2007–2008 breeding season; Nene 2 was tending her second nest. The nests were located approximately 100 m apart and within 10 m of refuge buildings frequented by refuge staff and volunteers. The females were thus habituated to people. Both nests were located on the ground beneath naupaka shrubs (*Scaevola sericea*) within about 2 m of grass lawns (seashore paspalum, *Paspalum vaginatum*), where the two Nene and others often foraged. Each nest contained three eggs.

We monitored incubation by placing an infrared charge-coupled device (CCD) video camera near each nest and continuously recording the video signal with a PVR-330 digital video recorder (Bolide Technology Group, San Dimas, CA) after passing the signal through a SuperCircuits electronic time/date stamp. We analyzed the video records with VirtualDub video software. From the birds' behavior and the day length at our study site, we established daytime as the interval from 06:30 to 18:30 Hawaiian-Aleutian Standard Time (HST), which was 6-8 min longer (depending upon the date) than the period from the onset of morning civil twilight until the end of evening civil twilight.

We typically initiated video recording in the morning between 10:17 and 12:23 HST (5 of 7 days) and consequently undersampled the early morning hours, which is when Nene typically take their first daytime nest recess (Banko et al. 1999). Still, our video records encompassed the transition from nighttime to daytime on 4 of 7 days for Nene 1 and on 3 days of 7 days for Nene 2.

Our video equipment was powered by motorcycle batteries that provided <24 hr of power. Therefore, we obtained 17.7 ± 4.7 (standard deviation) hr (range 7.7–22.9 hr) of continuous video per 24-hr day (n = 7) for Nene 1 and 16.0 ± 3.7 hr (range 11.3–22.7 hr) per 24-hr day (n = 7) for Nene 2. We obtained six rather than seven nighttime video recordings of Nene 1 because a battery failed. We recorded a total of 126.7 hr of video for Nene 1, of which 46.1% was daytime, and 113.0 hr for Nene 2 (46.3% daytime). Thus our records are slightly biased toward nighttime.

We quantified nest attentiveness (percent of time spent on the nest incubating), the frequency of incubation recesses (number of recesses per day), the duration of incubation recesses (minutes off nest per recess and total recess minutes per day), and egg-turning frequency (number of bouts of turning per hour of incubation). We present values as means ± standard deviation and compare means by using two-sample t-tests, assuming equal variances and after arcsine-transforming proportions.

RESULTS

Egg Turning

A Nene turns its eggs by standing up, moving backward to the nest's rim, reaching down and hooking the farthest egg with its bill, then drawing the egg backward, thereby rolling it (Figure 1). We videotaped a total of 132 egg-turning bouts by Nene 1, of which 69 (52%) were nighttime bouts, and

Figure 1. The female at nest 1 turning one of her three eggs about its short axis.

105 bouts by Nene 2, of which 43 (41%) were nighttime bouts. Both females avoided turning eggs during rain.

An egg's location within the nest cup relative to the other eggs changed during 7 of 92 bouts (8%, data for both nests combined), as one egg was drawn over another and thereby displaced it. During 42 of 92 bouts (46%) females intentionally manipulated all three eggs. During nine bouts only one egg was manipulated. Yet even when females manipulated only one or two eggs, the unmanipulated eggs usually moved at least slightly. Occasionally we caught glimpses of eggs moving slightly as a female stood to initiate turning. Settling back on the eggs after a turning bout was accompanied by rocking motions and obvious movements of the female's legs as she repositioned herself atop the clutch. It seems likely that these movements also moved the eggs slightly.

The number of minutes that elapsed between a female's return to the nest following an incubation recess and the first time she intentionally turned her eggs did not differ for the two females (t = 0.97, P = 0.34, df = 61) and averaged 26.6 ± 22.3 min (range 2.4–94.4 min). On one occasion, each female departed on a subsequent recess without first turning the eggs. Nene 1 intentionally turned her eggs as soon as she uncovered them after only 5 of 31 recesses (16%); for Nene 2 these numbers were 4 of 30 recesses (13%).

The frequencies of egg turning in daytime were 1.10 and 1.20 turns/hr for Nene 1 and 2, respectively. The nighttime frequency was 1.05 and 0.72 turns/hr for Nene 1 and 2, respectively. Nene 2 turned her eggs more often by day than by night (1.20 versus 0.72 turns/hr), whereas for Nene 1 daytime and nighttime turning frequencies were similar (1.10 versus 1.05 turns/hr). The total number of egg-turning bouts per 24-hr day was 25.7 for Nene 1 and 22.7 for Nene 2.

Incubation Recesses

Before leaving the nest on incubation recess, both females always covered their eggs with a mixture of downy feathers, leaves, and twigs. Nene 1 took significantly longer to cover her eggs than did Nene 2 (58.9 ± 14.3 sec versus 45.2 ± 13.1 sec; t = 3.91, P < 0.01, df = 62), but the difference is small and of questionable biological significance.

We observed a total of 31 incubation recesses by Nene 1, of which 9 were taken at night, and 34 recesses by Nene 2, of which 4 were taken at night. Nene 1 averaged 0.38 recesses per hour of daylight video versus 0.57 recesses per hour for Nene 2. Nighttime recesses averaged 0.13/hr for Nene 1 and 0.07/hr for Nene 2. The pooled number of recesses per daylight hour was 4.7 times the number per nighttime hour. Because our Nene took fewer recesses at night, mean nighttime attentiveness exceeded mean daytime attentiveness (97.0 ± 3.1% versus 82.8% ± 7.2%; t = 6.56, P = 0.001, df=16).

Our Nene took recesses throughout the day but tended to favor either dawn or dusk (Figure 2). Nene 2 took significantly more recesses during the first 4 hr after dawn than at other times of day, whereas Nene 1 took more recesses in the last 2 hr before dusk (Figure 3). Overall, the duration of recesses (Figure 2) was not correlated significantly with time of day in either female (Nene 1, r^2 = 0.03; Nene 2, r^2 = 0.00).

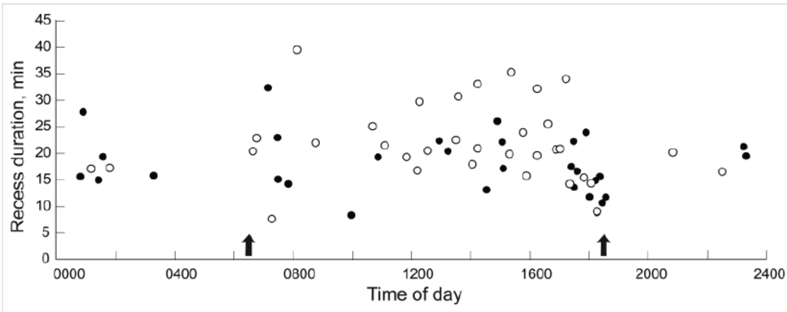

Figure 2. Recess duration versus time of day (HST) for Nene 1 (dots) and Nene 2 (circles) on the island of Kauai. Arrows denote the onset and end of civil twilight.

The duration of daytime recesses ranged from 7.7 to 39.5 min and was significantly longer for Nene 2 (22.4 ± 7.4 min) than for Nene 1 (17.7 ± 5.8 min; t = 2.41, P = 0.02, df = 50). For both females there was no significant difference between the length of nighttime and daytime recesses (Nene 1, t = 0.03, P = 0.98; Nene 2, t = 1.98, P = 0.06).

DISCUSSION

Some species of birds use their feet to turn their eggs (review by Deeming 2002), but in most species, the Nene included, only the bill is used to turn

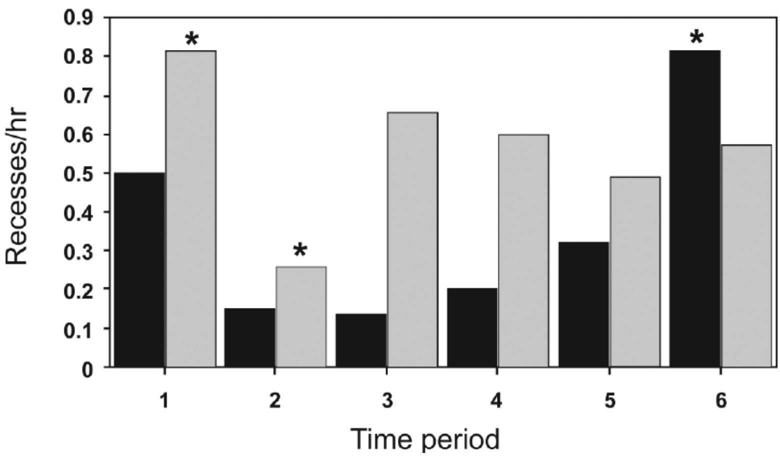

Figure 3. Number of recesses taken per hour of video for the six 2-hr intervals from dawn to dusk (1 = 06:30–08:30, 2 = 08:30–10:30, etc). Black bars denote Nene 1, shaded bars Nene 2. Asterisks denote values lying outside the 95% confidence interval of a given female's mean recess rate.

the eggs intentionally. Birds typically move their eggs by reaching beneath them with the bill and may turn them up to 180° or nudge them only slightly. Eggs may also move when a female changes position on the nest, but these egg movements are generally slight and seem unintentional. By observing natural markings on the eggs, we estimate that Nene typically rotated their eggs about their long axis by a maximum of 90° when turning them. In the Mallard (*Anas platyrhynchos*), the average angle of turn about the long axis when eggs are rolled is 61.2° (Caldwell and Cornwell 1975). Howey et al. (1984) stated that egg rotation in waterfowl is almost always about the long axis. Yet in 21% of bouts we observed, one egg (sometimes two) was rotated 180° about its short axis. Rotation about the short axis may be related to the Nene's relatively small clutch and/or large eggs.

Both females typically prodded the material covering the eggs with their bill a few times before settling on the still-covered eggs after returning to the nest following an incubation recess. The birds removed the material covering the eggs after settling on the nest by scraping backward with their feet while sitting on the nest. Uncovering generally required 2.5–5 min, during which time the females stood two to four times, turned roughly 90°, resettled on the nest, and resumed scraping the eggs' covering away with their feet. While uncovering the eggs, females often adjusted the nest material near their flanks with their bills. Because while being uncovered the eggs were not visible we could not determine if they moved.

The frequency of egg turning in daytime averaged 1.10 turns/hr for Nene 1 and 1.20 turns/hr for Nene 2, values similar to those reported for other waterfowl (Deeming 2002), including the Canada Goose (*Branta canadensis*) (1.2 turns/hr; Kossack 1947), from which the Nene is thought to have evolved (Banko et al. 1999). In three other species of waterfowl, the frequency of turning at night was about half that during the day (Howey et al. 1984). In the birds we observed, the nighttime egg-turning frequency was 95% of the daytime frequency in Nene 1 and 60% in Nene 2.

Incubation Recesses and Nest Attentiveness

Banko (1988) and Black et al. (1994) used time-lapse photography and/or video cameras to monitor incubation rhythms of Nene at Hawaii Volcanoes National Park on the island of Hawaii. In comparing our data with theirs and comparing data for the Nene with those for other geese, caution is warranted because of small sample sizes and differences between first and second nests of the Nene at both locations. At both sites, females spent substantially more total time per day off second nests than they did off first nests as a consequence of taking longer recesses. On Hawaii, they took recesses significantly more frequently (Table 1). On Kauai, the Nene on her first nest took more but shorter recesses than those on Hawaii (Table 1). On Kauai, more frequent but shorter recesses could result in higher average egg temperature and presumably result from foraging sites being nearer to nests on Kauai than at Hawaii Volcanoes National Park.

At Hawaii Volcanoes National Park, Nene took 85% of their incubation recesses during daylight hours, most near dawn or dusk (Black et al. 1994). The birds we observed on Kauai were similar in taking 83% of their incuba-

Table 1 Incubation Recesses of the Nene at Hawaii Volcanoes National Park, Island of Hawaii, and Kilauea Point National Wildlife Refuge, Kauai[a]

	Recess		
	Duration (min)	Number/day	Total time/day (min)
Kauai			
First nest[b]	17.7 ± 5.8	6.1	109.2
Second nest[b]	21.8 ± 7.2	8.2	173.8
Hawaii			
First nests (n = 4)[c]	28.8 ± 5.18	4.0 ± 0.71	112.1 ± 11.4
First nests (n = 5)[d]		3.4 ± 0.81	99.0 ± 25.9
Second nest (n = 1)[c]	18.9	10.7	199.7
Mean of all Nene[e]	24.8	4.4	119
Other geese[f]	19.4 ± 1.3	2.9 ± 2.0	68.5 ± 57.9
Canada Goose[g]	19.0 ± 5.2	3.3 ± 11.4	66.8 ± 40.3

[a]Values are mean ± standard deviation.
[b]Current study.
[c]Nests monitored 1979–1984 (Banko 1988).
[d]Nests monitored during 1991–1993 (Black et al. 1994).
[e]Mean of values above, adjusted for differences in sample size.
[f]Mean of seven species based on 17 studies (Afton and Paulus 1992).
[g]Mean of four races (Afton and Paulus 1992).

tion recesses during daylight but distributed their recesses more uniformly throughout the day (Figure 2). Nene resemble other geese in the duration and number of incubation recesses per day but spent longer away from the nest each day than the average goose, 119 min/day versus an average of 69 min/day for other geese (Table 1). Presumably, warm ambient temperatures in Hawaii permit Nene greater flexibility in their incubation recesses.

In 34 species of waterfowl daytime nest attentiveness ranges from 72.6 to 99.5% (mean 88.1 ± 1.0% standard error; Afton and Paulus 1992). In our Nene, daytime attentiveness averaged 83.3%, well within the range of other waterfowl. Nest attentiveness per 24-hr day averaged 89.9 ± 4.2% for both nests we observed.

Overall, the behavior of our Nene and that of those breeding on Hawaii differed little. Nene spend more time off the nest per day than other geese, which typically breed at higher latitudes (Table 1), but similarities between the Nene and other geese are more striking than the differences.

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