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PREDATION OF A WINTERING MIGRATORY SONGBIRD BY INTRODUCED RATS: CAN NOCTURNAL ROOSTING BEHAVIOR SERVE AS PREDATOR AVOIDANCE?

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Abstract. Many studies have demonstrated the deleterious effects of introduced predators on resident populations of island birds, but few have quantified their effect on the survival and space-use behavior of migratory species. We used radio telemetry to investigate the winter survival and roosting patterns of Bicknell's Thrush (*Catharus bicknelli*) at two sites in the Dominican Republic. Depredation by introduced rats was the only cause of mortality among 53 radio-tagged individuals monitored between January and March over multiple years; five (9%) marked individuals were depredated. Predator trapping revealed the presence of both the black rat (*Rattus rattus*) and Norway rat (*R. norvegicus*) and that the density of rats was higher in broadleaf cloud forest than in nearby pine forest. Some thrushes that used cloud forest exclusively during the day roosted at night in adjacent pine habitat. We suggest that introduced rats exert predation pressure on wintering Bicknell's Thrush in the Dominican Republic and that nocturnal arboreal rat predation could influence the thrush's space-use strategies.

Key words: Bicknell's Thrush, Catharus bicknelli, *Dominican Republic, introduced predators, migratory songbirds, predation,* Rattus, *roosting behavior.*

Depredación durante la Invernada de Aves Canoras Migratorias por Ratas Introducidas: ¿El Comportamiento de Descanso Nocturno Sirve para Evitar a los Depredadores?

Resumen. Muchos estudios han demostrado los efectos negativos de los depredadores introducidos sobre las poblaciones de especies de aves residentes en islas. Sin embargo, pocos han cuantificado sus efectos sobre la supervivencia y el comportamiento del uso del espacio de las especies migratorias. Usamos radio-telemetría para investigar la supervivencia durante el invierno y los patrones de comportamiento de descanso de *Catharus bicknelli* en dos sitios en la República Dominicana. La depredación por ratas introducidas fue la única causa de mortalidad en los 53 individuos marcados con transmisores que fueron monitoreados entre enero y marzo por varios años; cinco (9%) individuos marcados fueron depredados. Las capturas revelaron la presencia de *Rattus rattus* y *R. norvegicus* y que la densidad de ratas era más alta en los bosques siempre-verde de neblina que en los bosques de coníferas cercanos. Algunas aves que utilizaron los bosques de neblina sólo durante el día, descansaron durante la noche en los hábitats de coníferas adyacentes. Sugerimos que las ratas introducidas ejercen una presión de depredación sobre las poblaciones invernantes de *C. bicknelli* en la República Dominicana y que la depredación nocturna por ratas arbóreas podría influenciar las estrategias de uso del espacio de esta especie.

Predator avoidance has been proposed as one of several factors that influence space-use strategies of migratory songbirds on their nonbreeding grounds (Powell 1980). Relatively few studies have investigated the effect of predators on wintering songbirds explicitly, but at least two studies have supported the idea that predation exerts a proximate influence on nonbreeding birds' space-use strategies (Winker et al. 1990, Cuadrado 1997). Other factors influencing nonbreeding birds' use of space include the relative abundance and seasonal patterns of food resources (Johnson and Sherry 2001), intraspecific dominance hierarchies that result in the sexes segregating by habitat (Marra et al. 1993), and interspecific competition (Greenberg 1986).

On Caribbean islands, where native predators are less common than on the mainland (Vitousek 1988), several studies of migrants' ecology have discussed the influence of avian predators on their winter space use and roosting behavior (Latta and Faaborg 2001, Brown and Sherry 2008, Smith et al. 2008). To our knowledge, however, none have evaluated the potential effects of invasive mammalian predators. In the Caribbean, such potential predators include the feral cat (*Felis catus*), Indian mongoose (*Herpestes javanicus*), Norway rat (*Rattus norvegicus*), and the highly arboreal black rat (*R. rattus*). Although the extent of predation pressure on nonbreeding birds can be exceedingly difficult to determine (Sherry and Holmes 1996), many studies of resident populations of island birds have shown the extremely deleterious effects of invasive mammalian predators (e.g., Atkinson 1985, Robinet et al.

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1998, Nelson et al. 2002). Within the Caribbean, several studies have found that introduced mammals depredate nests, fledglings, and adults of both ground-dwelling and arboreal resident birds (Seaman and Randall 1962, Arendt 2000, Townsend et al. 2008). To date, however, there has been no documentation of predation by introduced mammals on overwintering migratory species.

We used radio telemetry to monitor the daily movements, survival, and nocturnal roosting behavior of wintering Bicknell's Thrushes (*Catharus bicknelli*) at two geographically and ecologically distinct sites in the Dominican Republic. Bicknell's Thrush is considered one of the nearctic–neotropical migrants of highest conservation concern (Pashley et al. 2000, Wells 2007), is classified as globally "vulnerable" by the International Union for the Conservation of Nature (BirdLife International 2000), and is experiencing population declines in parts of its breeding range (Campbell et al. 2008, Lambert et al. 2008). Additionally, we used live mark–recapture and removal trapping of rats to collect preliminary data on their relative population densities in different habitats used by Bicknell's Thrush at these two sites. Our goals were to (1) quantify the extent and causes of mortality of radio-tagged Bicknell's Thrushes, (2) quantify nocturnal densities of rats in different habitats used by Bicknell's Thrush, and (3) compare patterns of nocturnal rat density with diurnal movement and nocturnal roosting patterns of Bicknell's Thrush.

METHODS

We conducted radio telemetry at two 10–15 ha sites in the Dominican Republic during four consecutive winters from 2005 to 2008. The two sites are located in the southwestern and northeastern corners of the country, approximately 130 km apart. The southwestern site, Pueblo Viejo (hereafter "PUVI"), consists of primary, undisturbed montane cloud forest, both pine forest and hardwood forest, at 1600–1800 m elevation in the Sierra de Bahoruco (18° 12′ N, 71° 32′ W). The hardwood forest is characterized by a dense understory of vine tangles from trees felled in storms, complete canopy cover with trees reaching heights between 15 and 20 m, and an abundance of lianas and epiphytes (Veloz 2007). The pine forest is composed mainly of tall, straight Hispaniolan pines (*Pinus occidentalis*) with a sparse understory and few vines. At this site, the transition between pine and broadleaf forest is characterized by an abrupt ecotone of mixed forest <25 m in width. The northeastern site, Loma La Canela (hereafter "LOCA"), is located in primary and secondary rainforest at 350–600 m elevation in the Cordillera Septentrional (19° 25′ N, 70° 8′ W). The site is characterized by a more open understory, 85–90% canopy cover with trees 15–25 m tall, and some of the highest precipitation on the island (3000–4000 mm annually) as a result of orographic effects and the prevailing northeast winds (Sanchez and Hager 1997).

We captured Bicknell's Thrushes in 6- and 12-m 36-mm-mesh mist nets, primarily by playback of the species' vocalizations, and fitted all captured birds with 1.2-g radio transmitters (Model BD-2G, Holohil Systems, Ltd.), using the backpack-harness method of Rappole and Tipton (1991). We checked all birds for full leg and wing movement before release. We sexed the birds by DNA extraction and amplification by the polymerase chain reaction (Griffiths et al. 1998). We aged the birds by the shape of their rectrices (Collier and Wallace 1989). Using homing techniques (White and Garrott 1990), we located radio-tagged individuals with Wildlife Materials TXR-1000 receivers and 3-element hand-held Yagi antennas. To determine homing locations we approached the birds quietly and recorded points on hand-held Global Positioning System units (Garmin GPSmap 76) with an average accuracy of ±8 m. We located the nocturnal roosting sites of a subset of birds. We tracked the birds over a 4–6 week period between 1 January and 10 March each winter. We used the Animal Movement extension to ArcView 3.2 to model core diurnal territories with fixed-kernel use distributions (Hooge and Eichenlaub 2000).

We captured rats at PUVI during 2006 and at both PUVI and LOCA during 2008 and 2009. At PUVI in 2006, we deployed Sherman live traps in two sessions, one in January and one in February. Traps were open for three consecutive nights during each session. We placed 25 traps at 25-m intervals in broadleaf cloud forest and adjacent pine forest. Traps were baited with a mixture of oats and peanut butter placed both inside the trap and immediately outside its entrance. Captured rats were ear-tagged with a uniquely numbered aluminum band and released. In February 2008 and February 2009, we deployed 25 snap traps in both pine and broadleaf forest at PUVI and in mid-elevation rainforest at LOCA. Traps were baited with oats and peanut butter, and all dead rats were removed the following morning. In 2008 we trapped at PUVI for two consecutive nights in one pine forest and two cloud forest plots, in 2009 for three consecutive nights in one pine forest and one cloud forest plot. At LOCA we trapped for two consecutive nights in 2008 and four consecutive nights in 2009.

STATISTICAL ANALYSES

We determined trap success of both live trapping and snap trapping, calculating it as the number of animals trapped per number of traps available, corrected for sprung traps (Engeman et al. 2006). We examined proportion of captures as the response, weighted by the total number of traps set, in a generalized linear model (GLM) with habitat type (cloud forest vs. pine forest), trap type (snap vs. live), and date as predictors, specifying binomial errors and logit-link function in JMP v 7.0 (SAS Institute 2007). Nonsignificant effects were removed from the final model. In a separate GLM, we also compared trap success in rain forest at LOCA vs. that in cloud forest at PUVI, again with proportion of captures as the response and habitat as the predictor. There was no evidence of overdispersion of data in either model. Parameter estimates ($\beta \pm$ SE) are presented in logit scale. All other values reported are means ± SD.

RESULTS

Of 53 Bicknell's Thrushes radio-tagged and monitored for at least 30 days during the winters of 2005–2008, we documented the mortality of five (9.4%) (Table 1), all killed by introduced mammalian predators. All depredated individuals were male, and two of the five were juveniles. All other radio-tagged birds survived through the life of their transmitter's battery or the termination of our study. We recovered the carcasses and transmitters of all five depredated thrushes. In each case, physical evidence strongly indicated rat depredation. Four carcasses were found in shallow underground tunnels with openings approximately 5 to 8 cm in diameter from which we excavated their remains (sterna, tarsi, wings, feathers, transmitters). These underground tunnels are widespread at both sites and are known to provide underground refuge for introduced rats (JMT pers. obs.). The fifth carcass was found on the large horizontal limb of a broadleaf tree ~3 m above ground, surrounded by fresh rat excrement.

In a single model with habitat and trap type as predictors, trap success at PUVI was higher in broadleaf cloud forest than in adjacent pine forest ($\beta = 1.8 \pm 0.4$ cloud vs. pine; $\chi^2_1 = 23.5$,

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TABLE 1. Number of Bicknell's Thrushes depredated by introduced rats at a high-elevation cloud-forest site (Pueblo Viejo) and a mid-elevation rainforest site (Loma La Canela) in the Dominican Republic.

Site and year	Birds tracked (n)	Birds depredated (n)	Depredation of tracked birds (%)
Pueblo Viejo			
2005	20	1	5.0
2006	16	3	18.8
Loma La Canela			
2007	4	0	0.0
2008	13	1	7.7
Total			
2005–2008	53	5	9.4

$P < 0.001$) and was higher for snap traps than for live traps ($\beta = 1.1 \pm 0.3$ snap vs. live; $\chi^2_1 = 13.8$, $P < 0.001$). In a separate model comparing cloud forest at PUVI and rain forest at LOCA, trap success at these ecologically and geographically distinct sites did not differ (GLM, $\beta = -0.3 \pm 0.3$ cloud vs. rain; $\chi^2_1 = 1.0$, $P = 0.32$). Mean trap success in cloud forest by live trapping was 12.0% ± 2.9%, whereas in pine forest it was 3.5% ± 2.9% (Fig. 1). Mean trap success in cloud forest by snap trapping was 34.0% ± 7.9%, whereas in pine forest it was 4.6% ± 0.6% (Fig. 1). At LOCA, where we used only snap traps, mean trap success was 39.1% ± 2.8% (Fig. 1.) At all sites and by both trapping methods, we captured both black and Norway rats, but not all workers could distinguish the two species. We cannot, therefore, summarize their relative numbers and do not know which species was responsible for depredating thrushes.

At PUVI during winter 2005, we located nocturnal roosts (n = 75) of 12 individual Bicknell's Thrushes with discrete, minimally overlapping diurnal territories in cloud forest. Of these, nine maintained cloud-forest territories immediately adjacent to the transition to pine forest, so we refer to them as "border individuals." All nine border individuals roosted at least occasionally in the canopies of pines, at estimated heights of 10–15 m. We were unable to pinpoint the location of roosting birds visually, but on the basis of separation of the individuals' transmitter signals these birds appeared to roost singly. During the day, these individuals were never documented in pine forest (>30 diurnal locations per individual). Overall, 68% of roosting locations of border individuals were in pine forest (Table 2). Some individuals roosted exclusively in pine, whereas others roosted in pine as well as broadleaf (individual birds' percentage of roosting sites in pines ranged from 31% to 100%; Table 2). These individuals traveled a mean distance of 62.1 m ± 38.6 to reach roosts in pines. When border individuals were not found roosting in pine forest, they roosted either along the border between pine and broadleaf or within 12 m of their diurnal territories. Two of three individuals whose territories did not border pine forest ("nonborder individuals") and whose roosts we located left their territories to roost in pine forest. One, a first-winter male, traveled an average of 291.6 m to reach its roost in pine forest, and the other, a first-winter female, roosted on 5 of 6 occasions in her core diurnal territory but spent one night in pine forest 120.8 m from her core area. The third roosted in or within 12 m of its diurnal territory. Searching pine forest for the signals of other nonborder individuals produced no detections, and, on the basis of weak signals in the direction of these areas, we assumed that these birds roosted in or near their diurnal territories. We did not, however, track these birds to exact locations because of difficulties of navigating dense cloud forest at night. At LOCA, we found roost sites of three individuals on one night each. All roosts were within these individuals' diurnal territories. Nightly checking from a base camp in human-disturbed habitat adjacent to the forest study plot did not yield detections, only weak signals in the directions of diurnal territories within the forest.

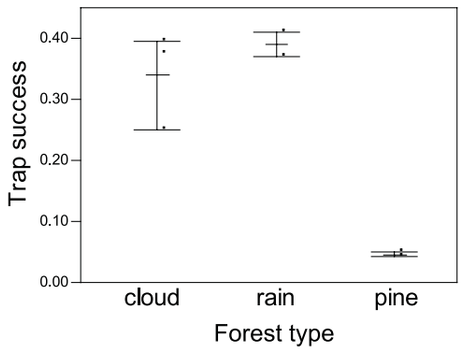

FIGURE 1. Rat-trap success per 100 corrected trap-nights for snap trapping (n) conducted in multiple habitats in the Dominican Republic, 2008–2009. Cloud = cloud forest (n = 3), rain = rainforest (n = 2), and pine = pine forest (n = 2). The middle horizontal bar represents mean trap success; the upper and lower bars represent the maximum and minimum values.

DISCUSSION

To our knowledge, these data are the first to document depredation of a migratory songbird on its nonbreeding grounds by introduced predators. We confirmed depredation of Bicknell's Thrushes in three of four winters of our study. In each incident, the evidence strongly suggests rats as the primary predator, but it is possible that the Indian mongoose was responsible for some of the depredations. We believe this is unlikely, however, for several reasons. First, the mongoose is rare in upper-elevation wet habitats of the Caribbean such as our study sites (Horst et al. 2001), and we never captured any in our traps. Next, we rule out the mongoose as the predator of the thrush found on a tree limb ~3 m above ground because in the Caribbean the mongoose is not known to be arboreal at such heights (Nellis 1989) and because we found rat excrement around the carcass. Further, all excavated tunnels from which we extracted the other four Bicknell's Thrush carcasses are known to be used by introduced rats and had narrow openings (~5 to 8 cm in diameter), unlikely to be large enough for the Indian mongoose, which makes wider burrows in loose soil. Finally, the remains recovered in these holes included sterna and tarsi with some flesh remaining, unlike the wings- and feathers-only remains of a songbird depredated by a mongoose and left in open habitat (Townsend 2006). We believe this evidence indicates rats as the responsible predators in each case. Furthermore, we suggest that on Hispaniola rat populations, which have expanded since introduction ~500 years ago, could reduce winter survival of migrant songbirds such as Bicknell's Thrush and influence their space-use strategies. Little is known about current trends in rat populations on Hispaniola, and our study is the first to monitor Hispaniolan rat populations in cloud forest and rainforest.

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TABLE 2. Number of nocturnal roost fixes, percentage of roosts in pine forest, and distance from diurnal core use areas to roost sites for nine Bicknell's Thrushes with diurnal territories in cloud forest bordering pine forest at Pueblo Viejo, Dominican Republic, 2005–2006. M = male, F = female, HY = hatching year, AHY = after hatching year.

Transmitter	Sex	Age	Roost fixes (*n*)	Fixes in pine (%)	Mean distance from roost to core area ± SD (m)
133	M	HY	12	83.3	46.3 ± 34.5
170	M	HY	6	100	66.6 ± 40.9
106	M	AHY	13	30.8	34.0 ± 3.3
267	M	AHY	10	70	73.7 ± 55.1
437	M	AHY	3	100	98.7 ± 27.3
734	M	AHY	3	66.7	82.8 ± 43.5
938	M	AHY	6	100	60.0 ± 20.4
899	F	HY	2	50	12.0
981	F	AHY	11	36.4	83.3 ± 19.3
All	—	—	66	68.2	62.1 ± 38.6

Our success rate with snap traps in both cloud forest and rainforest (25–41%) is higher than that of studies of introduced rats on islands in the Pacific, which generally report <10% trap success (Tamarin and Malecha 1972, Robinet et al. 1998). Our success rate is comparable, however, to that reported from mid-elevation wet forest in Puerto Rico's Sierra de Luquillo (33–44%), a rate among the highest known (Engeman et al. 2006). This Puerto Rican forest is used by a wide range of migrants, including Bicknell's Thrush (Rimmer et al. 2001).

Although during daylight hours rats may pose little threat to highly mobile and alert songbirds, at night they may be more successful in encountering immobile, roosting individuals. At dusk we frequently observed rats climbing at all vertical levels of the cloud forest and rainforest, from ground level to >15 m. At PUVI the use of nocturnal roosts in pine forest might be a space-use strategy to avoid nocturnally active and highly arboreal rats. At PUVI our rat-population indices show that numbers of rats in broadleaf forest exceed those in pine forest by several orders of magnitude. Pine forest is characterized by tall, straight trees with few lower branches and an open understory, which together may impede arboreal movements of rats. Broadleaf cloud forest, in contrast, is characterized by extensive horizontal and oblique branches and a dense understory of shrubs and vine tangles, features that may facilitate the movement of rats through the canopy. We suggest that birds that maintain diurnal territories in broadleaf forest but roost in adjacent pines may avoid predators.

An alternative to the predator-avoidance explanation is that birds roost nocturnally in a habitat better for thermoregulation (Walberg and King 1980, Merola-Zwartjes 1989), as has been suggested for several species of songbirds wintering in the Caribbean (e.g., Latta and Faaborg 2001, Smith et al. 2008). This possibility is unlikely at our sites, however, where minimum ambient nighttime temperatures in pine forest averaged 1° C lower than in cloud forest, significantly colder (Student's $t_{34} = 2.3$, $P = 0.02$, JMT, unpubl. data). Bicknell's Thrushes that roost in pine forest are therefore moving from the warmer and likely more protected microclimate of dense cloud forest to a colder, more exposed microclimate.

In contrast to the patterns observed at PUVI, at LOCA we did not detect nocturnal roosting by Bicknell's Thrushes outside of diurnal territories, although our data for LOCA are not extensive. There is no pine forest at or near this mid-elevation rainforest site. Neighboring habitats include pasture, shifting agriculture, agroforestry, and regenerating forest in various stages of succession; none of these appeared to provide microhabitats suitable for roosting. It might be that LOCA does not provide an alternative night refuge outside of diurnal territories, with negative consequences for Bicknell's Thrush survival, given that here we trapped rats at a rate as high as in cloud forest at PUVI.

Few other studies have investigated the benefits of habitat-specific roosting behavior on birds' nonbreeding grounds. Although at least four species of migrants wintering in Puerto Rico move from black mangrove (*Avicennia germinans*), white mangrove (*Languncularia racemosa*), and dry forest to night roosts in red mangrove (*Rhizophora mangle*), the proximate causes of this specialization in roosting habitat have yet to be identified (Reitsma et al. 2002, Burson et al. 2005, Smith et al. 2008). Brown and Sherry (2008) found that most Ovenbirds (*Seiurus aurocapilla*) wintering in dry forest in Jamaica roosted within their core diurnal territories and suggested that this even spacing across the landscape could confer an advantage in avoiding predators.

Although many factors influence the population dynamics and space-use strategies of migratory birds on their winter grounds, risk of mortality from introduced and naturally occurring predators should be considered an important potential selection pressure. High levels of predation in certain winter habitats could act in concert with other determinants of habitat quality (e.g., food resources, precipitation, intraspecific aggression, parasite prevalence) to affect winter survival negatively, thereby influencing overall demographics and population viability. Further study of introduced rat populations in multiple habitats on Hispaniola is needed to determine the extent and effects of predation on both migratory and resident birds and the potential for corrective management.

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