PATTERNS OF NESTING MIGRATIONS IN THE TUATARA (*SPHENODON PUNCTATUS*), A COLONIALLY NESTING ISLAND REPTILE

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Abstract: The costs of nesting to female animals can be substantial, and may dictate patterns of nest-site choice. In particular, females that travel longer distances to nest likely incur greater energetic costs and may be at greater risk of losing territories to conspecific competitors. We examined patterns of nesting migrations for a population of Tuatara on Stephens Island, New Zealand, over 5 yr. We found that only about 7% of female Tuatara observed nesting in a rookery also lived in that rookery. Of 140 females for which we had both residence and nesting locations, 42% traveled to a nesting rookery from their residential area. The average distance traveled by these females was 84 m, and travel was directed toward the rookery closest to a female's residence area. Our results demonstrate that female Tuatara on Stephens Island minimize the distance traveled on nesting migrations. We suggest that the patterns in nesting travel we observed in this population may be due to natal philopatry of nesting females, or to females minimizing the costs of nesting-related travel.

Key words: New Zealand; Reproduction; Rhynchocephalia; Stephens Island

Females of many species of reptiles migrate to nesting areas to lay their eggs. Nesting journeys range from brief, short-distance trips to a nesting area near an individual's home range (Macartney and Gregory, 1988) to the transoceanic migrations characteristic of sea turtles (Mortimer and Carr, 1987). Although such nesting-related travel is critical to the reproductive success of a female, it also presents several costs to individuals: females must invest energy in travel (Werner, 1983), nest construction (Rand and Dugan, 1983), and sometimes nest-guarding (Refsnider et al., 2009); females' body condition may decline as a result of not feeding while traveling to nesting areas (Madsen and Shine, 1999); and their vulnerability to predation (Shine, 1980), human exploitation (Suganuma et al., 1999), or incidental human-caused mortality (Haxton, 2000) may increase during migration. In species where only females engage in nesting-related travel and therefore are the only sex to incur these costs, high adult mortality during nesting migrations has the potential to skew sex ratios in reptile populations (Steen and Gibbs, 2004). Therefore, understanding the characteristics and costs of nesting migrations will enhance our understanding of life history traits and population dynamics, and aid conservation efforts by identifying potential risks to nesting females.

Nesting migrations are necessary because the habitat suitable for adults may not be suitable for embryonic and hatchling development. Indeed, thermal and/or hydric characteristics of nest microhabitat affect numerous hatchling phenotypes in reptiles including size (Brown and Shine, 2004), growth rate (Brooks et al., 1991), swimming speed (Miller, 1993), metabolism (Van Damme et al., 1992), predator avoidance behavior (Burger, 1989), and sex (e.g., Cree et al., 1995). To maximize fitness, reptiles must select sites for oviposition that, most importantly, produce surviving offspring, and secondarily produce high-quality offspring (Refsnider and Janzen, 2010). If such sites are not available within a female's activity center, she must travel elsewhere to find them.

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Many reptiles exhibit fidelity to nesting sites they have used in the past (e.g., Valenzuela and Janzen, 2001; Refsnider et al., 2010) and/or natal philopatry, wherein individuals return to nest at the site from which they hatched (e.g., Meylan et al., 1990; Bowen et al., 1992). These strategies may function by maintaining maternal lineages that produce large numbers of high-quality offspring from high-quality oviposition sites (Freedberg and Wade, 2001); occasional mistakes in natal homing would also result in colonization of new nesting habitat, which would foster gene flow and provide alternative nesting sites if previously used sites become unsuitable (Bowen et al., 1989). However, strong fidelity to nesting areas that are no longer suitable for offspring development due to anthropogenic alteration (Kolbe and Janzen, 2002) or that pose high mortality risk to nesting females (Refsnider and Linck, 2012) can create ecological traps. Thus, it is important to understand both the consequences of nest-site choice on female reproductive fitness and the costs to females of making a particular nest-site choice.

We studied a population of Tuatara (*Sphenodon punctatus*), the only extant species in the ancient reptilian order Rhynchocephalia (Hay et al., 2010), on Stephens Island, New Zealand (Marlborough Sounds, 40°40′S, 174°00′E, datum = GCS New Zealand 1949). The island is approximately 150 ha, and rises steeply to an elevation of 275 m along the summit ridge. Between the summit ridge and cliff faces are slopes of 12–38°; these areas were historically covered with dense native forest. Despite its small size, Stephens Island supports a Tuatara population estimated to consist of 30,000–50,000 animals (Newman, 1987). Most Tuatara on the island live in the closed-canopy forest along the summit ridge, where there are abundant invertebrates and seabird eggs and chicks on which they feed (Walls, 1981); the density of Tuatara in the forests on Stephens Island can reach 2700 individuals/ha (Moore et al., 2009a). Some Tuatara also live in lower-elevation open areas that were cleared for livestock grazing beginning in the 1890s (Dendy, 1899). However, the lower availability of food resources in these former sheep paddocks supports a much lower density of Tuatara than occurs in the forests (Gillingham et al., 1995), and Tuatara living in former pastures have higher parasite loads than those living in forests (Godfrey et al., 2008).

Tuatara live in underground seabird burrows and defend small territories against conspecifics (Gans et al., 1984). The spatial structure of territory ownership is highly stable over long periods of time (Moore et al., 2009a), as individuals have low energy requirements (Saint Girons et al., 1980), are very sedentary, and rarely leave territories voluntarily except to nest. Males are larger than females, and aggressively exclude intruding males from their territories (Gillingham et al., 1995), which often encompass the territories of several females (although females also physically attack intruding females; Ramstad et al., 2012). The species is seasonally monogamous, and males mate with a female whose territory overlaps their own; body size is the primary predictor of male reproductive success, with larger males excluding smaller males from most mating opportunities (Moore et al., 2008b, 2009b). Tuatara are known to live at least 60 yr, and lifespans may be closer to 100 yr (Castanet et al., 1988). Females nest every 2–4 yr (Cree, 1994; Newman et al., 1994) in open areas, as soil temperatures in the forests are too low to support embryonic development (Thompson et al., 1996). On Stephens Island, Tuatara nest colonially in rookeries in former sheep paddocks and rock outcrops, but prior to human colonization of the island, nesting habitat was limited to rock outcrops, cliff faces, and tree-fall gaps in the forest. Some females remain to guard their nests for several days against destruction by later-nesting conspecifics (Refsnider et al., 2009). Females also show high fidelity to nesting areas they have used in the past (Refsnider et al., 2010), although whether this results from natal philopatry is currently unknown.

In an intensive study of the nesting ecology of this population, approximately 1400 gravid female Tuatara have been individually marked on nesting rookeries (NJN, personal observation). However, the locations of those females' residence areas, and thus distances traveled to nesting rookeries, are unknown. Regular observations of nonreproductive adult females on nesting rookeries during the nesting season

suggest that some females live in the nesting rookeries throughout the year (Nelson et al., 2004), but it is unknown whether such females live and nest in the same rookery, or whether they travel elsewhere to nest in a different rookery. Our study had two primary objectives. First, we aimed to determine the residence sites of females nesting in specific rookeries, and to estimate the proportion of nesting females that also live permanently in rookeries. For the purposes of this study, we define a female's "residence area" as the area in which the female lives throughout the year, with the exception of a nesting season during which the female reproduces. Second, we wanted to explore patterns in the spatial relationship between females' residence areas and nesting rookeries. Specifically, we tested the following hypotheses: (1) females tend to nest in the rookery nearest their residence area, and females that live in a rookery also nest in that same rookery, and (2) all females living in a given residential area also nest in the same rookery.

Materials and Methods

Data were collected during 2002–2007 from a population of Tuatara on Stephens Island (Takapourewa Nature Reserve, 40°40′S, 174°00′E), Cook Strait, New Zealand. We collected nesting-season locations of female Tuatara during the austral springs of 2002–2006, inclusively. During November and early December in 2002–2006, researchers patrolled seven Tuatara nesting rookeries nightly (Fig. 1; Nelson et al., 2004; Refsnider et al., 2009). Adult female Tuatara were captured by hand and palpated to determine whether they were gravid (e.g., Goodman, 2006). Females determined to be gravid by the presence of shelled eggs in the oviducts were individually marked upon original capture by subcutaneous injection of passive integrated transponders (PIT tags; ISO FDX-B, Allflex), which allowed females to be identified individually when recaptured years later. Occasionally, we captured females that were not gravid at the time of capture, but showed evidence of having recently laid eggs (i.e., their abdomens were distended but empty); these females were also classified as reproductive and were marked. We scanned all females captured on

nesting rookeries, regardless of reproductive status, for the presence of a PIT tag. For all captured females, we recorded individual identity and capture location using a handheld global positioning system (GPS) unit.

Residence locations of females were obtained in two ways. First, during periodic trips to Stephens Island during March and September in 2005–2007 (i.e., outside the nesting season), we captured female Tuatara from both nesting rookeries and nonnesting habitat. All PIT-tagged individuals were identified and their capture locations were recorded using a handheld GPS unit. Residence locations were known for some females that lived in established study plots in the Keeper's Bush forest (Moore et al., 2009b) and in three rookeries (Godfrey et al., 2008). In March 2007 we also expanded our search area by conducting nightly patrols along all established trails on the island (Fig. 1). All female Tuatara encountered along trails and around buildings were captured and scanned for PIT tags, and marked individuals were identified and their capture locations were recorded. Aside from the nesting rookeries, we did not survey any undisturbed areas (such as native forest or cliff faces) for marked Tuatara to avoid damage to the extensive and fragile network of seabird burrows located throughout the island. The second way in which females' residence locations were established was by including records of nonreproductive females captured on nesting rookeries during the nesting season. Because females on Stephens Island nest, on average, only every 2.5 yr (Refsnider et al., 2010), a substantial proportion of the population is nonreproductive during any given nesting season; thus, the locations of nonreproductive females during the nesting season represent residence locations of such females.

We compiled records for all females for which we had both a nesting and a residence location. These locations were plotted on an aerial photograph of Stephens Island using ArcGIS 9.2 (ESRI). For each female, we measured the straight-line distance between residence and nesting locations to determine the minimum distance traveled by females from residence sites to nesting areas. Stephens Island's small size and high elevation
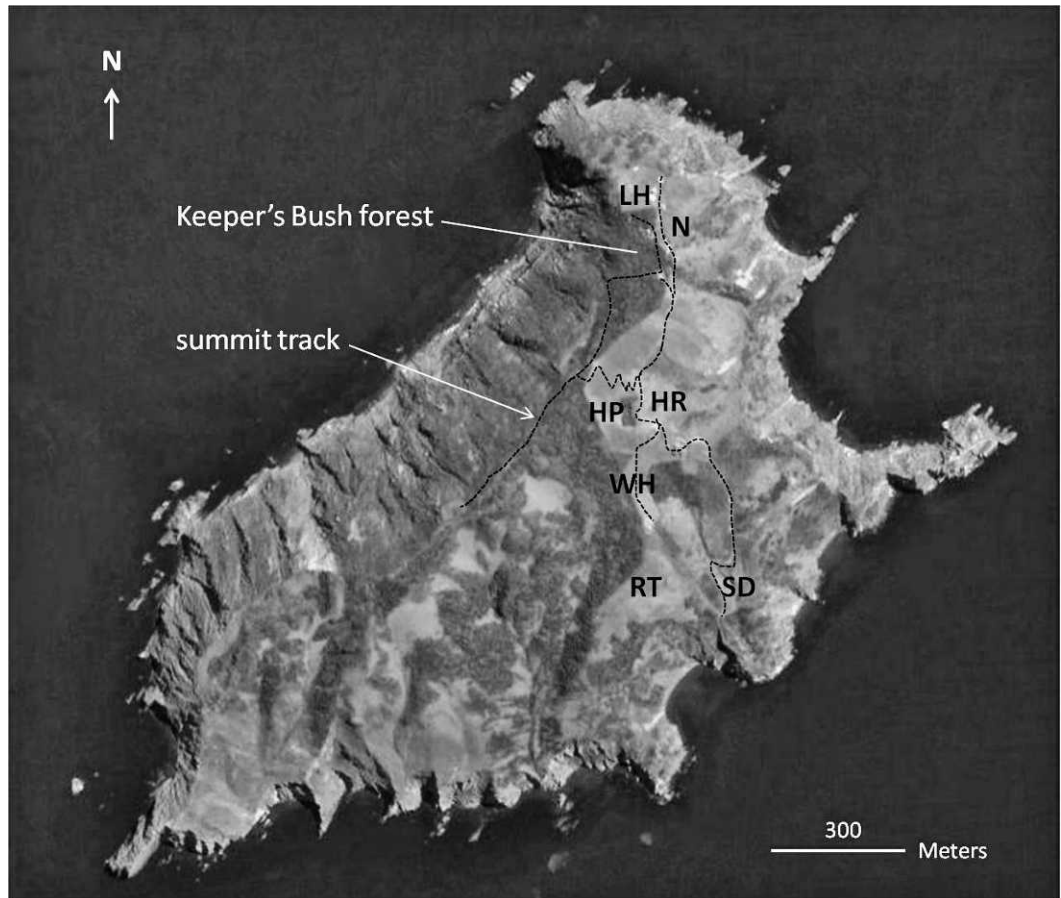
Fig. 1.—Stephens Island (Takapourewa Nature Reserve, 40°40′S, 174°00′E), Cook Strait, New Zealand. Dashed lines are established trails; rookeries are labeled as follows: LH = Lighthouse; N = Nursery; HP = House 3 Paddock; HR = House 3 Road; WH = Winch House; RT = Robyn's Tree; SD = Sand Dunes.

result in steep slopes across much of the island's surface; therefore, we also measured the surface-length distance traveled by nesting females using a 25-m digital elevation model for Stephens Island. Because surface lengths take into account the topography of a landscape, they provide a more accurate estimate of distance when significant topographic features (such as steep slopes) exist.

We tested for directional movement from residence areas to nesting rookeries using Rayleigh tests for circular uniformity with a specified mean direction (Durand and Greenwood, 1958). For this analysis, we standardized the specified mean direction across all females by converting to North (0°) the direction from each residence area to the nearest nesting rookery (as in Streby and Andersen, 2013). Finally, we determined the number of nesting rookeries through which females traveled from their residence location to the rookery in which they were captured when reproductive. Females whose residence was within the nesting rookery in which they were also captured when gravid received a 0 for this measure, females whose residence area was in an adjacent rookery or forest patch to their nesting area received a 1, and females that traveled through one or two rookeries between their residence and nesting areas were assigned a 2 or 3, respectively, for this measure.

TABLE 1.—Nongravid female Tuatara captured in established nesting rookeries during the nesting seasons in 2003–2006, and outside the nesting season in 2007, on Stephens Island, New Zealand.

Rookery	2003	2004	2005	2006	March 2007
House 3 Paddock	8	7	4	8	20
House 3 Road	2	0	4	2	3
Lighthouse	3	1	3	2	0
Nursery	1	1	2	3	6
Robyn's Tree	1	2	1	5	8
Sand Dunes	0	0	0	2	3
Winch House	5	1	4	6	17

RESULTS

We PIT-tagged 1360 reproductive female Tuatara during the nesting seasons in 2002–2006. The total number of individual females nesting on each rookery throughout the five nesting seasons ranged from 31 to 432 ($\bar{X}$ = 192), and tended to increase as rookeries increased in area ($P = 0.07$; $R^2 = 0.51$). Of the 1360 marked females, we identified at least one residence location for 140 individuals (10.3%). We had an average of 1.3 residence locations for each female, and 1.2 nesting locations for each female. Forty-two of these 140 females were captured only during the nesting season, but in both reproductive and nonreproductive states in different years; the other 98 females were captured when gravid during the nesting season as well as in residence locations outside the nesting season (Table 1). We captured 25 females in nesting rookeries both outside the nesting season, as well as during the nesting season but when nonreproductive, indicating that those females do in fact live in nesting rookeries year-round. Therefore, nonreproductive females captured on nesting rookeries during the nesting season most likely lived in the rookery.

Hypothesis 1: Females Tend to Nest in the Rookery nearest Their Residence Area

Of the 140 females for which we had both nesting and residence locations, 81 (57.8%) lived and nested in their nesting rookery, 47 (33.6%) traveled from a residence area to a rookery during the nesting season, and 12 (8.6%) lived in one rookery but nested in a different rookery. However, because our sampling effort was biased toward nesting rookeries during the nesting season, we were more likely to detect females whose residences were in rookeries rather than forests or other areas outside nesting rookeries. Therefore, our estimate that 57.8% of female Tuatara on Stephens Island live and nest in the same rookery probably overestimates the true value. To achieve a more realistic estimate, we calculated the proportion of all females observed nesting in each rookery that also lived in that rookery. This estimate was similar for all seven rookeries and ranged from 3.4% to 9.7% ($\bar{X} = 6.9\%$; Fig. 2).

For those females that traveled to a rookery to nest ($n = 59$), the mean ± SD straight-line distance traveled was 84 ± 64 m (range 17–362 m), and the mean surface-length distance traveled was 86 ± 66 m (range 17–373 m). The mean number of nesting rookeries through which females traveled was 1.0 ± 0.3, indicating that most females that traveled from a residence location to a nesting rookery traveled to a rookery adjacent to their residence area. Indeed, females' movements from residence areas to nesting rookeries were directed toward the nesting rookery nearest a female's residence area ($u_{59} = 4.13$, $P < 0.001$).

Hypothesis 2: Females Living in the Same Residential Area Also Nest in the Same Rookery

Although female Tuatara generally nested in a rookery adjacent to their residence area, and movements to nesting rookeries were directed toward the nearest rookery, not all females living in a given residential area traveled to the same rookery to nest. For example, females that lived in the forest along the summit track traveled to the House 3 Paddock, House 3 Road, and Robyn's Tree rookeries to nest, whereas females that lived in the Keeper's Bush forest nested in either the Lighthouse or Nursery rookeries. Conversely, females that nested in a single rookery came from multiple residence areas. For example, females nesting in the House 3 Paddock rookery had residence areas in the Keeper's Bush forest, the Winch House rookery, the summit track, and the House 3 Paddock itself. Thus, a female's nesting location seemed to be independent of the nesting locations of females living in the same
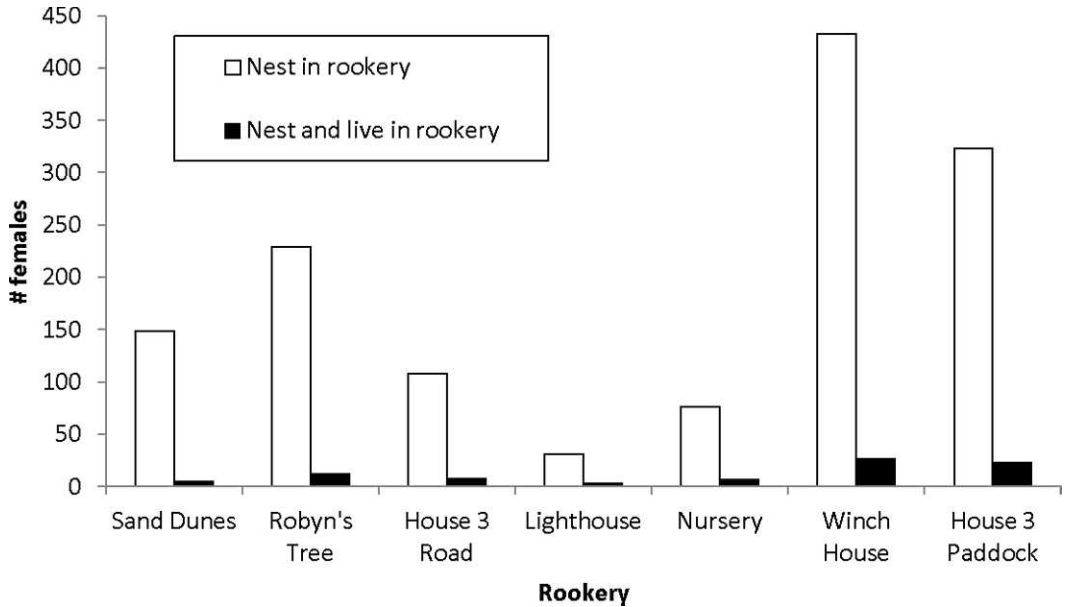
Fig. 2.—Comparison of number of female Tuatara (*Sphenodon punctatus*) nesting only vs. both nesting and living in seven rookeries on Stephens Island, New Zealand. Rookeries are shown in order of increasing elevation.

residence area, and females nesting in a particular rookery came from a variety of residence areas.

DISCUSSION

We examined patterns in nesting migrations of a population of female Tuatara on Stephens Island, New Zealand, over 5 yr. We found that a relatively low proportion (7%) of the Tuatara that nested in seven studied rookeries also lived in those rookeries. Those females that traveled to a nesting rookery generally undertook relatively short nesting migrations by traveling from their residence area to an adjacent rookery to nest. However, females that lived in a given residential area did not all nest in the same rookery, which seems counterintuitive given that females nested in rookeries adjacent to their residential area; therefore females from the same residential area might be expected to all nest in the same rookery. Importantly, residential areas were large and generally adjacent to several rookeries (Fig. 1), and our results suggest that females within a given residential area directed their traveling toward the rookery closest to their home burrow rather than to another

rookery that was also adjacent to their general area of residence. Similarly, females nesting in the same rookery did not all travel from the same residential area.

Our results suggest that some female Tuatara do not engage in nesting travel, whereas those that do travel generally move to the rookery nearest to their area of residence. Tuatara on a nearby island also traveled only very short distances from their home burrow to a nest site (Mitchell et al., 2010), although the short travel distance may be explained by the extremely small size of the island. Why might females travel only short distances to nest, rather than travel to more distant rookeries that might have advantages such as, for example, higher quality or the promotion of increased gene flow? We suggest two alternative hypotheses that may explain the pattern we observed in this study: natal homing by nesting females, or attempts to minimize the costs experienced by nesting females.

First, our observation that females minimized travel by nesting in rookeries adjacent to their area of residence may result from natal philopatry of nesting females. In such a scenario, juvenile females might disperse

short distances from the rookery in which they hatched to a residence area, and then return as adults to nest in their natal rookery. Female Tuatara in the study population are known to show strong fidelity to nesting rookeries they have used in the past (Refsnider et al., 2009), and it is possible that this site fidelity may arise through natal homing. Neither males nor females appear to be philopatric as adults in residential areas (Moore et al., 2008a), but far less is known about dispersal in juvenile Tuatara. Although most of the females that traveled to nest used a rookery that was adjacent to their residence area, a few exceptions were observed where females traveled greater distances during nesting migrations. Occasional individuals that travel greater distances to nest in rookeries farther from their residential areas may foster gene flow and promote outbreeding, which is important in isolated island populations (e.g., Miller et al., 2009).

An alternative hypothesis to explain why female Tuatara travel only short distances to nest is that minimizing travel distances might also minimize costs to nesting females. A specific risk faced by nesting female Tuatara on Stephens Island is the potential loss of their home burrow to conspecifics. Nesting habitat on Stephens Island does not appear to be limited (Nelson et al., 2004), whereas high-quality residential areas may be in greater demand. In forested areas, Tuatara occur at sufficiently high density (up to 2700 individuals/ha; Moore et al., 2009b) that individuals may be resource-limited (Moore et al., 2007). The wide availability of suitable nesting habitat on Stephens Island, along with strong competition for resources in residential areas, may combine to favor females that travel only as far as necessary to reach nesting habitat and then return as quickly as possible to reclaim home burrows in densely populated forest habitat. Indeed, females do not always return to the same home burrow after nesting (Moore et al., 2009a), and if this results from losing a burrow to a competitor while away nesting, females that spend less time nesting may decrease the risk of burrow loss. By nesting in the nearest available rookery, females may also be able to spend less time and expend less energy in traveling to a nesting rookery, and spend more time guarding completed nests against destruction by other females competing for the same nest site (Refsnider et al., 2009). Moreover, by nesting in familiar sites they have used in the past (Refsnider et al., 2010), females minimize time spent searching for suitable nesting habitat, again allowing them to return more quickly to residential areas.

Our results demonstrate that female Tuatara on Stephens Island minimize the distance traveled on nesting migrations by nesting in the rookery closest to their residential area. The patterns in nesting travel observed here may be due to natal philopatry of nesting females, or it may be to minimize the costs of nesting-related travel in this population. Future research should focus on determining whether natal philopatry occurs in Tuatara, and on quantifying the costs of nesting migrations in Tuatara, which could include declines in body condition, increases in parasite loads, and the risk to a nesting female of losing her home burrow to a competitor while she is on a nesting migration.

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