

## DISPERSAL OF NEONATAL GALÁPAGOS MARINE IGUANAS *AMBLYRHYNCHUS CRISTATUS* FROM THEIR NESTING ZONE: NATURAL HISTORY AND CONSERVATION IMPLICATIONS

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**Abstract.**—Neonatal dispersal is an essential component of metapopulation systems, resulting in changes in demography, population dispersion, colonization, and gene flow. We studied the dispersal of neonate Marine Iguanas (*Amblyrhynchus cristatus*) from their nesting zone on Santa Cruz Island, Galápagos. Dispersal patterns appeared to be related to coastal topography, as Marine Iguanas sought out necessary habitat requirements for foraging, refuge, and thermoregulation. We also observed that the dispersal of hatchlings was highly synchronized with the tidal schedule and exposure of algae in the intertidal zone through low tide. The timing of low tide influenced dispersal such that when it occurred at daybreak, early morning, or late afternoon, the iguanas did not disperse. Low ambient temperature (overcast days) and the presence of avian predators also significantly diminished dispersal. We observed 894 (range: 0–128/2h per day) neonate iguanas (both marked and unmarked) dispersing from the nesting zone along the coastline of Santa Cruz for distances sometimes > 6 km. Of the 246 marked iguanas we found outside nesting grounds, > 94% dispersed westward, while only 5% dispersed eastward. These observations indicate that abiotic and biotic pressures may result in trade-offs in how neonates select particular habitats out of their natal area. They also may account for previous reports of the negligible survivorship of some Marine Iguana populations on islands with introduced predators.

**Key Words.**—dispersal; habitat requirements; natural history, neonates; orientation; population

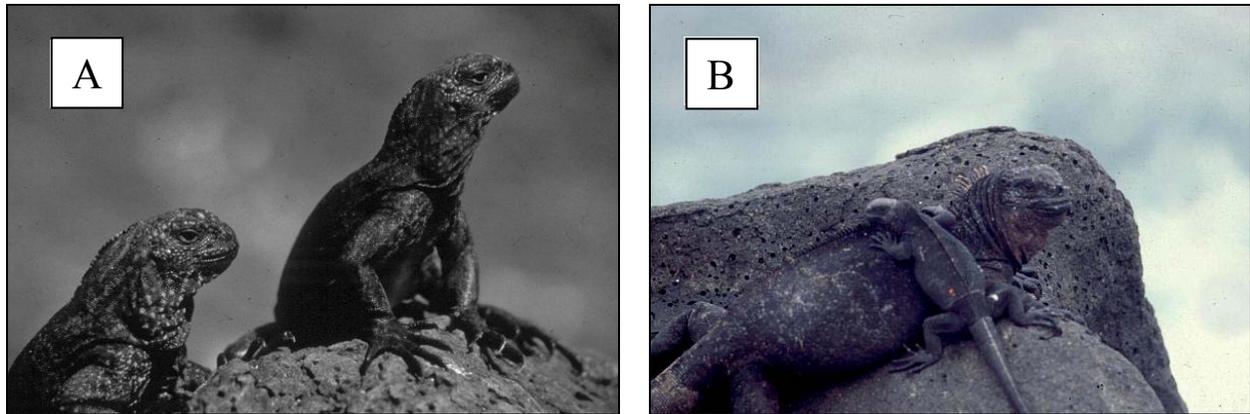
### INTRODUCTION

One of the most important demographic processes influencing species distribution, population regulation, and metapopulation survival is dispersal (Hanski 2001; Heino and Hanski 2001; Ujvari et al. 2008). Its outcome is considered of vital importance in the evolutionary trajectory of natural populations, strongly affecting their gene flow and genetic diversity (Bohonak 1999; Clobert et al. 2001). Natal dispersal, the movement of a juvenile from its place of birth to another location where it will breed (Howard 1960; Kenward et al. 2001), has received considerable attention from an evolutionary and ecological perspective (Clobert et al. 2001; Bullock et al. 2002). Fragmentation of the landscape and global climatic change, with the resulting extinction of species, has made dispersal studies highly relevant in conservation biology (Macdonald and Johnson 2001; Watkinson and Gill 2002; Davis and Stamps 2004; Trakhtenbrot et al. 2005).

Natal dispersal has been observed in a broad range of animal taxa. Mammals and birds have been the most common subjects of dispersal studies (Greenwood and Harvey 1982; Sutherland et al. 2000; Byrom 2002; Le Galliard et al. 2006, 2007). Biologists have studied dispersal to a more limited extent in amphibians (*Rana*

*catesbeiana*, Austin et al. 2003; *Rana temporaria*, Palo et al. 2004; *Ambystoma maculatum*, Montieith and Paton 2006). Most recently, there has been extensive development of theoretical models and empirical studies seeking to identify the ultimate (evolutionary) and proximate (triggering) factors that determine the timing and nature of dispersal behavior in reptiles (i.e., availability of habitat, intra- and inter-specific interaction, and predation; Clobert et al. 2001; Massot et al. 2003; Clobert et al. 2004; Ryberg et al. 2004). The determinants of the movement of reptiles are not yet completely understood (for a review, see Clobert et al. 2001; Mayer et al. 2002; Benard and McCauley 2008). Therefore, among reptiles, lizards have been a particularly studied taxon (e.g., *Uta stansburiana*, Doughty and Sinervo 1994; Doughty et al. 1994; *Sceloporus occidentalis*; Massot et al. 2003; *Niveoscincus microlepidotus*, Olsson and Shine 2003). The most detailed information is available for the Common Lizard, *Zootoca vivipara* (formerly *Lacerta vivipara*; Massot and Clobert 2000; Clobert et al. 1994; Le Galliard et al. 2005; Cote and Clobert 2007).

Here we extend work on the dispersal of lizards by analyzing for the first time the natal dispersal of recently-hatched Marine Iguanas (*Amblyrhynchus cristatus*) from their nesting area in the Galápagos



**FIGURE 1.** A: Neonate Marine Iguanas (*Amblyrhynchus cristatus*) basking in lava rocks. (Photographed by Maryn McFarland). B: A neonatal iguana with color marks on her dorsum. (Photographed by Milton Yacelga).

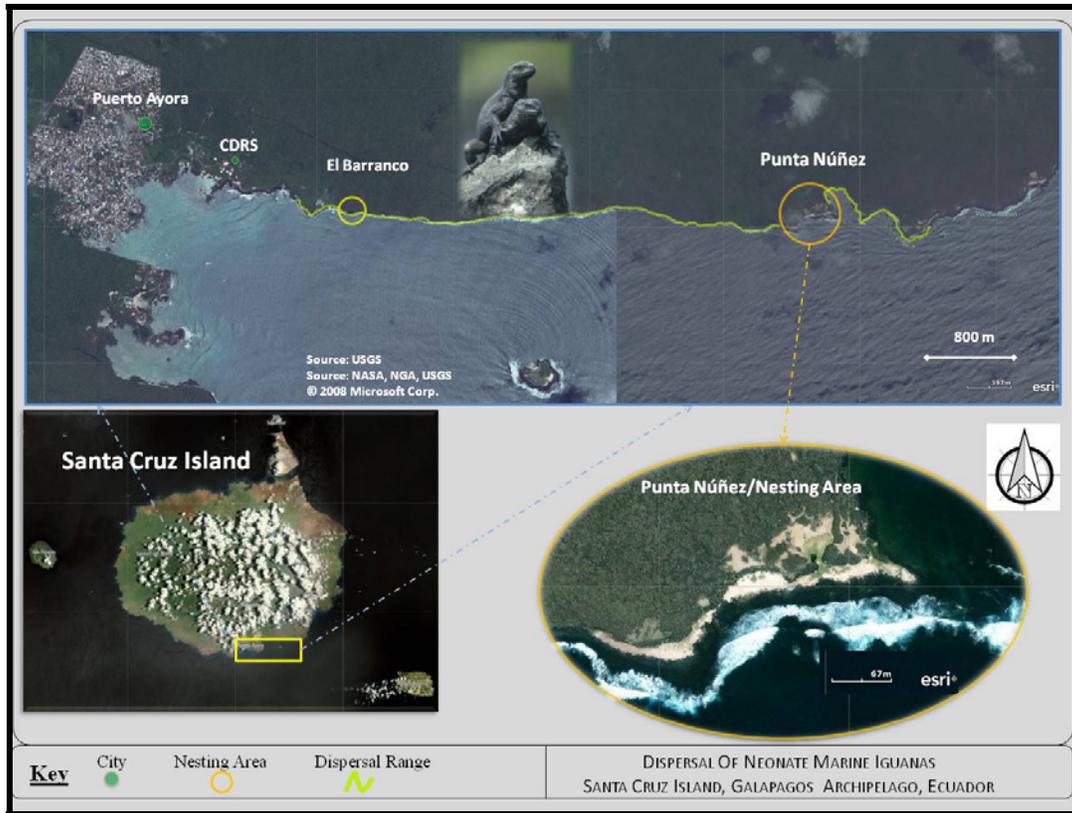
Islands. Marine Iguanas (Fig. 1) occur in patches along the coast on all islands of the Galápagos Archipelago. Their concentration is associated with shallow reefs, algal production, and cliff edges (Boersma 1984). Strictly herbivorous, Marine Iguanas are restricted to day time tidal rhythms to feed on macrophytic marine algae (Wikelski and Hau 1995). Hatchlings and juveniles are restricted in their feeding to intertidal foraging, exploiting exposed algae during low tide while adult animals are subtidal foragers; iguanas swim out on the sea and make several dives to reach the algae at depths of up to 15 m (Wikelski and Trillmich 1994; Wikelski and Hau 1995). Egg-laying takes place about five weeks after mating. Females move to traditional locations for nesting and lay one to six eggs depending on their body size (Boersma 1984). In Santa Cruz hatching can take about four weeks in May and June (Yacelga 1995). Upon emergence, hatchlings run to the nearest cover and eventually they make their way to the shore seeking lava crevices for thermoregulation and foraging (White 1973). Marine Iguanas live along the rocky coastline. During most of the day, they rest on rocks, in crevices, or on top of cliffs up to 60 m high (Wikelski and Hau 1995).

Marine Iguanas are found throughout the Galápagos Archipelago, though their survival is threatened on some islands (Laurie 1983; Cayot et al. 1994). Over the last two decades, observations of marine iguana populations on islands with introduced predators have suggested an alarming imbalance in the structure of the populations due to the lack of recruitment and survival of juveniles, and their growth to reproductive age (Laurie 1983; Cayot et al. 1994). Researchers have attributed the low survivorship of juveniles in these populations to predation by introduced mammals, in particular feral cats (*Felis catus*) and/or feral dogs (*Canis familiaris*; Laurie 1983; Cayot et al. 1994). Rauch (cited in Laurie

1983) and Yacelga (1995) reported nearly no survival of iguanas within a few months of hatching in Punta Núñez, Santa Cruz Island, the study site for the current work. The devastating effects on survivorship of hatchlings led to our present study, which characterizes the neonatal dispersal of a population of Marine Iguanas on Santa Cruz Island. We report results on dispersal rate and the distance dispersed by individual iguanas, as well as the possible factors that might influence such behaviors. To our knowledge, the dispersal patterns of Marine Iguanas have never been reported in the literature before. Our findings provide new insight on the population dynamics and natural history of the species.

#### MATERIALS AND METHODS

We studied the dispersal of hatchlings on the southern coast of Santa Cruz, at Punta Núñez (S. 0.74558°, W. 90.25537°) from May to June and October 1995 (Fig. 2). Because definitions of dispersal include adults breeding at the dispersal site, we define natal dispersal as young leaving their nesting ground > 1 km to new areas to forage and not returning for the length of the study. Santa Cruz, the central island of the Galápagos Archipelago, has the largest human population and many exotic species, including predators such as cats and rats. Punta Núñez, an area of extensive intertidal zones and beaches 6 km east of the Charles Darwin Research Station (CDRS), has excellent nesting areas for Marine Iguanas, totaling approximately 6,000 m<sup>2</sup> on roughly 3 ha, distributed in patches along approximately 600 m of coastline (Figs. 2, 3). We believe that this is probably the most suitable area for nesting on the island. The topography of the coastline from Punta Núñez to the east (approximately 6 km) is characterized by extended areas of flat rocks (Fig. 4A). In contrast, the ground to the

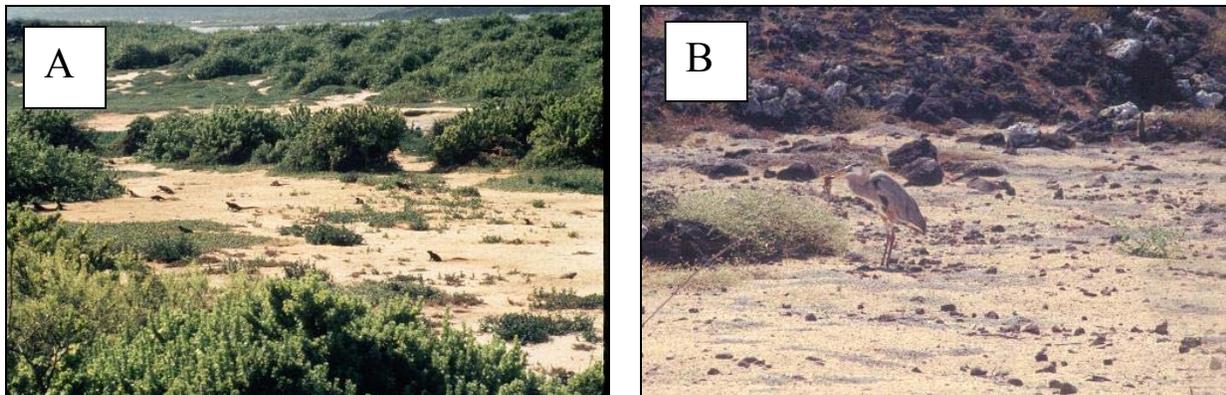


**FIGURE 2.** The study area at Punta Núñez, Santa Cruz Island, Galápagos. The map shows the dispersal direction of neonate Marine Iguanas (*Amblyrhynchus cristatus*) along the coast line and El Barranco as a main dispersal destination. (Neonatal Marine Iguanas photographed by Maryn McFarland).

west, for a distance of 5 km, is characterized by steep cliffs ranging from 5 to 25 m in height (Fig. 4B).

We estimated the population size of recently-hatched Marine Iguanas using mark-recapture technique twice a month during May and June 1995. Each marking period lasted two days, followed by one day of recapture. We walked the intertidal zone from east to west during low

tide searching for neonatal iguanas that were found in groups basking or foraging within the study area. We painted two spots on the dorsum of each animal using harmless waterproof non-permanent paint of different colors during each marking period. We chose this marking technique because it does not harm iguanas and the readily visible mark enable selective recapture,



**FIGURE 3.** A: Female Marine Iguanas (*Amblyrhynchus cristatus*) digging borrows in the nesting area at Punta Núñez (Photographed by Maryn McFarland). B: Great Blue Heron (*Ardea herodias*) eating emerging neonate Marine Iguanas. (Photographed by Milton Yacelga).



**FIGURE 4.** A: View of the extensive intertidal zone at Punta Núñez (Santa Cruz Island, Galápagos) adjacent to the nesting area; the point of initial dispersal of neonate Marine Iguanas (*Amblyrhynchus cristatus*). B: Looking at El Barranco (west-east view) towards Punta Núñez and the coastal topography where Marine Iguanas dispersed. (Photographed by Milton Yacelga).

preventing the over handling of any of the iguanas. Spots did not affect the behavior of the iguanas or the reaction of other animals (avian predators) towards the painted iguanas. We then estimated the number of animals in the population using the Petersen Index, calculated as the number of individuals that we marked initially, multiplied by the total number of individuals we observed (marked and unmarked) during the recapture period, divided by the number of marked individuals observed during the recapture period (Seber 1973). We used this method in preference to more complex methods of mark-recapture population estimation because it is the simplest and most easily interpreted method for the rapid dispersal of neonates observed. We solely wanted to indicate the order of magnitude of changes in the population of neonatal iguanas during both emerging from nesting grounds and dispersing from the study area. During mark-recapture periods, it was not possible to estimate day by day immigration (new hatchlings) and emigration (hatchlings dispersing).

To facilitate the scoring of iguana spatial patterns immediately after hatching, a segment of the beach with a clear vantage point was used to observe lizards. This vantage point allowed observation of the marked

neonates both prior to and at the onset of dispersal (Fig. 4). During and immediately following the hatching season, we determined the dispersal of hatchlings by counting the number of individuals that crossed the beach segment.

For neonatal Marine Iguana, foraging may represent their maximum daily activity, which includes excursions to the sea at low tide to feed on exposed algae. Thus, during hatchling season (May - June), we set up observation periods around the time of low tide. The observation periods averaged 2 h per day (range: 0.5–3.5 h) during which we monitored the activity of neonates and registered the number of individuals crossing the beach segment. The length of each observation depended on the activity level of the iguanas, which varied with weather conditions and the level of the tides. When no individuals were observed dispersing within 30 min, the observation period was terminated. Marine Iguanas restrict their activities during daytime hours because they need high body temperature for physical performance (moving on land or swimming) and efficient feeding in addition to the need of daylight for vision (Wikelski and Trillmich 1994). We made random observations during the peak of dispersal period (21–30 May) to eliminate the possibility of dispersal during high

**TABLE 1.** The number marked, number recaptured, population size estimates ( $\pm$  SE) using the Petersen Index, and density of neonatal Marine Iguanas (*Amblyrhynchus cristatus*) in Punta Núñez, Santa Cruz Island, Galápagos, for four periods during hatching season through May and June 1995.

Dates	Mark-recapture Marked	No. Iguanas Recaptured	No. Iguanas Population Size	Estimated Density/ha
10 May	237	101	544 $\pm$ 40.0	181
25 May	539	214	892 $\pm$ 38.0	297
10 June	195	100	330 $\pm$ 20.7	110
25 June	128	103	154 $\pm$ 5.98	51

and low tide periods during dawn-early morning and twilight, including nighttime hours. The observation time was determined by a concurrent study that included a 24 h observation period of the introduced predators during hatching season of iguanas. While monitoring the dispersal of the iguanas, we observed the activity of potential avian predators, such as the Great Blue Heron (*Ardea herodias*) and the Lava Gull (*Butorides sandevalli*), that either preyed upon neonatal iguanas or prevented their dispersal.

Because we observed recently hatched iguanas dispersing, not only to the west but also to the east, in May and June two observers walked along the coastline from Punta Núñez to CDRS (6 km west) and from Punta Núñez to the east (also 6 km) for 4–5 h during low tide counting the number of recently hatched iguanas (marked and unmarked) within each 200 m section of the study area. We also counted one-year old iguanas (juveniles from cohort of 1994). We counted recently hatched iguanas, marked and unmarked, twice, and one-year old iguanas three times, when the lowest tide was between 0900 and 1100. We made a final count of hatchlings in October 1995 both to the west and to the east of the nesting area.

We used hierarchical multiple regression analysis to determine whether the number of dispersed neonates Marine Iguanas was affected by either ambient temperature or the presence of an avian predator in the dispersal path. Although predator is a categorical variable, we were able to use multiple regressions for this analysis by converting this measure to an indicator variable. We took air temperatures from the meteorological data base of the Charles Darwin Foundation. We also investigated using precipitation but it rained only three days during the study period; thus, the variable was dropped from the analysis. Further, we used Analysis of Variance (ANOVA) with weather (overcast and sunny days) and when an avian predator was present in the dispersal route as factors and the number of individuals dispersing as the dependent variable to assess dispersal rate of iguanas from the nesting area. Marine Iguanas live around cliff edges and shallow reefs, which are exposed to wave action and where algae appear to be more prolific (Boersma 1984). Thus, in the next analysis, we examined the relationship between the number of iguanas we observed dispersing and the height of the cliffs using regression analysis.

Results were considered significant at  $P \leq 0.05$ . We conducted all statistical tests using SPSS version 16.0 for Windows.

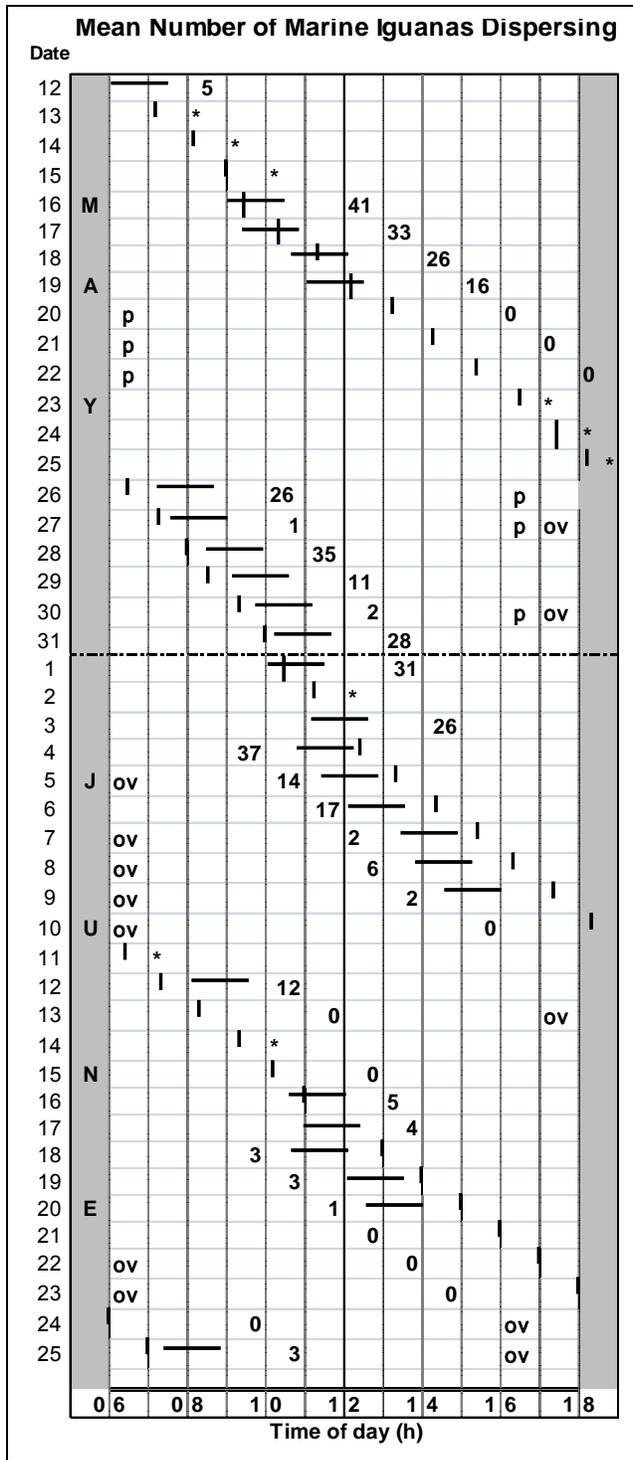
## RESULTS

The highest estimate of population size of Marine Iguana hatchlings was in the second period (25 May), with an estimate of 892 individuals (214 recaptures) resulting in a density estimate of 297 neonates/ha (Table 1). At the onset of the hatching season (beginning of May), the number of hatchlings in the nesting area gradually increased to a peak at the end of May, followed by a rapid decline (Table 1). By the end of June, the population was estimated at 154 individuals (51 neonates/ha), which represented 17% of the estimated population of Marine Iguanas in the nesting area 25 May.

During 36 days of monitoring hatchling iguanas in Punta Núñez, we observed dispersal of neonates within two days of the start of the hatching season, on 10 May. Of the marked hatchlings that dispersed, 95% moved to the west and 5% dispersed to the east, although not by more than 1 km. We recorded 894 (marked and unmarked) iguanas crossing the beach, moving from the area of greatest concentration of iguanas that hatched, which was east of the beach (Fig. 4A). By October, 98% of hatchlings moved completely out of the nesting area.

We observed neonate iguanas dispersing in synchrony with the timing of low tide. Hatchlings left the nesting area around low tide during the daytime, with the prime dispersal period beginning 2 h before and ending 2 h after the low tide. Of 894 dispersing neonates, 626 (70%) dispersed when the low tide occurred between 1000 and 1200. When low tide occurred early in the morning (between 0600 and 0800), iguanas dispersed mostly during the second half of the low tide (90 individuals; 10%). When low tide occurred after 1300, the hatchlings dispersed during the first half of the low tide period (178 individuals; 20%; Fig. 5).

Temperature accounted for a significant effect on the number of neonate iguanas dispersing ( $F_{1,34} = 6.59$ ,  $P = 0.015$ ,  $r^2 = 0.16$ ). When the avian predator variable was entered into the regression model after temperature has been factored in, the predator variable did not have a significant effect on dispersal beyond the effect of temperature ( $F_{1,33} = 1.80$ ,  $P = 0.190$ ,  $r^2 = 0.21$ ).

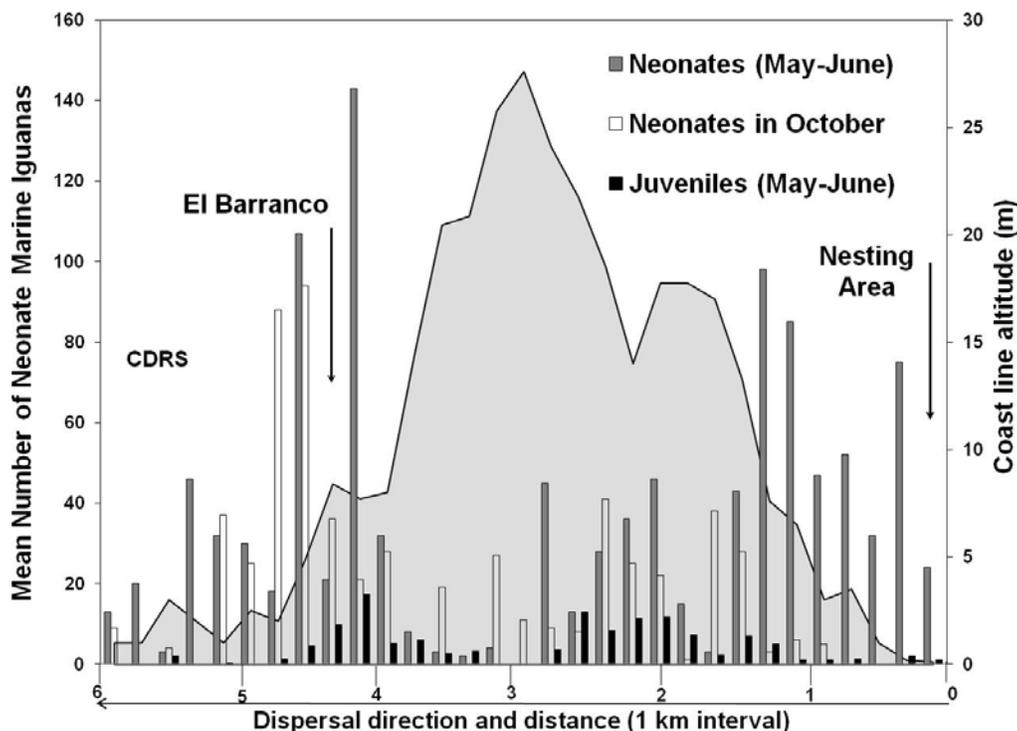


**FIGURE 5.** Actogram showing the dispersal activity of hatchling Marine Iguanas (*Amblyrhynchus cristatus*) from Punta Núñez, Santa Cruz, during May and June 1995. Numbers indicate the mean number of individuals dispersing/h. Consecutive days are arranged from top to bottom. Vertical lines show the time of low tide. The symbol “\*” indicates no observation made. Abbreviations “p” and “ov” indicate predator present and overcast days respectively. Horizontal lines across the line of time of low tide indicate when the majority of dispersal took place; that is, before, during, and after low tide.

However, the predicted power with predator in the model went up from 16% to 21%. Time periods with low temperatures and overcast skies dramatically reduced the number of hatchlings dispersing from the nesting ground to the west. Although avian predators did not show predictive power in the analysis, perhaps because predators were in the dispersal path only in six days, the outcome of dispersal in those specific days was influenced to a degree (Fig. 5). Further, we found a significant reduction in the intensity of dispersal on overcast days from the level of dispersion on sunny days ( $F_{1,21} = 6.32, P = 0.02$ ). There was a significant reduction when an avian predator was present ( $F_{1,21} = 408.0, P = 0.05$ ). The collective effect of these factors was clear at the peak of the hatching season (the end of May and the beginning of June). On 26 May (a sunny day), for example, the mean number of individuals dispersing was 26, whereas on 27 May (an overcast day), the mean number was only one. The next day, when it was sunny, the mean number of dispersing iguanas increased to 35 (Fig. 5).

A Great Blue Heron was present in the nesting zone on 30 of the 36 days of observation. On 15 of those 30 days, we observed the heron eating hatchling iguanas. Predation usually occurred within the nesting zone. On one occasion, we saw the bird eat five hatchlings in one bout upon emergence from the nesting ground (Fig. 3). However, when the predator was in the surrounding rocky areas by the dispersal route, feeding was more difficult. Lava Gulls were occasionally present during the observation period. Although we never saw them attacking iguanas, their presence in the dispersal route reduced the dispersal of iguanas.

Of the 246 marked iguanas (from the four mark-recapture periods) we found outside the Punta Núñez nesting zone, 233 (95%) migrated to the west and only 13 (5%) migrated to the east. We observed no iguanas farther than 1 km to the east. Neonates dispersed long distances towards the west, and many did so very rapidly. For example, within two days of the second marking period, in which we marked more than 500 hatchlings at Punta Núñez, we found 90 outside the nesting area, some up to 3 km away. We observed one individual 6 km to the west (at the CDRS dock) on the sixth day after marking at Punta Núñez. We received additional reports of marked iguanas in the Puerto Ayora, outside the Galápagos National Park (GNP), 7 km from Punta Núñez (Fig. 2). During the counts we made along the 6 km of coastline from Punta Núñez to CDRS, we observed a large number of hatchlings distributed along the lava reef at the foot of the cliffs, with the greatest concentration at kilometer marker one and at El Barranco (Figs. 2, 6). Both areas are characterized



**FIGURE 6.** Mean number of hatchling (1995 cohort) and juveniles (1994 cohort) Marine Iguanas (*Amblyrhynchus cristatus*) observed over 200 m intervals along the coast as a function of distance from Punta Núñez (PN) and CDRS (6 km) and cliff's altitude. Additionally the graph includes the number of hatchling Marine Iguanas (1995 cohort) taken during a final observational period in October 1995. The graph shows El Barranco and kilometer marker one as areas with high concentration of dispersed iguanas.

by medium high cliffs (6–9 m). Few individuals remained in the nesting zone after five months of hatching. The one-year old iguanas (the 1994 cohort) showed similar distribution patterns, but with even fewer individuals within the nesting zone at Punta Núñez (Fig. 6). We found no significant relationship between the number of neonate iguanas observed and the height of the cliffs ( $F_{1,29} = 3.80, P = 0.06, r^2 = 0.11$  and  $F_{1,29} = 3.45, P = 0.07, r^2 = 0.10$  for juveniles, 1994 cohort). The final count of recently-hatched iguanas in October 1995 reconfirmed that the distribution of the iguanas along the coastline was not related to the height of the cliffs ( $F_{1,29} = 0.02, P = 0.90$ ).

### DISCUSSION

Although the population size estimates may not be precise, they indicate the order of magnitude of the change in population size of neonates from the beginning to the end of the hatching period in the vicinity of the nesting ground. The differences in population estimates among the mark-recapture periods are clear evidence of the influx of neonates from the nesting grounds and their eventual exile from the study area. Recruitment and dispersal of iguanas within

marking periods resulted in population size estimates that were somewhat unreliable. Punta Núñez evidently cannot support the large number of iguanas that hatch there; the dispersal of hatchlings seems to indicate an adaptive response to the lack of local resources (i.e., food, refuge), with dispersal presumably increasing survivorship. The extent of dispersal of neonatal Marine Iguanas in our study varied with thermal environment, both in time and in space. In terms of time, dispersal was restricted to ocean tides. Our observations suggest that the timing of the low tides is a factor that constrains neonatal Marine Iguana daily dispersal, causing hatchlings to synchronize their foraging with their subsequent departure from the nesting area. Our results agree with Wikelsky and Hau (1995) who suggested that Marine Iguanas have an endogenous nature of foraging rhythms. That is, iguanas walk to their foraging grounds in a rhythm highly correlated with times of low tide. In the daytime, perhaps anticipating the low tide, neonates likely leave their crevices to thermoregulate before venturing into the intertidal zone to forage on more or less exposed algae. Immediately after foraging in the cool and wet intertidal zone and post feeding thermoregulation, neonates leave their basking rocks and start dispersing.

The synchronization of foraging and dispersal during low tides appears to have adaptive advantages. Natal dispersal is energetically expensive (Dufty and Belthoff 2001). Thus, neonates that disperse within a day or two of hatching need to acquire energy that would enhance their physiological performance at the time of departure (i.e., speed, avoidance of predators, and endurance while traveling).

The preferential dispersal during low tides between midmorning and early afternoon (e.g., 1000–1400) may provide advantages to hatchlings in terms of the digestion of food and energy intake before dispersal. Marine Iguanas depend on high body temperatures 36.7 °C, even under cool air temperature of 32 °C (Wikelski et al. 1993), for efficient feeding and physical performance during feeding. Trillmich and Trillmich (1986) suggest that iguanas may have insufficient time to warm up before foraging on early morning low tides or after foraging on late evening low tides. In addition, it may be important for iguanas to re-warm after feeding to attain efficient digestion (Wikelski and Trillmich 1994; Wikelski and Hau 1995) and for neonates in particular, to trigger their dispersal. Dispersal occurs during times periods when high temperatures prevail (resulting in a  $T_b > 33$  °C). Yacelga (1995) determined significant differences in body temperature of neonates while basking (33.8 °C) and at the onset of dispersal (37.0 °C). These physiological requirements appear to explain why neonatal Marine Iguanas restrain their dispersal to specific hours of the day. Moreover, they also seem to explain the drastic reduction in the number of individuals dispersing during low temperatures and overcast days.

In terms of space, the rapid and directionally oriented dispersal distributes neonates widely over suitable habitats throughout the area of dispersal (approximately 7 km). The differences observed with respect to the direction and distance of dispersal strongly suggest that topographical features resulted in a largely unidirectional dispersal. To the east, the coastline is low and rocky, with extensive intertidal zones (approximately 40–70 m at low tide), very similar to the nesting zone. During low tide, hatchlings have to search out exposed algae, which is not abundant in flat areas (Wikelski and Trillmich, 1994; Milton Yacelga, pers. obs.), exposing the animals to predation. To the west, an area with steep cliffs ranging from 5 to 28 m in height, algae is abundant and close to the iguanas' basking areas and refuges. However, we did not find a significant relationship between number of neonate iguanas and the height of the cliffs. We hypothesize that neonates and adult iguanas may prefer moderate-size cliffs that are not too tall, such as the ones observed in the dispersal route between kilometer markings two and four, which measure 13–28 m in height. It seems mid-size cliffs with low reefs, such as the ones found at El Barranco and near the kilometer

marker one, offer the most suitable habitat. Another explanation for this apparent lack of relationship was the time constraint for the counts during low tide when neonates were not observed found foraging or basking. For example during counts on a hot day, neonates were already under shades after they had foraged. Thus, we have not counted all individuals present, which may have led to an underestimate in the number of iguanas on the higher cliffs.

Wikelski and Trillmich (1994) suggest that foraging on steep rocks or at the front of reefs permits small iguanas to maintain their body temperatures. This allows them to forage for a greater time period than if they were on a flatter area of the intertidal zone where the energetic cost/walking distance is 75% higher than swimming (Gleeson 1979). The distribution patterns of hatchlings and one-year old iguanas suggest that the height of the cliffs may not be a critical factor in the dispersal patterns. We nevertheless noted that the cliffs at El Barranco and at the first kilometer marking do not have nesting areas, yet they offer habitat patches appropriate for the regulation of temperature, protection from predators, and they are easy for foraging during low tide. Yacelga (1995) determined 57% survivorship of neonate iguanas at El Barranco nine months after hatching compared to 5% in Punta Núñez. Additionally, individual body mass and size is significantly higher at El Barranco compared to iguanas at Punta Núñez. It is likely then that the distribution is related to the presence of good foraging areas in the intertidal zone in close proximity to warming sites and refuges. Burghardt et al. (1977) pointed out that the directed dispersal of Green Iguanas (*Iguana iguana*) in Panama, which shows a similar pattern to the dispersal of Marine Iguanas, is a response to ecological conditions, with rapid movement of young iguanas from a region with a high risk of predation to a more secure habitat with more abundant resources.

The majority of intensive ecological studies of Marine Iguanas in Galápagos have taken place on islands with abundant forage and with adequate refuges from predators (Wikelski and Trillmich 1994; Wikelski et al. 2001). Therefore, there are no factors that would prompt an immediate dispersal away from the nesting zones. On the small island of Caamaño, where Marine Iguanas are numerous and widely distributed throughout the islet, there is an abundance of food and we have observed hatchling iguanas moving among the various areas of iguana concentrations (Milton Yacelga, pers. obs.). This suggests that other factors stimulate these movements. Olsson and Shine (2003) suggested that mode of reproduction may contribute to dispersal patterns. Females of oviparous species often travel significant distances to locate nesting areas. As a result, offspring may be born in unsuitable habitat, and therefore will have to travel to locate more suitable areas. The

availability of nesting sites may be a limiting factor in Santa Cruz, where favorable laying sites are scarce on the predominantly rocky coast. Therefore, the majority of females move from the areas they inhabit during most of the year to their nesting locations.

Finally, our results indicate the effect of both abiotic (air temperature) and biotic (avian predators) factors and their interaction constraining the daily onset of dispersal by neonatal iguanas. Low air temperature (overcast days), crucially influenced dispersal (reducing mean dispersal rate, in some days, close to zero), suggesting that optimal temperature range in Marine Iguanas has a major influence on the relative performance of the physiological system (e.g., locomotor ability, foraging, and predator avoidance; White 1973; Wikelski et al. 1993). To our knowledge, our observations of neonatal dispersal in Marine Iguanas have not been documented in the literature before. Our findings suggest that further research is warranted to fully understand the selective pressures that favor dispersal in our studied population. Future research should include studies of the movement of adults (i.e., breeding dispersal) on different islands, both with and without introduced predators. This is particularly important because the dispersal we found in this study not only influences the overall population dynamic of the species and helps us understand the natural history of the species, but also has implications for the conservation of Marine Iguanas, and for the better management of these and other threatened populations.

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