

Influence of nest location and yolkless eggs on the hatching success of leatherback turtle clutches in French Guiana

Stéphane Caut, Elodie Guirlet, Pascal Jouquet, and Marc Girondot

Abstract: The hatching success of leatherback turtles, *Dermochelys coriacea* (Vandelli, 1761), is influenced by heterogeneously distributed ecological factors. However, the hatching success according to nest-site selection has rarely been studied and little is known about the role of nest-site selection and infertile (yolkless) egg production on the predation rate and development of fertile eggs in leatherback turtle nests laid in French Guiana. A field study of 99 leatherback turtle nests was conducted to quantify the relationships between hatching success and (i) the nest-site selection (i.e., vegetation line, sea tide line) and (ii) the infertile eggs, especially their state after incubation (i.e., hydrated or dehydrated) and their effects on predation rate. We found that hatching success on this beach was very low (38.2%). This study illustrates that nest-site selection influences the predation rate and the dehydration of yolkless eggs, while the production of yolkless eggs by leatherback turtles has consequences on nest success. The proportion of yolkless eggs in the clutch, as well as their status at the end of incubation (hydrated or not, preyed upon), correlates with predation rate, development of yolked eggs, and hatching success. There was a significant relationship between nest location (relative to high tide line and vegetation line) and both the predation rates of eggs and the percentage of dehydrated yolkless eggs within a clutch. The production of yolkless eggs was related to hatching success and supports the hypothesis that yolkless eggs have a positive effect on the future of the clutch.

Résumé : Le succès de l'éclosion chez la tortue luth, *Dermochelys coriacea* (Vandelli, 1761), est influencé par la distribution hétérogène des facteurs écologiques. Cependant, le succès de l'éclosion a rarement été étudié en fonction de la sélection du site de ponte et peu de choses sont connues sur le rôle du choix du site de ponte et des œufs infertiles (sans jaune) sur le taux de prédation et le développement des œufs fertiles dans les nids de tortue luth pondus en Guyane française. Une étude de terrain s'est déroulée sur 99 nids de tortue luth pour quantifier les relations entre le succès de l'éclosion et (i) la sélection du site de ponte (c.-à-d., ligne de végétation, ligne de marée) et (ii) les œufs infertiles, spécialement leur état après incubation (c.-à-d., hydraté ou déshydraté) et leurs effets sur le taux de prédation. Nous avons trouvé un très faible taux de réussite de l'éclosion sur cette plage (38,2 %). Notre étude montre que la sélection du site de ponte influence le taux de prédation et la déshydratation des œufs infertiles, alors que la production de tels œufs infertiles chez la tortue luth a des conséquences sur le taux de réussite du nid. La proportion d'œufs infertiles dans la ponte, comme leur état à la fin de l'incubation (hydraté ou non, détruits par prédation), sont corrélées avec le taux de prédation, le développement des œufs fertiles et le succès de l'éclosion. Il y a une relation significative entre la position du nid (en rapport avec la ligne de marée haute et la ligne de végétation), d'une part, et le taux de prédation des œufs et le pourcentage des œufs infertiles déshydratés à l'intérieur de la ponte, d'autre part. La proportion des œufs infertiles est reliée au succès de l'éclosion, ce qui est en accord avec l'hypothèse qui veut que les œufs infertiles aient un effet positif sur le sort de la ponte.

Introduction

Hatching success for organisms that lay eggs in a nest is believed to be influenced by a number of interacting ecological factors, which include temperature, moisture, and water salinity. To improve the nest microclimate, animals can select particular locations, thereby modifying the properties of the nest (e.g., gecko, Bragg et al. 2000; insects, Korb and Linsenmair 1998; Mallon et al. 2001; birds, Reid et al. 2000; Giese and Cuthbert 2003; and spiders, Bilde et al. 2002). Nest-site selection has been studied in various reptiles, particularly sea turtles. A wide range of biological, chemical, and physical factors have been reported to influ-

ence the location of successful sea turtle nests, including oxygen and salinity level (Ackerman 1980); moisture content (Mortimer 1982; McGehee 1990; Bjorndal and Bolten 1992); temperature (Stoneburner and Richardson 1981; Mrosovsky et al. 1984); sand texture, type, and density (Mortimer 1982; Horrocks and Scott 1991; Cardinal et al. 1998); artificial lights on the beach (Salmon et al. 1995); or beach topography (Hays et al. 1995). The distance of the nest to the supra-littoral vegetation and to the high tide line may also be important ecological factors that influence nest-site selection (Hays et al. 1995; Wang and Cheng 1999; for more information see Bjorndal and Bolten 1992).

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The forces governing nest-site selection by sea turtles are still not fully understood. Nest-site selection may have consequences on nest success (i.e., development and predation rate of embryos) or on emergence and survival of newborn turtles. For example, flooding of nests by sea water leads to egg mortality from suffocation (Whitmore and Dutton 1985) and (or) chloride toxicity (Bustard and Greenham 1969); alternatively, hatchlings that emerge far above the high tide line may take longer to reach the sea, may be unable to find the sea at all, or may be more susceptible to predation on the beach (Mrosovsky 1983; Horrocks and Scott 1991). Moreover, nests excavated among supra-littoral vegetation may suffer high egg mortality as a result of roots invading the egg chamber (Leslie et al. 1996). However, Horrocks and Scott (1991) showed that the hawksbill turtle (*Eretmochelys imbricata* (L., 1766)) may prefer to nest among the vegetation, a strategy tentatively accounted for by the fact that vegetated nest sites were less compacted than non-vegetated ones and had a higher hatchling escape success rate. Predators of sea turtle nests include dogs, birds, rats, lizards, frogs, crabs, and insects (Brown and Macdonald 1995; Baran and Turkozian 1996; Broderick and Godley 1996; Leslie et al. 1996; Broderick and Hancock 1997; Yerli et al. 1997; Baran et al. 2001; Maros et al. 2003); predation rates may also vary according to the location of the nest.

Many leatherback turtle nests are often prone to erosion and flooding by the tide (Mrosovsky 1983; Eckert 1987). Consequently, mean nest success of leatherback turtles ranges 20%–70%, depending on the year, the beach, and the method used to evaluate nest success (Whitmore and Dutton 1985; Girondot et al. 1990; Leslie et al. 1996; Sarti et al. 1996; Spotila et al. 2000; Bilinski et al. 2001; Bell et al. 2004). Moreover, leatherback turtle clutches have a higher frequency of eggs without yolks, commonly referred to as yolkless eggs, than other sea turtle clutches. Leatherback turtle clutches contain, on average, 58–114 yolked eggs and 21–56 yolkless eggs (Leslie et al. 1996; Bell et al. 2004; Maros et al. 2003). These yolkless eggs are smaller than fertile yolked eggs, almost exclusively contain albumin (Pritchard 1971), are thin-shelled and irregular in shape, and are generally the last of the eggs laid in a clutch. The role or function of yolkless eggs in leatherback turtle nests is not well understood, but they may provide some selective advantage by improving the hatching success of the viable eggs (Whitmore and Dutton 1985).

In this paper, we investigated the possible relationship between nest-site selection of leatherback turtles and hatching success. Additionally, we investigated the possible influence of yolkless eggs on hatching success and on the protection of yolked eggs from predation.

Materials and methods

Study site and species

Research was carried out on the Awala Yalimapo beach in French Guiana (5°45'N, 53°57'W), located within the Amana Nature Reserve, on the inshore plain of coastline between the Mana and the Maroni rivers. The beach is 4 km long and varies from a few metres to 20 m wide, depending on the tide line. For this study, we chose a 300 m long section of beach that was sufficiently frequented by turtles but also sufficiently distant from sites visited by tourists.

The beach of Awala Yalimapo has one of the highest nesting densities of leatherback turtles, with about 30%–40% of the world's population of nesting females and approximately 50% of all leatherback turtles nesting in the region of French Guiana and Suriname from March to August (Girondot and Fretey 1996; Fretey and Lescure 1998; it should be noted that the exact proportion varies according to the year). The high concentration of eggs on Awala Yalimapo beach could attract animals such as dogs, black vultures (*Coragyps atratus* (Bechstein, 1793)), Atlantic ghost crabs (*Ocypode quadrata* (J.C. Fabricius, 1787)), and mole crickets (*Scapteriscus didactylus* (Latreille, 1804)) that prey on both leatherback turtle eggs and hatchlings (Maros et al. 2003).

Data collection

The nests analyzed in the study were laid from 20 May to 4 June 2002. For each freshly laid nest encountered, we used a plastic measuring tape to measure the minimum distance from the nest to (i) the last high tide line ("sea distance"), to (ii) the vegetation line (slight vegetation (*Ipomea*), sand still visible), and (iii) the width of the beach (high tide line – vegetation line). At the time of oviposition or later during nest covering, we measured the minimum straight carapace length of the nesting female (SCLmin) (Bolten 1999) and the female identity was recorded (passive integrated transponder (PIT) tags). All nest locations were localized to within 1 m by triangulation to numbered stakes placed every 10 m along the vegetation of the beach. To locate specific nests after incubation, we placed a ring of plastic isolated copper in the sand above the clutch when the female was covering the nest and then used a metal detector to locate nests at the end of incubation. After 50 days of incubation, we monitored nests daily for signs of emergence. All nests were excavated 48 h after signs of emergence. Nest contents were examined and divided into categories. The number of shell fragments (*S*), live hatchlings (*L*), dead hatchlings (*D*), emerged hatchlings ($E = S - (L + D)$), undeveloped yolked eggs (UD), yolkless eggs (*Y*), and the number of yolked and yolkless eggs preyed upon by Atlantic ghost crabs (described in Viseux 2001) and mole crickets (described in Maros et al. 2003) were counted. Yolked and yolkless eggs are included in the estimate of predation rate. We defined three categories of yolkless eggs: yolkless eggs still filled with albumin (hydrated eggs), yolkless eggs intact without albumin (dehydrated eggs), and yolkless eggs without albumin because they had been preyed upon (preyed upon eggs). Hatching success (HS) was determined by dividing the number of eggs that successfully produced hatchlings that left the nest (estimated by number of shell fragments, *S*) by the total number of yolked eggs originally laid by the female ($YE = S + UD$).

Statistical analysis

To determine the consistency of nest-site selection relative to distance from the sea and distance from the vegetation, we tested the normal distribution with the Shapiro–Wilk *W* test because of its good power properties compared with a wide range of alternative tests (Shapiro and Wilk 1965). An important aspect of the "description" of a variable is the shape of its distribution, which tells us the fre-

quency of values from different ranges of the variable. If the skewness (which measures the deviation of the distribution from symmetry) is clearly different from zero, then the distribution is asymmetrical, whereas normal distributions are perfectly symmetrical. If the kurtosis (which measures "peakedness" of the distribution) is clearly different from zero, then the distribution is either flatter or more peaked

than normal; the kurtosis of a normal distribution is zero. Analyses were done using STATISTICA® version 6.0 (Statsoft Inc. 2001b).

A generalized linear model (GLM) was used for the analysis of hatching success. One model with first-order interactions was fitted as follows:

$$G(\text{hatch}) = \text{adult size} + \text{sea distance} + \text{vegetation distance} \\ + \text{number of yolless eggs in the clutch (dehydrated, preyed upon, hydrated)} + \text{number of yolked eggs} \\ + \text{interactions} + \text{error}$$

where G is a link function and hatch represents hatching success. Adult size, sea distance, vegetation distance, number of yolless eggs (in the clutch, dehydrated, preyed upon, hydrated), and number of yolked eggs were treated as continuous independent variables. As dependent variables were percentages, we used binomial error distribution and logit link function (GLMStat). The significance of factors and interactions were tested and only significant terms were left in the final model. However, a nonsignificant term was kept if its interaction with another factor was significant. We started from a complete model on which we applied a backward elimination procedure to obtain the final model using the following criteria: the variable with the maximum nonsignificant probability was excluded at each step (Dobson 1990). The final model was attained when all variables retained were statistically significant ($p < 0.05$). Moreover, we used this model to obtain the percent deviance accounted for by each variable when compared against the null model (Martínez et al. 2003).

GLM with binomial error distribution and logit link were performed to look for possible correlations of paired variables. Different parameters related to hatching success, yolless eggs (in the clutch, hydrated, preyed upon, dehydrated), and yolked eggs (in the clutch, undeveloped, preyed upon) were dependent variables and distance from the sea and the vegetation were continuous independent variables. A similar GLM was used to test for the correlation between yolless eggs and yolked eggs preyed by mole crickets.

All calculations were performed using GLMStat version 5.5 (StatSoft Inc. 2001a). For all statistical tests, $\alpha = 0.05$.

Results

Nests

Over a period of 15 days, we marked all nests laid ($n = 99$) along a 300 m stretch of beach. At the end of the study, five nests were lost to erosion, six nests to dog predation, and two nests to human poaching. Therefore, 99 nests were analyzed for nest-site selection, and 86 nests were analyzed for hatching success and the role of yolless eggs (because the 13 lost nests were not excavated).

Leatherback turtle nests ($n = 86$) had, on average, 87.8 (SE 2.3) yolked eggs and 24.7 (SE 1.1) yolless eggs per clutch. All nests had some yolless eggs. The overall hatching success of all nests was 38.2% (SE 2.4%) with 74/86 nests hatched. Mole cricket predation was recorded in 94.2% of the nests (81/86 nests), with an egg predation rate

of 16.6% (SE 1.0%) and a mean of 17.7 (SE 1.2) eggs preyed per nest. Mole crickets preyed upon yolless eggs significantly more often than yolked eggs ($F_{[1,85]} = 9.180$, $p = 0.003$, $n = 86$; Fig. 1), with a yolked egg predation rate of 14.3% (SE 0.9%) and a yolless egg predation rate of 22.5% (SE 2.0%). In the case of Atlantic ghost crabs, the predation rate was 48.9% of nests (42/86 nests), with an egg predation rate of 4.9% (SE 0.5%) and a mean of 4.1 (SE 0.4) eggs preyed per nest. Atlantic ghost crabs preyed only on the yolked eggs. At the end of nest incubation, yolless eggs were found to be intact but dehydrated (mean 59.1%, SE 2.4%), still filled with albumin (mean 17.8%, SE 2.5%), preyed upon by mole crickets (mean 22.5%, SE 2.0%), or indeterminate (mean 0.6%, SE 0.8%).

Nest-site choice

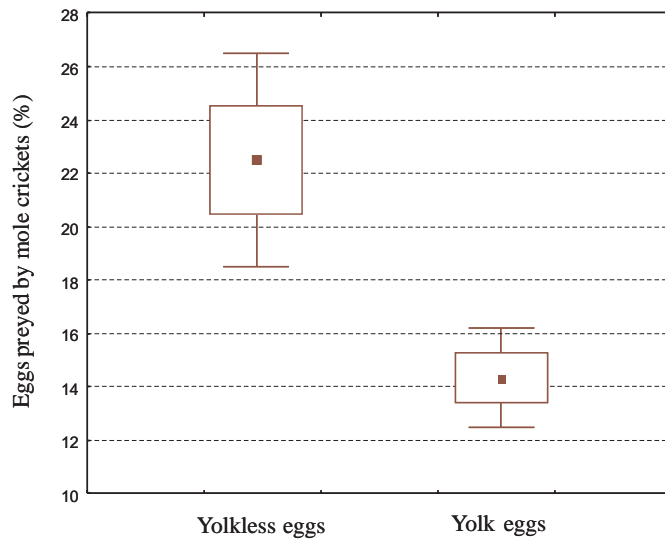
Leatherback turtles tended to lay their clutches away from the sea and near the vegetation behind the beach ($n = 99$) (Fig. 2). The distribution of the distance from the sea was normal ($W = 0.99$, $p = 0.94$, skewness = -0.08 , kurtosis = -0.14). In contrast, the distribution of the distance from the vegetation was leptokurtic ($W = 0.91$, $p < 0.001$, skewness = 1.08 , kurtosis = 0.81).

Correlations of paired variables with different parameters relating to hatching success and nest site showed that the distance to the vegetation line and predation rate by mole crickets on eggs ($F_{[1,98]} = 5.980$, $p = 0.0166$), especially on yolked eggs ($F_{[1,98]} = 4.726$, $p = 0.0325$), was negatively significant and the number of yolless dehydrated eggs ($F_{[1,98]} = 4.482$, $p = 0.0372$) was positively significant. All other possible correlations of paired variables were nonsignificant. Clutch size (yolked eggs + yolless eggs) did not vary from the tide line to the vegetation line. The quantities of yolked and yolless eggs were not correlated, and clutch proportions were similar across the nesting zone. Finally, the proportion of undeveloped yolked eggs and the proportion of yolked eggs preyed upon by Atlantic ghost crabs were not significantly correlated with the distance between the nests and the vegetation or between the nests and the high tide line.

GLM analysis models

The model for hatching success accounted for 25.69% of the original deviance (Table 1). Some factors that are directly involved in hatching-success estimation were not used. For example, number of undeveloped yolked eggs (%) directly influences hatching success. Sea distance and vege-

Fig. 1. Proportion of yolkless and yolked eggs of leatherbacks (*Dermochelys coriacea*) preyed upon by mole crickets (*Scapteriscus didactylus*) ($n = 86$).



tation distance were not significant alone, but their interaction was highly significant ($p = 0.003$) and accounted for 44.72% of model deviance. The interaction term between yolkless dehydrated eggs and yolkless hydrated eggs was found to be significant ($p = 0.0167$); however, only the factor of dehydrated yolkless eggs was significant ($p = 0.0015$) and represented 33.49% of the model deviance. Hatching success increased with yolkless dehydrated eggs and the interaction between sea distance and vegetation distance.

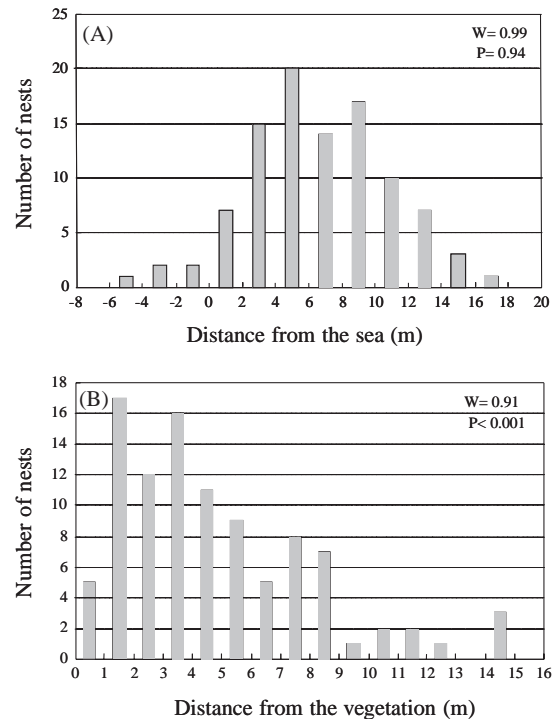
We used a simple GLM model for hatching rate to account for the sea distance \times vegetation distance interactions ($G(\text{hatch}) = \text{sea distance} + \text{vegetation distance} + \text{interaction} + \text{error}$). The hatching rate was higher near the vegetation line if the beach was narrow and greatest in the middle of the beach if the beach was wide (Fig. 3). It appears as if actual hatching rates remain relatively constant near the vegetation line, even as the beach widens.

Discussion

Impact of yolkless eggs on hatching

Several studies report the presence of larvae of two polyphagous fly families (Phoridae and Sarcophagidae) in the nests of sea turtles (Acuna-Mesen and Hanson 1990; Trauth and Mullen 1990; Disney 1994; Broderick and Hancock 1997). Three genera of flying Sarcophagidae are known to attack the supple shell of sea turtle eggs (Lopes 1982; Lopez Barbosa 1989; Andrade et al. 1992; Vasquez 1994; McGowan et al. 2001). These studies indicate that the eggs are vulnerable to predation by insects. However, the level of this impact is unknown and we have no idea whether eggs that show signs of predation are actually viable at the time when the inferred predation occurs. Moulis (1997) describes a reduction of 15% of hatchling emergence for some *Caretta caretta* (L., 1758) nests infested by the invasive red fire ant (*Solenopsis invicta* Buren, 1972) compared with noninfested nests. Although the level of egg predation by insects is suspected to be very high, it has rarely been documented for the leatherback turtle. During this study, predation occurred

Fig. 2. Frequency distribution of the distance between nest sites and (A) the sea tide and (B) the vegetation for all nests measured ($n = 99$). Negative values in A indicate nests that were laid below the sea tide. We tested the normal distribution of the data with the Shapiro–Wilk W test.



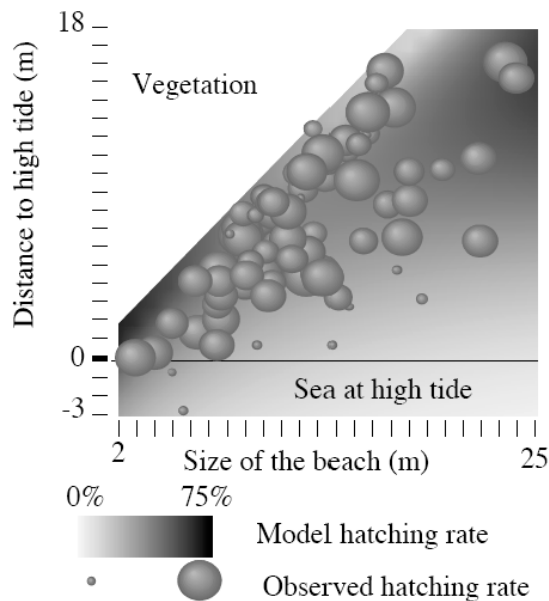
mainly by Atlantic ghost crabs and mole crickets. Sea turtle eggs are rarely the principle food source of Atlantic ghost crabs (Arndt 1994; Loegering et al. 1995; Watts and Bradshaw 1995; for more information see Hill and Green 1971) and we found that their impact on leatherback turtle eggs may be relatively small (predation rate 2.4%, $n = 86$). In terms of predation by mole crickets, our results are consistent with those of Maros et al. (2003) who found that about 18% of leatherback yolked eggs laid on this beach were preyed upon by mole crickets (10 nests). As shown in Leslie et al. (1996), we found that the predation rate was related to the position of the nests. In particular, we found that the proportion of eggs preyed upon by mole crickets increased near the vegetation zone, especially for the yolkless eggs. This is consistent with Maros et al. (2003) who found a greater density of mole crickets near the vegetation line.

Most of the yolkless eggs were dehydrated at the end of incubation (approximately 59%). The proportion of eggs preyed upon by mole crickets was negatively correlated with the vegetation distance, whereas the proportion of dehydrated yolkless eggs was positively correlated. As yolkless eggs dehydrate, they might release substances into the surrounding egg chamber that act as deterrents to mole crickets (Dutton and McDonald 1995). Most of the yolkless eggs are laid at the top of the egg mass; therefore, yolkless eggs may be the first eggs encountered by mole crickets if they dig straight down from the surface of the sand. Our data showed that hydrated yolkless eggs were more often preyed upon than yolked eggs. Consequently, yolkless eggs could act, in part, as an efficient means of protection against

Table 1. Generalized linear model (GLM) for the hatching success of leatherback turtles, *Dermochelys coriacea*, in Guiana.

	Estimate	Deviance	df	<i>F</i>	Prob. > <i>F</i>	Percent deviance
Hatching success model		516.8	6	5.40	<i>0.0001</i>	25.7
Constant	0.5808					
Yolkless eggs						
Dehydrated	<i>1.615 × 10⁻²</i>	173.1	1	10.86	<i>0.0015</i>	33.5
Hydrated	<i>-5.658 × 10⁻²</i>	6.46	1	0.41	0.5261	1.6
Sea distance	-0.1505	9.04	1	0.57	0.4538	1.7
Vegetation distance	-2.439	1.65	1	0.10	0.7482	0.3
Sea distance × vegetation distance	0.2823	231.1	1	14.5	<i>0.0003</i>	44.7
Yolkless dehydrated × yolkless hydrated	<i>5.583 × 10⁻³</i>	95.33	1	5.98	<i>0.0167</i>	18.4

Note: The percent deviance accounted for by each variable and by the model (compared with a null model) are shown. Only significant terms were left in the final model; adult size, number of yolkless eggs (in the clutch and preyed on), and number of yolked eggs were dropped. Values in italic type are significant at $p < 0.05$.

Fig. 3. Hatching rate according to the size of the beach and the distance to high tide. Shading represents the model hatching rate (GLM analysis) and spheres represent the observed hatching rates.

the mole cricket predation of yolked eggs in French Guiana. As such, three scenarios may occur when mole crickets find a leatherback turtle clutch: (1) mole crickets encounter yolkless eggs with greater probability than yolked eggs; (2) if yolkless eggs are hydrated, the mole crickets preferentially feed on them rather than on yolked eggs; and (3) if yolkless eggs are dehydrated, some substances from the eggs may inhibit the actions of mole crickets.

Although we have evidence of the role of yolkless eggs on the development of yolked eggs, they may have several positive impacts. The more hydrated yolkless eggs there are at the end of the incubation period, the less likely that yolked eggs will successfully complete their development. These results support the hypothesis that yolkless eggs might help maintain physicochemical conditions (e.g., moisture by dehydrated eggs) (Dutton and McDonald 1995). Dutton and McDonald (1995) did not find a significant difference in hatching success between clutches with or without yolkless eggs, probably because few predators are present in St. Croix (especially mole crickets) and clutches were collected as they were laid and reburied at sites on sta-

ble areas of the high beach platform. Altogether, these results suggest that yolkless eggs could play an important role in the successful incubation of the nest; some may act as decoys for predators, while others may be important for successful incubation of yolked eggs and the escape of hatchlings from the nest (Dutton and McDonald 1995).

Nest-site selection and hatching success

Nest-site selection of leatherback turtles has been described as being highly variable and widely dispersed (Weishampel et al. 2003), with some clutches suffering near complete mortality following wash over by high tides on the day of laying (Mrosovsky 1983; Eckert 1987). In contrast, we found that few leatherback turtle nests (5%) were laid below the high tide line and most nests were strongly aggregated in the upper part of the beach.

The beach of Awala Yalimapo has one of the lowest hatching success rates of leatherback turtles in the world (Girondot et al. 2002). The hatching success of sea turtles is thought to be strongly related to the distance that the nest is laid from the sea and from the vegetation behind the beach (Hays and Speakman 1993; Godley et al. 2002). Our data indicates a strong relationship between hatching success and the interaction between sea distance and vegetation distance, except for the predation by mole crickets that increases significantly toward the vegetation line. It is likely that various micro-environmental factors such as sand content and compaction; oxygen, chloride, and moisture levels; and temperature varied from the vegetation to the sea level. Nests placed closer to the vegetation are likely to encounter a substrate with reduced moisture, temperature, and compaction (Spotila et al. 1987; Weisrock and Janzen 1999; for more information see Godfrey et al. 1996). It is also likely that the low overall hatching success rate on this beach made it difficult to determine the interactions among the nest location, relative proportions of yolked and yolkless eggs, and hatching success. It should be noted, however, that the hatching rate was close to 80% when eggs from French Guiana were incubated under laboratory conditions (Girondot et al. 1990). The principal factors that affect hatching success may be different from those considered in this study. We suggest that other ecological factors in the beach of Awala Yalimapo (i.e., organic matter, oxygen exchange, and moisture contents) may limit the development of eggs (Ackerman 1980; McGehee 1990). Another probably important variable

related to egg mortality is bacterial and fungal attacks (Girondot et al. 1990).

Nest-site selection as an integrative response

The correlation between hatching success and nest location leads to the question of how and why leatherback turtles choose their nest site. There are probably many factors influencing nest success (i.e., predation rate, the physiological state of yolkless eggs, and soil properties), which may vary along the beach and interact with each other. Moreover, as suggested by Horrocks and Scott (1991), the length of beach crawl may be an important factor influencing the nesting behavior of turtles. The large size of leatherback turtles and the slow speed of their hatchlings may make the length of the crawl on land critical, and may partly explain the tendency for leatherback turtles to nest closer to the sea compared with green turtles (*Chelonia mydas* (L., 1758)), which also nest on beaches in the Guianas (Whitmore and Dutton 1985). Mrosovsky (1983), at the population level, and Eckert (1987), at the individual level, suggested that leatherback turtles have developed a scattered nesting strategy, whereby nests are randomly distributed throughout a beach to maximize clutch survival over an unpredictable nesting area. But Nordmoe et al. (2004) showed that the leatherback turtle preference for open sand at Playa Grande is consistent with that seen in Malaysia (Chua 1988). On Krofajapasi beach in Suriname, Whitmore and Dutton (1985) found a general preference for open sand nest sites among leatherback turtles, in contrast to the green turtle preference for vegetative cover. In a recent study, Kamel and Mrosovsky (2004) suggested that nesting patterns cannot be characterized in a simple manner, and there appears to be two main aspects of this behavior: one aspect emphasizes nonrandom repeatable choices and the other reflects scatter in the actual nesting pattern. During our study, we saw four adult turtles attacked by packs of stray dogs on the beach, illustrating that nesting can be dangerous for females. Nest site also influences the proportion of dehydrated yolkless eggs, which in turn may influence the predation rate by mole crickets. Our results on nest-site selection showed that leatherback turtle females nest at intermediate distances from the tide and near the vegetation, and these results correspond with those of Kamel and Mrosovsky (2004). Nest-site selection may be a trade-off between decreasing the loss of nests from tidal flooding or erosion when laying at a short distance from the sea and increasing possible predation rates on females and hatchlings when nests are laid near the vegetation (Mrosovsky 1983).

Conclusion

Leatherback turtles that nest in French Guiana represent about 30%–40% of the world's breeding population (Girondot et al. 2002). The serious decline in female populations at many of the world's leatherback turtle rookeries (Spotila et al. 2000) increases the urgency in obtaining a better understanding of the status of the species at Awala Yalimapo beach. Previous workers at the site have proposed that nesting success was a significant factor governing population dynamics (Fretey and Lescure 1979). We found that hatching success on this beach was very low (38.2%) compared with the values observed for this species at Culebra

(75%, Tucker 1989) and at St. Croix (67%, Boulon et al. 1996). Several factors affecting incubation success are known for Surinamese and French Guianan beaches. Our results indicate that the nest site may affect hatching success, especially with regard to mole cricket predation. In Awala Yalimapo beach, the predation rate was 16.6%; however, preliminary results indicate that 40% of leatherback turtle eggs in Galibi beaches are predated by mole crickets (Hoekert et al. 1998). We find that yolkless eggs have a positive effect on the future of the clutch. This is an important result, as yolkless eggs are often ignored in hatchery studies with relocated nests and laboratory incubators, and as such, highlights the fact that they should be included in such studies.

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