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The effect of incubation temperature on hatchling quality in the olive ridley turtle, *Lepidochelys olivacea*, from Alas Purwo National Park, East Java, Indonesia: implications for hatchery management

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Abstract Nest protection through egg relocation from natural nests into protected hatcheries is a common practice used at rookeries around the world to increase hatchling recruitment into sea turtle populations. However, rarely have the impacts of this practice on hatchling recruitment and quality been assessed. This study investigated the influences of the thermal nest environment of olive ridley turtles *Lepidochelys olivacea* on emergence success and quality of hatchlings of hatchery nests in Alas Purwo National Park, East Java, Indonesia (2009 and 2010 nesting seasons). Nest temperatures above 34 °C for at least 3 consecutive days during incubation in the hatchery resulted in decreases in emergence success and locomotor performance of hatchlings. The use of the hatchery is recommended due to extremely high predation rate of nests left on the beach; however, altering hatchery management practice by spacing nests one meter apart and providing shade should improve hatchery outcomes now and into the future.

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Introduction

Population decline in sea turtles has mainly been attributed to anthropogenic-induced changes to sea turtle habitat (King et al. 1989; Lagueux 1991; Lutcavage et al. 1997; Engeman et al. 2003; Cornelius et al. 2007). Such changes include global warming with its associated rise of sea level, accumulated pollutants in the sea including plastics, increased harvesting of eggs and adults for human food consumption and non-turtle-friendly fishing methods (Heppell et al. 2003; Lewison et al. 2004; Hawkes et al. 2007; Fuentes et al. 2011). Various mitigation programs have been introduced in an attempt to counter the global decline in sea turtle populations which include introduction of turtle-friendly fishing methods (Crowder et al. 1994), environmental education (Vieitas et al. 1999; Jones et al. 2011), collaboration between countries (Shillinger et al. 2008; Huang 2011), but one of the biggest areas of effort has been to target nesting beaches which include application of nest predator controls (Stancyk 1995; Engeman et al. 2006; Barton and Roth 2007) and translocation of clutches of eggs into protected areas (Boulon 1999; Garcia et al. 2003).

Nest protection through the transfer of egg clutches from natural nests into hatcheries is a common strategy employed around the world in an attempt to increase hatchling recruitment into the sea and thus potentially increase the population of sea turtles (Boulon 1999; Mortimer 1999). However, hatchery use as sea turtle conservation strategy has attracted criticisms and controversy (Parmenter 1980; Frazer 1992; Grand and Beissinger 1997; Garcia et al. 2003; Kornaraki et al. 2006) because of potential undesirable outcomes such as inconsistent hatching rate (Wyneken et al. 1988; Abella et al. 2007), skewed sex ratios (Mrosovsky and Yntema 1980; Morreale

et al. 1982), detrimental influences on embryonic devel-
opment (Blanck and Sawyer 1981; Patino-Martinez et al.
2012a), decreased hatchling fitness (Patino-Martinez et al.
2012b), and improper methods of hatchling release which
result in high rates of hatchling mortality (Mortimer 1999).

The micro-environment within a hatchery plays a vital
role in determining the incubation success of turtle eggs
and the phenotype of hatchlings (Ackerman 1997; Van de
Merwe et al. 2006). The specific environment inside the
nest is a result of interactions between biotic factors (e.g.,
microorganisms and the developing turtle embryos them-
selves) and abiotic factors (e.g., sand characteristics, gas
exchange, moisture levels, and temperature) which can
vary temporally and spatially during the nesting season
(Ackerman 1997). Both bacteria and fungus in nesting sand
can infect eggs and result in reduced incubation success
(Phillot et al. 2002; Güçlü et al. 2010) and have been
documented to also influence phenotype in the hatchery
situation (Patino-Martinez et al. 2012a). Nest temperature
is particularly important to developing sea turtle embryos
because it influences hatching sex ratio (warmer tempera-
tures produce more females, cooler temperatures more
males) (Standora and Spotila 1985), hatchling quality in
terms of hatchling size and the amount of yolk converted to
hatchling tissue before hatching (Booth et al. 2004), and
hatchling locomotor performance (Burgess et al. 2006).
Hence, differences in the nest micro-environment between
natural beach nests and artificial hatchery nests may
influence incubation success as well as the quality of
emergent hatchlings which may in turn affect the recovery
and survival status of sea turtle populations in the future
(Wibbels 2007). Therefore, if hatcheries are used as part of
sea turtle conservation programs, they need to be carefully
assessed in terms of emergence success and hatchling
quality to ensure they are meeting their conservation
objectives.

Studies examining the microenvironment of olive ridley
turtle (*Lepidochelys olivacea*) nests are limited and have
focused on populations exhibiting the *arribada* nesting
phenomenon (Trullas and Paladino 2007; Honarvar et al.
2008). Studies on the incubation environment for solitary
nesting populations are scarce with no information
regarding the quality of hatchlings. Alas Purwo National
Park is one of the largest rookeries for olive ridley turtles in
Indonesia and a hatchery was established in 1983 at this
site (Conant et al. 2007). The management practice for over
25 years is to relocate all clutches of eggs laid on the
surrounding beach to a single protected beach hatchery;
however, no evaluation of the effectiveness of this program
in terms of emergence success or hatchling quality has
been made. For this reason, the current study investigated
the nest thermal environment of olive ridley hatchery nests
of Alas Purwo National Park to evaluate the effect of

incubation temperatures on the emergence success and
quality in terms of hatchling mass, size (carapace dimen-
sions), and locomotor performance (self-righting ability
and crawling speed) of the hatchlings generated from these
nests.

Materials and methods

Study site

This study was carried out in the 2009 and 2010 nesting
seasons (April–July) in Alas Purwo National Park (APNP).
APNP is situated on the south eastern tip of Java, Indo-
nesia, between 8°26′46″–8°47′00″S and 114°20′16″–
114°36′00″E (Fig. 1). The beach of APNP provides nest-
ing habitat for four species of sea turtles: green (*Chelonia
mydas*), hawksbill (*Eretmochelys imbricata*), leatherback
(*Dermochelys coriacea*), and olive ridley (*Lepidochelys
olivacea*). The total length of the beach is 18 km and
consists of Pancur Beach (2 km) and Marengan Beach
(16 km).

Data collection

Nests were categorized into three groups; (1) natural nests,
(2) protected nests, and (3) hatchery nests. Natural nests
were left to incubate naturally in situ after an initial
excavation to determine clutch size. Protected nests were
also left at the natural site but were protected with a
cylindrical wire cage. Both natural and protected nests
were purposely selected from nests that were constructed
by females within 200 m of the hatchery in order to
facilitate regular monitoring. Hatchery nests consisted of
clutches of eggs relocated to the hatchery and buried in
artificially dug nests. Standard park management procedure
is to collect and relocate to the hatchery all clutches of eggs
laid on beaches within the park; the ones chosen for
monitoring in this study were a haphazard sub-set of these
nests.

All nests were excavated immediately after adult
females finished their nesting activities. Nests were dug out
by hand and eggs were removed and counted. Eggs were
then placed back into the nest, and an *ibutton* temperature
data logger (Model DS1922 L, Maxim, Dallas, USA) set to
record temperature once every 2 h was placed in the center
of egg mass (Booth and Freeman 2006). Nest location was
marked with two wooden stakes with red ribbon attached.

Eggs transferred to the hatchery were transported from
the nest site to the hatchery by motorbike. Eggs were
transported on top of a layer of sand (to minimize the
shocks to eggs during transport (Mortimer 1999)) in either
a plastic bag, bucket, or styrofoam box. The same protocol

Fig. 1 Study site. Pancur and Marengan Beaches, Alas Purwo National Park, East Java, Indonesia
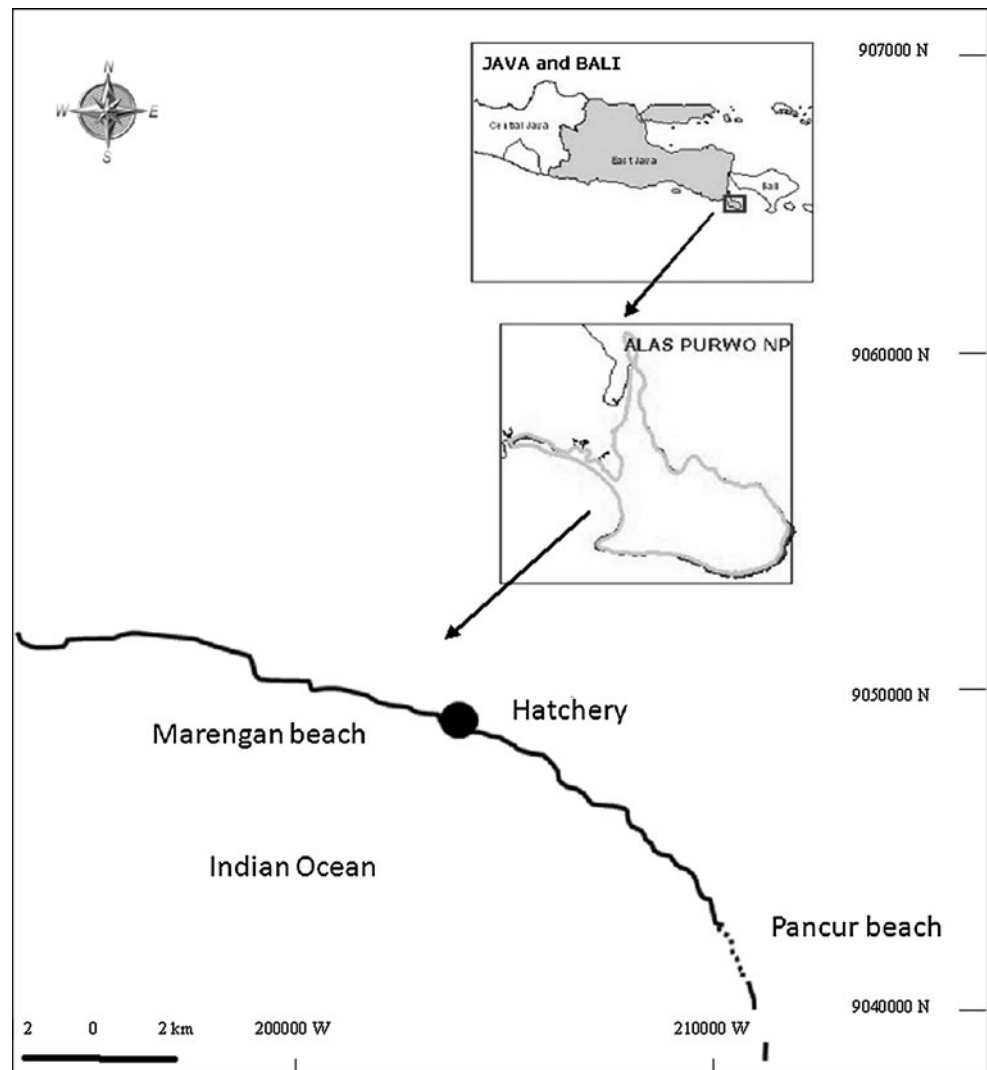
was used in setting up artificial nests in the hatchery, with the bottom of the artificial nest located 40 cm below the sand surface (Whiting 1997; Whiting et al. 2007). Because of management directives, in 2009, all relocated nests were placed in western part of the hatchery, while in 2010, all relocated nests were placed in the eastern part of the hatchery. Approaching the anticipated hatching date, cylindrical plastic cages were placed on top of nests to enable collection of hatchlings as they emerged from nests. Frequent visits to the cages were carried out during this period to check for, and release, emerging hatchlings. Nests were excavated 3 days after the first hatchlings emerged from nests in order to determine emergence success (number of hatchlings successfully emerged from a nest divided by total number of eggs in nest) and to retrieve the data loggers.

Daily rainfall data recorded at a weather station 18 km north of the park was obtained from the local bureau of meteorology at Banyuwangi. For analysis of the possible influence of rainfall on emergence success and hatchling quality, cumulative rainfalls were calculated for each nest by summing together the rainfall from each day of incubation (i.e., from laying to nest emergence). Sand temperatures at nest level (40 cm below sand surface) were monitored by deploying *ibutton* temperature data loggers at Marengan beach-sector 109 which was located close to the hatchery and in the eastern and western parts of the hatchery. These loggers recorded temperature every 2 h.

Measurement of hatchling quality

Carapace length and width of hatchlings emerging from nests were measured using a digital calliper. These two measurements were multiplied to give a carapace size index (Booth and Astill 2001; Booth et al. 2004). The mass of hatchlings was measured using a spring balance ($\pm$1 g) in 2009 and a digital balance ($\pm$0.01 g) in 2010. The spring balance was checked against the digital balance and found

to read lightly differently so a conversion factor was used to correct mass measurements taken in 2009 before analyzing body mass data.

Two measurements of hatchling locomotor performance were made. In the first, crawling speed was recorded by measuring the time taken by each hatchling to crawl along a raceway of 1.5 m, 100 mm wide PVC guttering. The track was lined with moist sand, and a dull flashlight was placed at one end of the raceway. This measurement was repeated three times for each hatchling and a mean time calculated for each hatchling. Crawl time was converted to crawl speed (cm s^{-1}). If hatchlings failed to move within 240 s of being placed in the raceway, they were assigned to a failed to crawl category. The body temperature of the hatchlings was measured immediately after the completion of the crawling trial by inserting a thermocouple (25G Type K) connected to a digital thermometer (Omega 871A) 1 cm into the cloaca.

In the second measurement of locomotor performance, in a random sample of 15 hatchlings from each nest, the time taken for hatchlings to self-right themselves was measured when they were placed upside down on their carapace. This was repeated three times for each hatchling. If an individual took more than 60 s for any righting attempt, a 30-s rest period on their plastron was given before the next attempt was made. This procedure provided two different metrics: (1) the mean time for a hatchling to self-right (the average of the successful self-righting events) and (2) a score from 0 to 3 indicating self-righting propensity depending on the number of times hatchlings self-righted during self-righting trials. Hatchlings which took <60 s to self-right in all three trials were given a score of 3. Hatchlings that self-righted in <60 s in two of the three trials were given a score of 2. Hatchlings that self-righted in <60 s in only one of the three trials were given a score of 1. Hatchlings that failed to self-right within 60 s in all three trials were given a score of 0. The body temperature of the hatchlings was measured immediately after the completion of the self-righting trial by inserting a thermocouple (25G Type K) connected to a digital thermometer (Omega 871A) 1 cm into the cloaca.

Data analysis

Initial ANOVA in which nest was a random factor found significant inter-nest variation in all hatchling variables measured ($P < 0.01$ in all cases) so nest means for each variable were calculated and these used in further analysis. Nest emergence success was found to decline significantly when the average maximum nest temperature experienced over three consecutive days during incubation (T3dm) exceeded 34 °C (Maulany et al. in press). For this reason, hatchling morphology and performance data were grouped

into T3dm < 34 °C and T3dm > 34 °C. Because no nests experienced T3dm < 34 °C in 2010, year could not be used as an independent factor in further analysis, but was factored into analysis by generating three groups (T3dm < 34 °C in 2009, T3dm > 34 °C in 2009, and T3dm > 34 °C in 2010). Mode of transport (plastic bags, bucket, styrofoam box) was also integrated into the GLM analysis (T3dm and transport mode fixed factors) for each hatchling variable. Post hoc Tukey tests adjusted for unequal sample size were used to make multiple comparisons between experimental groups. Pearson correlation was used to explore relationships between T3dm and hatchling variables, and body temperature and locomotor performance variables. Multiple regression models with T3dm and cumulative rainfall as explanatory variables were used to explore relationships with hatchling variables in hatchlings experiencing T3dm < 34 °C and T3dm > 34 °C. If more than one regression model was statistically significant, the model with the highest value of adjusted R^2 was designated as the best fitting model. PASW Statistics 18.0 was utilized for statistical analysis. Data are reported as means ±1 SE. Statistical significance was assumed if $P < 0.05$.

Results

A total of 64 nests were studied in 2009 and 75 in 2010 (Table 1). All nests, both caged and non-caged, left on the beach to incubate were 100 % depredated by natural predators within 3 days of nest construction in both 2009 and 2010.

Nest temperature profiles

There was no obvious effect of daily rainfall on nest temperature (Fig. 2). Total rainfall during the monitored period was higher during 2010 (181 mm) than 2009 (96 mm). The mean temperature profiles of nests in 2009 and 2010 indicated differences in the temporal variation in nest temperature between and within years (Fig. 2). Nests that were shaded for some part of the day in 2009 experienced T3dm < 34 °C and nest temperature averaged 29.5 °C for the first 25 days of incubation and then steadily

Table 1 Number of nests studied during 2009 and 2010 nesting seasons

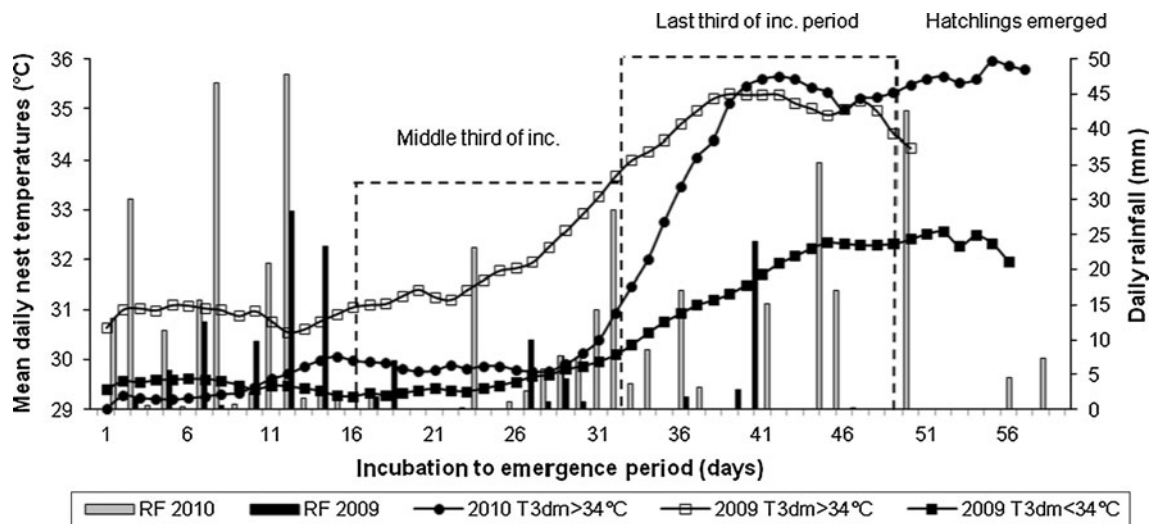| Nesting season	Natural nests		Hatchery nests	Total nests
	Caged	Non-caged		
2009	5	6	53	64
2010	5	14	56	75

Fig. 2 Temperature profiles of hatchery nests (experiencing T3dm < 34 °C in 2009 and T3dm > 34 °C in 2009 and 2010) and daily rainfall during the incubation period

Table 2 The effect of maximum temperature experienced for 3 days in a row on Olive Ridley turtle hatchling morphology and performance from 2009 to 2010 nests

Parameter measured	T3dm below 34 °C in 2009 ($n = 31$ nests) Mean ± SE (min–max)	T3dm above 34 °C in 2009 ($n = 22$ nests) Mean ± SE (min–max)	T3 above 34 °C in 2010 ($n = 56$ nests) Mean ± SE (min–max)	P value
Tmid (°C)	$29.7^a \pm 0.2$ (28.0–31.8)	$31.8^b \pm 0.2$ (29.9–33.5)	$30.1^c \pm 0.1$ (28.1–31.3)	$P < 0.001$
T2 weeks (°C)	$32.2^a \pm 0.2$ (30.2–33.6)	$34.9^b \pm 0.3$ (32.2–36.6)	$35.4^c \pm 0.1$ (33.3–36.5)	$P < 0.001$
Tinc (°C)	$30.4^a \pm 0.2$ (28.6–32.1)	$32.4^b \pm 0.2$ (30.5–33.6)	$31.6^c \pm 0.1$ (29.7–32.4)	$P < 0.001$
T3dm (°C)	$32.8^a \pm 0.2$ (30.1–33.9)	$35.7^b \pm 0.2$ (33.2–37.2)	$36.3^c \pm 0.1$ (34.1–37.9)	$P < 0.001$
Nest emergence success (%)	$81.7^a \pm 2.3$ (46.7–98.3)	$61.6^b \pm 4.1$ (30.4–96.6)	$54.2^b \pm 2.7$ (12.9–87.4)	$P < 0.001$
Body mass (g)	15.5 ± 0.3 (12.1–17.8)	15.4 ± 0.3 (12.7–19.7)	16.2 ± 0.3 (10.9–18.9)	$P = 0.073$
Size index (mm²)	$1438^a \pm 19$ (1281–1571)	$1367^b \pm 17$ (1180–1545)	$1350^b \pm 11$ (1091–1459)	$P < 0.001$
Crawling speed (cm/s)	$3.1^a \pm 0.1$ (2.3–3.9)	$2.5^b \pm 0.1$ (1.5–3.5)	$2.1^c \pm 0.1$ (0.2–3.7)	$P < 0.001$
Self-righting time (s)	$15.7^a \pm 3.1$ (2.2–41.5)	$27.2^b \pm 2.9$ (3.8–59.5)	$25.1^b \pm 1.9$ (2.2–50.1)	$P = 0.015$
Self-righting propensity	$2.8^a \pm 0.1$ (1.2–3)	$1.9^b \pm 0.2$ (0.1–3)	$2.1^b \pm 0.1$ (0.9–3)	$P < 0.001$

Tmid the mean temperature in the middle third of incubation period, *T2 weeks* the mean temperature during the last 2 weeks of incubation period, *Tinc* the mean temperature during the entire period of incubation), *T3dm* the maximum temperature experienced by a nest for 3 consecutive days. *P* values are from ANOVA analysis. Superscript letters indicate differences between groups (Tukey multiple-comparisons test adjusted for unequal sample size)

increased to 32 °C from 25 days to 45 days and remained at 32 °C until hatching (Fig. 2). Nests that were exposed to full sun for the entire day in 2009 experienced T3dm > 34 °C, and nest temperature averaged 31.0 °C for the first 25 days of incubation and then steadily increased to 35 °C from 25 to 40 days and then decreased slightly from 35 to 34 °C at hatching (Fig. 2). Hence, in 2009, there was an approximate 2 °C difference in nest temperature between nests exposed to full sun and those that experienced shade for part of the day (Table 2). In 2010, all nests were exposed to full sun for the entire day and experienced T3dm > 34 °C. These nests averaged 29.8 °C for the first

30 days of incubation and then rapidly increased to 35.5 °C from 30 to 40 days and averaged 35.5 °C until hatching (Fig. 2). In 2010, sand temperature in the eastern hatchery increased from 29 to 34 °C between 35 and 45 days, and sand temperature rose from 29 to 32 °C at Marengan beach-sector 109 during the same period (Fig. 3).

Effect of T3dm and rainfall on nest emergence success and hatchling quality

GLM analysis indicated that both T3dm (Table 2) and mode of transport of eggs (Table 3) affected hatchling

Fig. 3 Temperature profiles of beach sand at 40 cm depth (Marengan-Sector 109), sand at 40 cm depth among nest within the hatchery, and hatchery nests during the 2010 nesting season
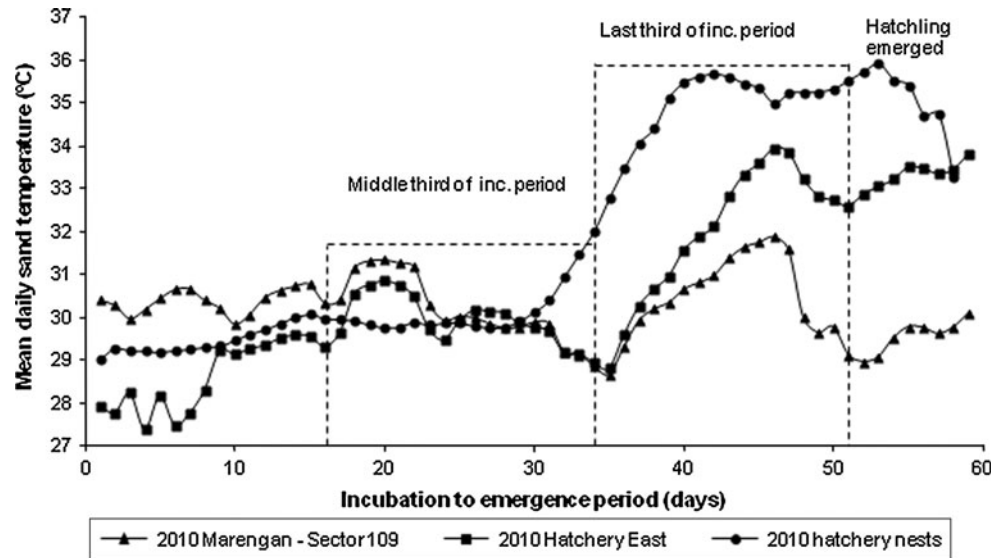

Table 3 The effect of mode of transport of eggs on Olive Ridley turtle hatchling morphology and performance

Parameter measured	Plastic bag ($n = 45$ nests) Mean ± SE (min–max)	Bucket ($n = 17$ nests) Mean ± SE (min–max)	Styrofoam box ($n = 47$ nests) Mean ± SE (min–max)	P value
Nest emergence success (%)	57.7[a] ± 3.7 (12.9–87.4)	66.1[b] ± 4.9 (21.2–95.9)	68.9[b] ± 2.7 (30.3–98.3)	P = 0.042
Body mass (g)	15.7 ± 0.3 (10.9–18.9)	15.7 ± 0.4 (13.2–17.9)	15.6 ± 0.2 (12.1–19.7)	P = 0.918
Size index (mm^2)	1350[a] ± 11 (1091–1459)	1367[a] ± 17 (1173–1552)	1438[b] ± 19 (1180–1571)	P = 0.027
Crawling speed (cm s^{-1})	2.4 ± 0.1 (1.2–3.7)	2.7 ± 0.1 (1.3–3.5)	2.6 ± 0.1 (0.2–3.9)	P = 0.156
Self-righting time (s)	30.1[a] ± 2.5 (2.2–50.1)	20.1[b] ± 3.4 (3.8–44.3)	17.8[b] ± 1.9 (2.2–59.5)	P = 0.015
Self-righting propensity	1.8[a] ± 0.1 (1.2–3)	2.4[b] ± 0.2 (0.1–3)	2.5[b] ± 0.1 (0.9–3)	P < 0.001

P values are from ANOVA analysis. Superscript letters indicate differences between groups; Tukey multiple-comparisons test adjusted for unequal sample size

variables, and that there was no interaction between these two factors. Nest emergence success was greatest in nests that experience T3dm < 34 °C, and with the exception of body mass, hatchling variables varied significantly across T3dm/year combinations (Table 2). Carapace size, crawling speed, and self-righting propensity were greater, and self-righting time was shorter in hatchlings that experienced T3dm < 34 °C (Table 2). T3dm was not correlated with body mass ($r^2 = 0.018$, $P = 0.159$, $n = 109$ nests), negatively correlated with carapace size index ($r^2 = 0.212$, $P < 0.001$, $n = 109$ nests), crawling speed ($r^2 = 0.448$, $P < 0.001$, $n = 109$ nests), and self-righting propensity ($r^2 = 0.206$, $P < 0.001$, $n = 109$ nests) and positively correlated with self-righting time ($r^2 = 0.281$, $P < 0.001$, $n = 109$ nests). Hatchling crawling speed was not correlated with body temperature ($r^2 = 0.004$, $P = 0.513$, $n = 109$ nests), and self-righting time was not correlated with body temperature ($r^2 = 0.001$, $P = 0.814$, $n = 109$ nests).

Multiple regression indicated no relationships between accumulated rainfall and T3dm with any hatchling variables in hatchlings that experienced T3dm < 34 °C (Table 4). For hatchlings that experienced T3dm > 34 °C, there were no relationships between accumulated rainfall and T3dm with hatchling body mass or carapace size, but significant relationships between these variables and crawling speed, self-righting time and self-righting propensity (Table 5). In all three hatchling performance variables, T3dm was significantly correlated, while accumulated rainfall increased the correlation strength in self-righting time and self-righting propensity.

Effect of mode of transport of eggs on emergence success and hatchling quality

Mode of egg transport influenced nest emergence success, self-righting time, and self-righting propensity (Table 3). Eggs transported in styrofoam boxes resulted in hatchlings with larger carapaces, while those transported in plastic

Table 4 Relationship between hatchling body mass, size, crawling speed, self-righting time, and self-righting propensity and the maximum temperatures experienced by nests for 3 consecutive days (T3dm), and cumulative rainfall (RF) in nests that experienced T3dm below 34 °C in 2009 (*n = 31 nests*)

Parameter measured	Model	T3dm (P value)	RF (P value)	R^2
Body mass	T3dm	0.844	–	0.001
	RF	–	0.106	0.00
	T3dm + RF	0.853	0.931	0.002
Size index	T3dm	0.612	–	0.009
	RF	–	0.702	0.005
	T3dm + RF	0.591	0.670	0.016
Crawling speed	T3dm	0.732	–	0.004
	RF	–	0.428	0.022
	T3dm + RF	0.679	0.415	0.028
Self-righting time	T3dm	0.187	–	0.059
	RF	–	0.050	0.127
	T3dm + RF	0.111	0.032	0.203
Self-righting propensity	Mean T3dm	0.143	–	0.073
	RF	–	0.080	0.102
	T3dm + RF	0.088	0.051	0.192

None of these regression models were statistically significant

Table 5 Relationship between hatchling body mass, carapace size, crawling speed, self-righting time, and self-righting propensity and the maximum temperature experienced by nests for 3 consecutive days (T3dm) and cumulative rainfall (Rf) in hatchlings from nests that experienced T3dm above 34 °C in 2009 and 2010 (*n = 78 nests*)

Parameter Measured	Model	T3dm (P value)	Rf (P value)	R^2
Body mass	T3dm	0.671	–	0.002
	Rf	–	0.144	0.028
	T3dm + Rf	0.373	0.099	0.038
Size index	T3dm	0.063	–	0.045
	Rf	–	0.587	0.004
	T3dm + Rf	0.077	0.990	0.045
Crawling speed	**T3dm**	**0.000**	**–**	**0.231**
	Rf	–	0.182	0.023
	T3dm + Rf	0.000	0.886	0.231
Self-righting time	T3dm	0.000	–	0.160
	Rf	–	0.094	0.036
	T3dm + Rf	**0.000**	**0.002**	**0.262**
Self-righting propensity	T3dm	0.001	–	0.130
	Rf	–	0.090	0.037
	T3dm + Rf	**0.000**	**0.003**	**0.227**

The best model fit for models that were statistically significant is highlighted in bold

bags had lower nest emergence success, and produced hatchlings with longer self-righting times and lower self-righting propensity (Table 3).

Discussion

No nests left to incubate on the beach survived in the 2 years of study, both caged and non-caged nests were 100 % depredated by natural predators. Therefore, no comparisons can be made between the natural nests and hatchery nests in terms of temperature profiles or hatchling quality. The shallow nests were easily dug up by monitor lizards which simply tunneled under the protective cage barrier. For this reason, the most effective management option is to relocate freshly laid eggs to a protected hatchery for incubation, but this makes optimal management of eggs incubated in the hatchery a high priority.

Nest conditions emergence success and hatchling quality

In 2009, all monitored nests were located in the western side of the hatchery, part of which was shaded. As a consequence, some nests were exposed to full sun all day, while others were shaded for part of the day, and these partly shaded nests experienced a similar pattern of temperature change during incubation to nests exposed to full sun, but the absolute temperature they experienced was 2 °C lower than nests exposed to full sun (Fig. 2, Table 2). This indicates that the provision of shade can effectively decrease potential detrimentally high nest temperatures to lower optimal nest temperatures and be a useful rookery management tool particularly if, as predicted, sand temperatures increase in the future (Patino-Martinez et al. 2012b). In 2010, all monitored nests were located in the eastern side of the hatchery and were exposed to full sun all day and as a consequence also experienced the high overall mean nest temperatures seen in nests exposed to full sun in 2009. The difference in the nest temperature between shaded and full sun exposed nests has consequences for emergence success and hatchling quality.

In 2010, sand temperature in the hatchery measured between incubating nests became approximately 2 °C warmer than sand temperature monitored on the beach. This difference is probably the result of the combined metabolic heat produced by developing embryos in adjacent nests that were located 30 cm apart. Within-nest metabolic heating is well documented in sea turtle nests and typically elevates nest temperature 1–3 °C above general beach sand temperature by the end of incubation (Broderick et al. 2001; Godley et al. 2001, 2002; Booth and Freeman 2006), but the raising of general sand temperature due to close proximity of adjacent nests is unusual, only being reported in an *arribada* rookery of olive ridley turtles (Valverde et al. 2010).

Nests that experienced T3dm greater than 34 °C had lower emergence success than nests that experienced T3dm

lower than 34 °C. Indeed, at T3dm greater than 34 °C nest emergence success decreased as T3dm increased (Maulany et al. in press). Continuous incubation of sea turtle eggs at temperatures above 34 °C is fatal (Miller 1997), but sea turtle embryos become more tolerant to high temperatures late in incubation as evidenced by studies that have reported successful nest emergences after experiencing nest temperatures expecting 34 °C during the last weeks of incubation, but usually with reduced emergence success (Matsuzawa et al. 2002; Chu et al. 2008; Ishcer et al. 2009), and the observation that the thermal tolerance of reptilian embryos increases as development progresses (Deeming and Ferguson 1991). Reduced emergence success after exposure to high temperatures can result from increased incidences of teratogenic mistakes during embryonic development (Miller 1985; Milton and Lutz 2003) or a general weakening of hatchlings so that they fail to reach the beach surface (Chu et al. 2008).

Body mass of hatchlings was the only variable not correlated with T3dm. This is consistent with previous studies that indicate sea turtle hatchling body mass is independent of incubation temperature (Booth 2000; Reece et al. 2002; Ishcer et al. 2009) but more affected by genetic and maternal features such as the egg size (Glen et al. 2003; Andrews 2004; Özdemir et al. 2007) where larger eggs result in larger hatchlings (Van Buskirk and Crowder 1994). In contrast, hatchling carapace was larger at lower temperatures as has been previously reported and attributed to more yolk material being converted to hatchling tissue during a longer incubation period at lower temperature (Ishcer et al. 2009). Of more significance from a hatchery management point of view was the correlation of hatchling crawling and self-righting ability with T3dm, higher temperatures resulted in slower crawling, longer self-righting times, and lower self-righting propensity. High nest temperatures have been associated with decreased crawling (Ishcer et al. 2009) and swimming performance in green turtle hatchlings (Booth and Evans 2011). High incubation temperatures have also been reported to decrease locomotor performance in freshwater turtles (Ashmore and Janzen 2003; Du and Ji 2003; Du et al. 2006). Clearly, prolonged exposure to high incubation temperatures influences the developing physiological systems so that hatchlings have their locomotor performance compromised to some extent which ultimately could result in decreased fitness of hatchlings.

Decreased locomotor performance can potentially expose hatchlings to an increased chance of predation. Slower crawling speeds and decreased self-righting ability potentially prolong the time hatchlings are exposed to terrestrial predators such as sea gulls and other avian predators as they crawl from their nest to the water's edge. Although in the hatchery situation, this is not such a

problem because hatchlings are generally shepherded to the waters edge by hatchery staff. However, once in the water where the majority of predation on hatchling sea turtles occurs (Gyuris 1994, 2000; Pilcher et al. 2000), decreased swimming performance will increase the time that hatchlings are exposed to the relatively high density of fish predators found in near-shore waters. The larger size of hatchlings from cooler nests may also increase a hatchling's fitness by increasing its chances against gape-limited predators (Burgess et al. 2006), and indeed, field experiments have indicated that larger green turtle hatchlings have a greater chance of surviving the near-shore swim compared to smaller hatchlings (Gyuris 2000). In summary, high nest temperatures are detrimental to embryos/hatchlings of olive ridley turtles as evidenced by decrease emergence success, decrease in hatchling size, and decrease in hatchling locomotor performance.

Although water availability in the nest can affect embryonic development and hatchling quality of turtle eggs, particularly in species like sea turtles that lay pliable shelled eggs (Packard and Packard 1986; Janzen et al. 1990; McGehee 1990), these effects are only obvious in very wet nests (which result in embryos drowning) or dry nests where embryos are in negative water balance. In between these extremes, the developing embryo is sufficiently buffered against variations in nest hydric conditions that embryonic development is little affected. Hence, despite the difference in the amount of cumulative rainfall experienced, nests at APNP in 2009 and 2010, there was no detectable effect on hatchling size or locomotor performance because the hydric environment of nests remained within the optimal range throughout the incubation period.

Mode of egg transport emergence success and hatchling quality

Eggs transported in plastic bags had lower nest emergence success. A possible explanation for this finding is that eggs transported in plastic bags are exposed to greater rotational movement during the transporting process. Rotational movement is known to be fatal to sea turtle eggs once the 'white spot' has formed when the vitelline membrane attaches to the inter shell membrane surface (Limpus et al. 1979). However, all eggs were transported before this process occurred in the present study and mode of transport did not influence the percentage of undeveloped eggs (P = 0.468). The increased mortality of eggs transported in plastic bags occurred in eggs that had clear signs of embryonic development but failed to hatched and it is difficult to speculate on a mechanism that transport mode could have on this category of embryonic mortality. Likewise, it is difficult to find a mechanism that might explain why eggs transported in plastic bags also had

decreased self-righting ability and how transport in styrofoam boxes might result in larger carapace size. Nest temperatures of eggs transported in styrofoam boxes were not different from those transported in plastic bags or buckets so differences in carapace size cannot be explained by the influence of nest temperature.

Hatchery management and the way forward

The current sea turtle rookery management practice at Alas Purwo National Park is to relocate all clutches of eggs into a protected beach hatchery and this practice has been in place for over 25 years. The predation of all nests left on the beach, even nests that had protection barriers erected around them within the first few days of oviposition, justifies the practice of translocating all natural nests into the protected hatchery. However, this study demonstrates that current management procedures could be fine-tuned to increase hatchery success and quality of hatchlings produced in the hatchery. The practice of transporting eggs from natural nests to the hatchery in plastic bags should be replaced with transporting them in styrofoam boxes lined with a layer of sand. This change should increase nest emergence success and contribute to maximizing hatchling locomotor performance and carapace size.

Currently, the biggest problem in the hatchery is excessively high nest temperatures that result in reduced nest emergence success and a clear reduction in hatchling quality as demonstrated by smaller hatchling carapace size and decreased locomotor performance. High nest temperatures are caused by a combination of metabolic heating and high sand temperature. Current management practice is to place nests 30 cm apart in the rookery and this practice results in a general rise in hatchery sand temperature because of the combined metabolic heat generated by closely located clutches of eggs. Close location of nests and subsequent lethally high nest temperatures have also been reported in a natural *arribada* nesting population of olive ridley turtle (Valverde et al. 2010). Spacing the nests at least one meter apart should be implemented in order to limit the synergistic metabolic heating effect of closely located nests (Boulon 1999; Mortimer 1999; Patino-Martinez et al. 2012b). Generally, high sand temperatures in areas that are exposed to full sun all day are also a major cause of high nest temperatures within the hatchery. The use of a section of the hatchery that receives shade for part of the day reduced nest temperatures by about 2 °C in 2009 and the use of shade is a viable strategy that has previously been recommended to reduce undesirably high nest temperatures at sea turtle rookeries (Reece et al. 2002; Chu et al. 2008; Patino-Martinez et al. 2012b). Hence, placing hatchery nests into areas of full and partial shade as well as leaving a few nests in full sun will provide a range of nest temperatures and reduce the incidence of undesirably high nest temperatures. Indeed, if as predicted, general sand temperatures increase in the future as a consequence of global warming, the provision of shade may be the only viable option for providing suitable nest temperatures at current rookery sites in the future (Patino-Martinez et al. 2012b).

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