Management and Conservation Article

Impact of Clutch Relocation on Green Turtle Offspring

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ABSTRACT For species with temperature-dependent sex determination, such as marine turtles, global climate change poses numerous threats. At the nesting beach, rising temperatures are predicted to further skew already female-biased sex ratios and increase embryonic mortality; sea-level rise and resultant coastal squeeze may leave few alternative breeding habitats in developed regions. As a result, clutch relocation, a commonly used management tool to reduce egg loss, may become necessary for safeguarding populations. Although studies have examined the impact of relocation on clutch success, few have examined the impact of this practice on the sex or phenotypic characteristics of hatchlings produced. We used a randomized block design experiment to examine effects of relocation on green turtle (*Chelonia mydas*) clutches. We compared hatching success, thermal conditions, and size (length and mass) of hatchlings from in situ control clutches with those subjected to 2 relocation methods, while controlling for maternal and other environmental effects. Relocated clutches did not vary significantly from control clutches in incubation temperature or inferred sex ratios during the critical middle third of incubation when sex is thought to be determined. Hatchling size was also unaffected by relocation. Both relocation methods, however, resulted in a 20% reduction in hatching success in comparison to in situ clutches. Clutch relocation is, however, likely to affect the population primary sex ratio, when clutches are relocated from sites in proximity to the sea where tidal inundation is a threat. Here, cooler conditions are likely to produce more males than are the warmer female-producing temperatures higher up the beach. For clutches at risk, relocation is a viable process and does not appear to affect hatchling size or predicted sex ratios if relocation sites are selected in areas utilized by other females. We urge caution, however, when moving clutches from potentially male-producing sites, particularly given predicted impacts of climate change on already female-biased sex ratios. (JOURNAL OF WILDLIFE MANAGEMENT 73(7):1151–1157; 2009)

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Clutch relocation is a common management tool used by marine turtle conservation programs, whereby clutches are moved from a threatened site to a safer location, be it to an enclosed hatchery area or simply to another section of beach. Where clutches would otherwise have been lost to predators or illegal human take, relocation may be necessary. Similarly, where clutches are at risk from tidal inundation or erosion, clutches are frequently moved. These aptly named doomed clutches (Dutton and Whitmore 1983, Mrosovsky 2006) can account for 20% of clutches laid by green turtles (*Chelonia mydas*) in certain areas (Dutton and Whitmore 1983, Hoekert et al. 1998).

Relocating clutches of eggs does not come without its own issues (Mrosovsky 2006). Relocation can sometimes have a negative effect on hatching success when compared to natural nests left in situ (Eckert and Eckert 1990, Marcovaldi and Laurent 1996, Rees et al. 2002, Özdemîr and Türkozan 2006) or a positive effect when compared to doomed nests left in situ (Wyneken et al. 1988, Hoekert et al. 1998). Furthermore, Mrosovsky (2006) recently suggested that consistent relocation of doomed clutches could lead to distortion of gene pools, via relaxation of selection pressure against females nesting too near the water.

Of greater immediate concern is the potential impact of relocation on the thermal conditions within the clutch. In marine turtles, temperature during incubation affects the physical phenotype of hatchlings (Glen et al. 2003), including sex of offspring, through the mechanism of temperature-dependant sex determination (TSD; Mosovsky and Yntema 1980, Girondot 1999, Qualls and Andrews 1999, Shine 1999, Xiang et al. 2006). Temperature-dependent sex determination relies upon the existence of a pivotal temperature, described as the temperature at which a 50:50 sex ratio is produced (Ackerman 1997). In marine turtles, the pivotal temperature is around 29° C (Mrosovsky 1994, Wibbels 2003) and at temperatures exceeding this, most embryos develop into females, whereas below this threshold males are mostly produced (Yntema and Mrosovsky 1980). The main sensitive period of development for sea turtle eggs is reported to be in the middle third of incubation, when gonadal development is thought to occur (Mrosovsky 1980). Temperature also affects success of the clutch, with high incubation temperatures causing an increase in embryonic mortality (Ackerman 1997, Broderick et al. 2001, Godley et al. 2001*a*).

Considering that most studies to date have recorded female-biased primary sex ratios (see Wibbels 2003 for review), the predicted rise in both temperatures and sea level as a result of global climate change may have major impacts on marine turtle populations (Fish et al. 2005, Hawkes et al. 2007, 2009). If females cannot change the latitude or phenology of breeding, a possibility given that they exhibit natal philopatry and site fidelity to nesting beaches, and continue to breed in current locations, clutches will incubate

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at higher temperatures, further skewing sex ratios and potentially increasing embryo mortality. In addition it is likely that females will lose nesting habitat through a combination of sea-level rise and coastal squeeze (Fish et al. 2005).

Some doomed clutches, if left in situ, may indeed hatch (Mrosovsky et al. 1984, Whitmore and Dutton 1985), be it at reduced success, and these clutches, being in proximity to the sea, are likely to be cooler and could be critical in producing males for the population (Baptistotte et al. 1999, Naro-Maciel et al. 1999). As a result of global climate change, clutch relocation may become a vital management tool for preserving marine turtle populations and it is important that we further investigate and understand effects of such management protocols upon populations. Although studies have reported variation in hatching success between relocated and in situ clutches, none to our knowledge have effectively controlled for effects of extrinsic, as well as intrinsic factors, such as nest-site location, nest depth, temperature, and date of lay that may affect hatching success.

We examined effects of 2 commonly used methods of turtle clutch relocation on production of green turtle hatchlings. We compared thermal conditions within study clutches allowing us to predict resultant sex ratios and the physical phenotype of hatchlings produced. We also investigated how relocation may be influencing success of clutches.

STUDY AREA

We conducted our study on Ascension Island (United Kingdom), a small volcanic island in the South Atlantic Ocean (7°56′S, 14°22′W), the site of one of the largest green turtle rookeries in the world with a population estimated to be >11,000 females (Broderick et al. 2006). Nesting on Ascension occurs between December and July, peaking in March (Godley et al. 2001*b*). Nest relocation was not a common management practice at Ascension Island, in part because the large recovering nesting population required little direct management and also because of management choice to leave nests in their natural environment. With nesting occurring in such high densities, this site provided an ideal location for our study.

METHODS

Nest relocations took place between 12 March and 3 April 2006 on Long Beach, an uninterrupted stretch of sand 965 m long with no shading and no natural vegetation. We relocated clutches within 6 hours of laying. We used a random block design and established 23 study blocks. Each block consisted of 3 clutches, 2 of which were relocated clutches (each representing one of the 2 types of relocation method; i.e., treatments 1 and 2), and one was a natural undisturbed control nest. We chose the site of the control clutch effectively at random, because this clutch remained in the location chosen by the nesting females. We placed the 2 relocated clutches alongside the control clutch so that all 3 clutches within a block were equidistant to the waters edge. We randomly allocated the order of the clutches within the block to ensure no order effect of position within the block. Maximum distance between the outer 2 nests in each block was approximately 5 m.

We patrolled the beach until we found a nesting female. We recorded depth of the nest chamber prior to the female laying any eggs, and we placed a TinyTag temperature logger (Gemini Dataloggers, Chichester UK; resolution of 0.01° C; accuracy 0.3°) in the center of the clutch. We set all data-loggers to record temperature synchronously every hour throughout the incubation period. We then marked the site of the clutch and left the female to camouflage her clutch. Patrols were then continued to locate doomed clutches, this time focusing upon the tidal area of beach below the escarpment, which is at high risk of erosion and tidal inundation. Upon locating a nesting female, we applied one of 2 relocation methods to her clutch. The method used was often determined as a result of her stage of laying; if she had already laid eggs, we used treatment 1. Individual females were only ever used once in our experiment irrespective of the location of their subsequent clutches.

For treatment 1, we allowed the female to complete the nesting process undisturbed. We marked the exact site of the clutch within the nest at the time of laying, and we excavated eggs once the female had camouflaged her clutch and returned to the sea (within 1–6 hr after laying). Once located, using rubber-gloved hand we carefully placed the eggs in a clean plastic bag within a bucket and transported them to the site of the in situ control nest where we then reburied the clutch in a hand-dug nest, 1.5 m to the side of the control nest. We buried eggs at the same depth as the control nest. As with the control nest, we placed a temperature logger in the center of the clutch and marked the nest site with posts.

For treatment 2, we observed the female to be at the latter stages of preparation of her egg chamber and we closely observed her until the onset of laying. We removed eggs by rubber-gloved hand from the chamber as they were being laid and transferred them directly to a clean plastic bag within a bucket. Once the female had finished laying, we immediately transported the eggs to the control nest site and reburied them in a second hand-dug nest in exactly the same manner as treatment 1.

We measured the curved carapace length of all experimental nesting females (CCLn-t; Bolten 1999) using a 1.5-m soft tape, with 3 measurements to ensure accuracy and a mean CCLn-t calculated and used for subsequent analyses. We placed 4 wooden posts around each nest to mark its location and record nest details. Because nesting density was at its peak during our study, the posts also served to protect the clutches by preventing subsequent nesting females from digging them up.

Fifty days after laying, we placed wooden frames (60 × 60 × 10 cm) over nests with fly-screen netting securely attached to the top side to contain emerging hatchlings. We checked nests early every morning for presence of hatchlings. Following emergence, we measured straight carapace length (Bolten 1999) and mass of a random sample of 5–10 hatchlings from each nest. From 36 hours to

96 hours following hatchling emergence, we excavated nests by hand. We removed all eggs from the nest, and recorded numbers of each of the following: hatched shells, dead hatchlings, nonviable eggs (unyolked), and number of unhatched eggs. We incised unhatched eggs and categorized them according to developmental stage or absence of embryo. We categorized embryos smaller than the remaining yolk as less than halfway through development, and we counted those that were larger than the remaining yolk as more than halfway through development. We classified eggs yolked but with no gross signs of embryonic development simply as yolked, because it was unknown whether these were unfertilized or if early embryonic death had occurred.

We collected temperature loggers during excavation and used TinyTag software to download the data (TinyTag Explorer, version 4.2; Gemini, Chichester, United Kingdom). From these data, for each nest we calculated incubation duration (defined as time of laying to time of first hatchling emergence), mean daily incubation temperature, and mean daily temperature during the first, middle, and final thirds of incubation. Previously at this site, Godley et al. (2002) recorded temperature of in situ clutches and determined sex of offspring through histological examination of the gonads. We applied temperatures recorded in our study to results of Godley et al. (2002) to estimate sex ratios.

We analyzed data using either Residual Maximum Likelihoods (REML) or Generalized Linear Mixed Models (GLMMs) with Poisson error distributions and a log link function, dependent upon distribution of the error structures, using Genstat Release 8.1 (Genstat 2005). The REML and GLMMs allow both fixed and random factors as well as covariates to be fitted and random factors control for the use of repeated measurements (Schall 1991). We calculated the significance of fixed terms in REML and GLMMs using maximum likelihoods and assessed it by their Wald statistics, which were distributed as chi-squared for each term fitted last in the model. For all analyses we included the block within which nests were situated and the order of nests within this block as random factors and included nest treatment as a fixed factor.

Because incubation temperature is instrumental in determining sex of sea turtle hatchlings and we used clutch temperature during the middle third of incubation to estimate sex ratios, an investigation of variables possibly affecting temperature at this time period is essential. We used a GLMM approach to examine the effect of our nest treatment on clutch temperature during the middle third of incubation (when sex is determined) with the maximal model also including female size, incubation duration, date of laying, number of early stage dead embryos (ESD), number of late-stage dead embryos (LSD), and clutch size as covariates.

In our REML analyses of the physical phenotype of hatchlings, we used mean hatchling size (length) and mass as response variables, with maximal models including nest treatment, temperature (middle third of incubation), incubation duration, date of lay, clutch size, and female size as covariates. Because larger females are known to produce larger hatchlings (Glen et al. 2003), we retained female size in these models.

To determine whether relocation protocols were affecting overall hatchling production, we examined the effect of nest treatment on hatching success (arcsine-transformed) using REML analyses, with female size, incubation duration, date of laying, clutch temperature (middle third), and clutch size included as covariates. We used subsequent GLMMs to examine the effect of nest treatment on number of ESD and LSD occurring in clutches. Maximal models included clutch size, female size, clutch temperature (middle third), date of lay, number of yolked eggs, and incubation duration as covariates as well as the effect of nest treatment.

For each analysis we constructed the best-fitting model by stepwise deletion of the least significant term until only significant terms ($P < 0.05$) remained in the model, following Crawley (1993). For REML analyses we checked model residuals for normality and homoscedasticity at each step of removal. We computed post hoc comparisons of nest treatment by dividing the differences between the parameter estimates by differences between the standard errors of the parameters and interpreting the output as a *t*-test with degrees of freedom equal to the residual of the model (Zar 1999).

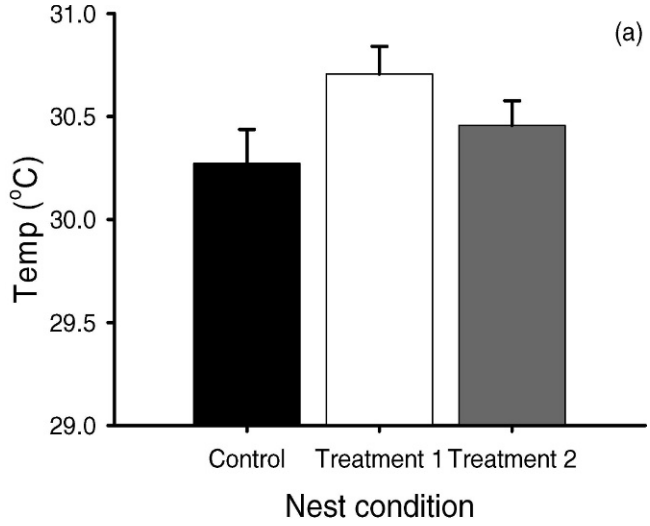
RESULTS

Of our 69 study clutches only one clutch failed to hatch (treatment 2) and we were unable to successfully locate a further 2 clutches (both relocated using treatment 1) owing to disturbance of clutches and markers by other nesting females. We included all hatched clutches in the models.

Using the temperature–sex ratio curve generated for this population (Godley et al. 2002) we estimated 87% (SD = 9%, range = 70–100%) of offspring from control clutches to be female. We estimated sex ratios from relocated clutches to be 94% (treatment 1; SD = 5%, range = 79–100%) and 92% (treatment 2; SD = 7%, range = 70–100%) female, although these were not significantly different from control clutches. There was no effect of clutch relocation on mean nest temperature during the middle third of development (Fig. 1a). We found clutch size (GLMM: W = 8.63, $P < 0.01$), date of lay (GLMM: W = 13.57, $P < 0.001$), number of early stage dead embryos (GLMM: W = 32.53, $P < 0.001$), and number of late-stage dead embryos (GLMM: W = 38.28, $P < 0.001$) all had positive effects on nest temperature during the middle third of incubation.

Relocation did not affect hatchling length (Fig. 1b) or mass. Date of laying did, however, have a negative effect on hatchling length (REML: W = 7.40, $P < 0.01$), with smaller hatchlings produced later in the season, and female size had a positive effect on hatchling mass (REML: W = 8.82, $P < 0.01$), with larger females producing heavier hatchlings.

Nest treatment affected hatching success (REML: W = 16.55, $P < 0.001$) with post hoc comparisons revealing that control clutches had greater hatching success ($\bar{x} = 0.86 \pm 0.16$, $n = 23$) than those from treatment 1 (REML post hoc comparison: $t = 4.68$, $P < 0.01$; $\bar{x} = 0.66 \pm 0.18$, $n = 21$) and treatment 2 (REML post hoc comparison: $t = 5.29$, $P < 0.01$; $\bar{x} = 0.67 \pm 0.19$, $n = 22$ [Fig. 2a]; control = 87%,



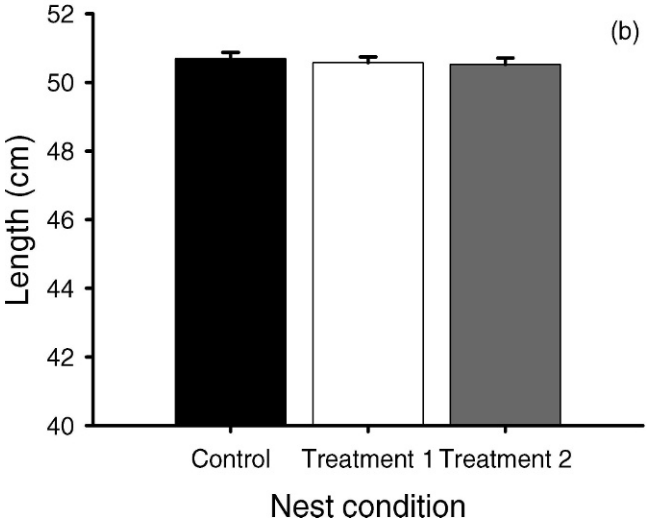
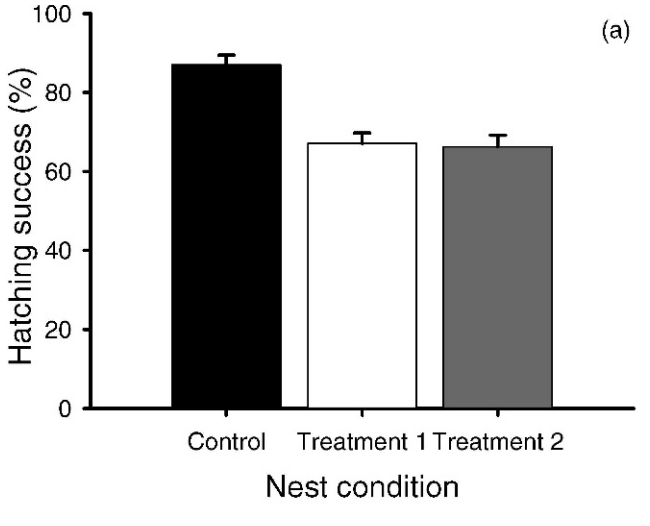


Figure 1. Effect of clutch relocation on (a) temperature during the middle third of incubation and (b) hatchling straight carapace length of green turtles at Ascension Island, United Kingdom, 2006. Shown are fitted values of the model, which account for the effect of all significant predictor variables in the model and reflect the true relationship. Error bars are 1 standard error.



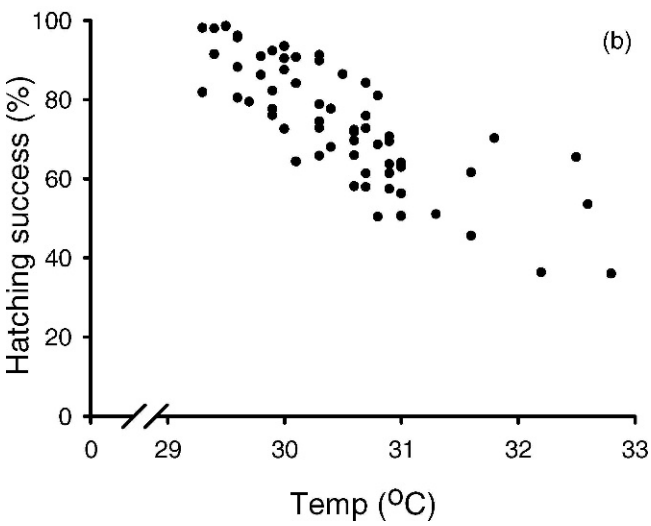


Figure 2. Effect of (a) nest relocation and (b) temperature during the middle third of incubation on mean hatching success of green turtle clutches at Ascension Island, United Kingdom, 2006. Shown are fitted values of the model, which account for the effect of all significant predictor variables in the model and reflect the true relationship. Error bars are 1 standard error.

treatment 1 = 67%, treatment 2 = 66%). There was no difference in hatching success for the 2 treatment types (REML post hoc comparison: $t = 0.59$, $P > 0.05$). Mean daily nest temperature during the middle third of incubation had a negative effect on hatching success (REML: W = 36.65, $P < 0.001$; Fig. 2b) as did clutch size (REML: W = 4.69, $P < 0.03$).

To investigate how relocation may be affecting hatching success we examined frequency of embryonic mortality within study clutches, dividing into late- and early stage embryonic mortality. In our model with number of early stage dead embryos as the response variable, we found nest treatment to have an effect (GLMM: W = 11.13, $P < 0.001$; Fig. 3a). Clutches relocated using treatment 2 had more dead early stage embryos than control nests (GLMM post hoc comparison: $t = 4.38$, $P < 0.01$) and treatment 1 nests (GLMM post hoc comparison: $t = 3.55$, $P < 0.01$), although there was no difference between control nests and treatment 1 nests (GLMM post hoc comparison: $t = 1.49$, $P > 0.05$). Clutch size (GLMM: W = 23.33, $P < 0.001$) and temperature during the middle third of incubation (W = 43.93, $P < 0.001$) also had an effect on number of dead early stage embryos in a clutch.

Nest treatment had an effect on number of dead late-stage embryos in a clutch (GLMM: W = 8.66, $P < 0.001$). Treatment 1 nests had more dead late-stage embryos than both control nests (GLMM post hoc comparison: $t = 3.94$, $P < 0.01$) and treatment 2 nests (GLMM post hoc comparison: $t = 2.39$, $P < 0.05$; Fig. 3b), although there was no difference between control nests and treatment 2 nests in number of dead late-stage embryos in a clutch (GLMM post hoc comparison: $t = 1.52$, $P > 0.05$). Clutch

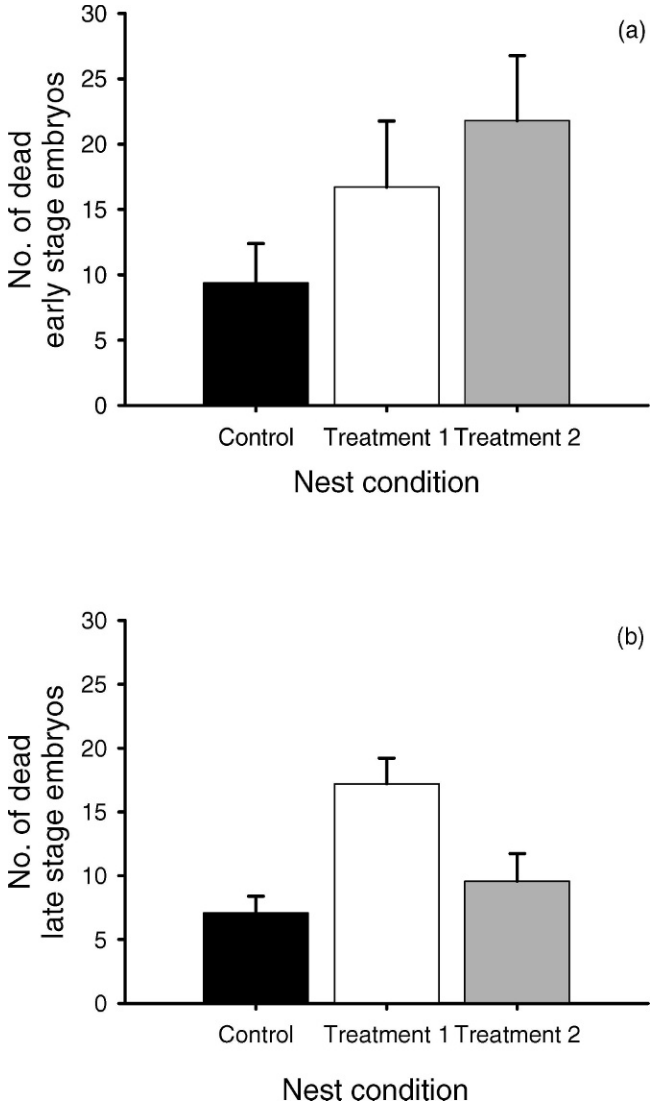


Figure 3. Effect of nest relocation on (a) the number of dead early stage embryos and (b) the number of dead late-stage embryos found in green turtle clutches at Ascension Island, United Kingdom, 2006. Shown are fitted values of the model, which account for the effect of all significant predictor variables in the model and reflect the true relationship. Error bars are 1 standard error.

size (GLMM: W = 17.54, $P < 0.001$) and clutch temperature (middle third; GLMM: W = 35.53, $P < 0.001$) both had positive effects on number of dead late-stage embryos, although number of early stage dead embryos (GLMM: W = 8.92, $P < 0.01$) and date of lay (GLMM: W = 5.89, $P < 0.05$) had negative effects.

DISCUSSION

Although we found that nest relocation reduced hatching success, nest relocation may be acceptable if clutches would otherwise fail. Most important, however, for an ectotherm with TSD, was that relocated clutches did not experience different temperature regimes in comparison to natural in situ clutches in the same area of beach, nor was there any effect on the resultant hatchling size, which is known to be influenced by temperature (Glen et al. 2003).

Other studies have reported temperature differences, with clutches relocated to hatcheries being warmer than undisturbed in situ clutches, raising concerns regarding altered sex ratios of hatchlings (Hoekert et al. 1998). The pivotal temperature for green turtles on Ascension Island is 28.8° C (Godley et al. 2002) and, thus, at 30.3° C, average temperatures within in situ nests during the critical sex-determining period were well above the pivotal value and were likely to have resulted in a female-skewed sex ratio of hatchlings. We assumed that sex ratios were unaffected; in reality, there may be other variables such as moisture that play a role in determining sex. Indeed, van de Merwe et al. (2005, 2006) examined effects of shading and nest depth on green turtle clutches and found no relationship between clutch temperature during the middle third of development and sex ratios produced. Such results, however, need to be carefully examined and may have been a result of the small range in temperatures recorded (27.5–29.3° C) and the resolution of data-loggers used to record temperature (DS1921 Thermochron iButtons, Dallas, TX; resolution ±0.5° C; accuracy ±1° C).

It is possible that we changed the temperature regime that doomed clutches would have been exposed to if left in place and in doing so may have further skewed the sex ratio in favor of a female bias. The potential effects of clutch relocation at a population level via alterations to the gene pool and the capacity for evolution due to relaxation of selection pressure for nesting too near the water (Mrosovsky 2006) are at present unknown but, with fewer males produced, could be profound. Our findings also reinforce issues raised by Mrosovsky (2006), who recommends projects that relocate every clutch in a season to a common hatchery should reexamine relocation as a conservation strategy for doomed clutches. With increasing climatic temperatures and predicted sea-level rises relocation may become a much more standard practice and we support recommendations of Mrosovsky (2006) that relocation take place with less alacrity and with more discussion and regulation than at present.

Further examination of the 2 methods we used to relocate clutches may aid us in understanding how relocation reduces hatching success. The physical handling of eggs during relocation may have caused reduced hatching success in relocated clutches by causing shock to developing embryos. Current practice assumes that handling is not harmful prior to attachment of the yolk sac membrane to the shell, thought to occur >24 hours after egg deposition (Limpus et al. 1979, Booth 2004), although clutches relocated up to 96 hours postlaying have been shown to be unaffected (Abella et al. 2007). Damage caused to the shell through handling and abrasion from the sand and removal of the protective layer of fluid secreted with the eggs by the female may also affect hatching success (Boulon 1999) and we may have inadvertently caused these effects during our relocation treatments.

One of the most likely explanations for our reduced hatching success is that our artificial man-made nests are probably of poorer quality in comparison to natural turtle nests. The egg chamber in man-made nests may have been different in terms of size and shape, which would affect how

the clutch is configured and may potentially affect the surface area that is available for gaseous exchange, either through configuration itself or increased sand coating of egg shells. The surface area of eggs available for gaseous exchange may affect hatching success. Furthermore, it is likely that we moved relocated clutches to nests of differing depths to those in which they had originally been laid, because we dug artificial nests to the same depth as the control nest. We may well have relocated clutches from deep chambers into shallow chambers and vice versa. It is unknown whether females choose to dig deeper chambers when laying larger clutches, but if such a phenomenon exists, by creating chambers either deeper or shallower than any given clutch would naturally be laid in, we may have affected its eventual hatching success. Nest-site selection, in particular nest depth, deserves further consideration in future research.

Female quality and quality of clutches that are relocated are greatly overlooked when considering relocation and reporting hatching success of relocated clutches. All relocated nests in our study came from females that were nesting in the tidal zone and females that attempt to nest there may be lower quality individuals compared to those that nest further up the beach. Therefore, the lower hatching success seen in relocated clutches may be because of female quality issues and not relocation per se. However, we did control for female size in our model, commonly shown to be related to egg and clutch size in marine turtles (Broderick et al. 2003).

An alternative explanation for reduced hatching success in relocated clutches is that females tailor clutches they lay for the area of beach where they are to be laid. Therefore, females that actively choose to nest below the inundation line may be selectively adjusting their clutch to produce males. By moving these clutches further up the beach we may have placed clutches in an environment that was less than ideal for that clutch, causing the resultant decrease in hatching success. Several recent studies on marine turtles have shown that nest-site location is highly repeatable within individual females and that females showed high fidelity to locations both within and between years (Kamel and Mrosovsky 2004, 2005, 2006) and that clutches tended to be larger the further inland they were laid (Kamel and Mrosovsky 2005). Repeatability of nest sites may indicate that females are selecting sites to manipulate offspring sex ratios or may be a result of larger females producing larger clutches and having the ability to travel further from the waters edge. Experiments to elucidate the exact nature of reduced success in relocated clutches, which in all likelihood will be different at different locations, would be useful to improve conservation management strategies.

Hatching success was lower in our relocated clutches than in natural ones, but if left to their own devices, we believe most relocated clutches would not have hatched due to inundation and beach erosion. The area from which we moved clutches was inundated for much of the postrelocation period and was subjected to harsh wave action. Most clutches laid in this zone are completely washed away. At sites such as Ascension Island, where nesting density is high, it is difficult to assess what proportion of clutches would be lost if left in situ. As a result, we collected no data on hatching success of undisturbed doomed nests, but past research on green turtles and leatherbacks (*Dermochelys coriacea*) in Suriname has shown that 65% of undisturbed clutches did not hatch, whereas only 18% of relocated clutches remained unhatched (Hoekert et al. 1998). In such cases any increase in hatching success achieved through relocation can be viewed as positive.

MANAGEMENT IMPLICATIONS

Clutch success was reduced in relocated clutches, with both methods producing similar (approx. 20%) reduction in success. Where clutches would otherwise have been lost, and where populations require intervention, clutch relocation may be an acceptable management practice for conservation of marine turtle populations. Many conservation projects, however, use clutch relocation as a management tool without prior assessment of the level of clutch loss and potential skewing of already female-biased sex ratios. We urge caution and stress the need for evidence-based conservation, especially in populations that do not require invasive action (Frazer 1992).

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