distance travelled, about 40% more than the direct distance, and numerous locations at
the same spots, both suggest a random searching pattern of emperor penguins on their
way to polynias.

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Assessing the nesting beach fidelity and clutch frequency of sea turtles by satellite tracking

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Satellite tracking can only be applied to marine animals if they spend time at the sea sur-
face or out of the water, thus enabling transmission of messages (uplinks) to the satellite.
For many species the probability of surfacing is low (Priede & French 1991). Sea turtles
spend almost their entire adult life at sea, but reproductive females emerge onto beaches
to lay their eggs in a chamber that they excavate in the sand. This provides an opportu-
nity for monitoring by satellite. As with many animal activities, nesting behaviour in turtles
is coupled to the diel cycle, occurring mainly at night. The satellites of the Argos system
also orbit in a fixed relationship to the diel cycle and at low latitudes there is not uniform
coverage over the whole 24-h cycle. The phase relationship between animal behaviour
and satellite overpasses is therefore an important factor in determining the success of
satellite tracking studies. Hays et al. (1991) have demonstrated the technical feasibility of
locating loggerhead turtles by satellite. This chapter considers the effects of the phase
relationship between turtle emergences and satellite overpasses for a particular locality,
and demonstrates methods for calculating the probability of detection using the Argos
system.

In addition to nesting emergences, sometimes a turtle will emerge onto a beach but
will not nest, such an event commonly being termed a ‘false-crawl’ (cf. Dodd 1988). It
has been assumed that when a turtle has false-crawled it will emerge and nest on either
the same or a subsequent night (Caldwell et al. 1959, Frazer 1984). False-crawls poten-
tially increase the probability of uplink acquisition and detection of nesting events.

By tagging nesting females with numbered flipper tags, it has been repeatedly demon-
strated that during a single season individuals may nest several times and with a pre-
dictable inter-nesting interval (cf. Frazer & Richardson 1985, Hays & Speakman 1991),
and may nest on more than one beach (Stoneburner & Ehrhart 1981, Bjorndal et al. 1983,
Iwamoto et al. 1985, Le Gall & Hughes 1987, Hays & Sutherland 1991). It is important to establish the true clutch frequency and beach fidelity of sea turtles. The number of clutches that turtles lay in a season is an integral component of their overall reproductive capacity, and is therefore an important factor in sea turtle population models (Frazer 1984, Crouse et al. 1987). Many sea turtle beaches are threatened by human developments (Corbett 1989) and the capacity of populations to survive may be influenced by their ability to select alternative nesting beaches. However, with conventional methods of personnel patrolling beaches at night it is logistically impossible to detect every nesting event. Satellite tracking may provide an alternative method of establishing clutch frequency and beach fidelity (Hays et al. 1991).

METHODS AND RESULTS

The framework of the model
To establish, by satellite tracking, that a turtle has laid a clutch, the turtle may be located on land on either a nesting emergence and/or a preceding false-crawl. If a satellite passes over while the turtle is on land, and messages are successfully received by the satellite, then a location may be obtained. Hence the probability of obtaining a location while the turtle is on land will be dictated by the interaction of (1) the satellite overpass times, (2) the time when the turtle is on land, and (3) the efficiency with which locations are obtained when the satellite is overhead ($L_e$) (Keating et al 1991). Each of these components may be quantified. The timing of satellite overpasses may be calculated from orbital prediction software. The time when a turtle may be on land can be revealed by

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Fig. 1. The length of time (min) that turtles spent on (a) nesting emergences, and (b) false-crawls.

Fig. 2. The observed time interval between consecutive emergences.
Assessing the nesting of sea turtles by satellite tracking

Fig. 3. (A) The time of day that turtles emerged on either nesting emergences (hatched area) or false-crawls (solid area) and the times at which NOAA 10 (B) and NOAA 11 (C) rose above 5° elevation on overpasses over Cephalonia.

Fig. 4. The probability distribution for the number of false-crawls that preceded a nest.

number and timing of false-crawls preceding nesting emergences. \( L_n \) may be calculated by positioning test platform transmitter terminals (PTTs) on nesting beaches.

Applying the model

I applied the model to loggerhead turtles (Caretta caretta) nesting on the island of Cephalonia, Greece (38.067°N, 20.758°E) from 1985 to 1991. Field data were collected by foot patrols on beaches on Cephalonia during the nesting season (June to September).

To calculate how long turtles spent on land while on false-crawls and while on nesting emergences, I only used ‘on-land’ times that were recorded if the turtle was encountered as it was still crawling up the beach and had not attempted to dig, i.e. times for turtles that had only recently (<10 min) emerged from the sea. I assumed that the unobserved period of the crawl out of the sea occurred at a speed of 5.75 m min\(^{-1}\) (Hays & Speakman in press). The mean time spent on the beach by turtles while they were on nesting emergences was 92.2 min (\( n = 20, \ SD = 21.7 \) min) (Fig. 1a). The mean time spent on the beach on false-crawls was 31.0 min (\( n = 12, \ SD = 18.9 \)) (Fig. 1b).

I assumed that the turtle had nested undetected if it was not seen within one week of a false-crawl. The time interval between successive emergences associated with the same
nest (i.e. between two false-crawls, or a false-crawl and a nesting emergence) ranged from 70 min up to four days (Fig. 2).

A frequency distribution for the time when turtles emerge from the sea will be influenced by the beach patrol protocol. For example, if the most rigorous beach patrols are conducted earlier on in the night, then this will skew the frequency distribution of emergence times to the left (i.e. to earlier in the night). Therefore, to calculate a frequency distribution of emergence times I only used data collected in 1991, as the most uniform and methodical beach sampling was achieved in this year (in only one out of a total of 33 nests was the turtle not observed). I calculated how long an encountered turtle had already been on the beach, using the mean times to complete the various processes associated with nesting reported by Hays & Speakman (1991). The time that individuals came out of the sea was recorded for 32 nesting emergences and 14 false-crawls. Turtles emerged during most of the night, with the peak number of emergences between around 2330 h and 0230 h (Fig. 3A).

To calculate the proportion of false-crawls to nesting emergences I also used data only from this year. False-crawls were identified by direct observation (n = 14), by the absence of any digging (n = 15) and, if digging had occurred, by the absence of any
hatching tracks later on in the season (n = 5). Turtles laid a total of 33 nests and made a total of 34 false-crawls, i.e. the proportion of false-crawls to nesting emergences was 1.03. Using this value for the intensity of false-crawls per nest, I calculated the probability density function (Poisson distribution) for the number of false-crawls preceding nesting emergences (Fig. 4). Most nests (>70%) would have either zero or one false-crawl preceding them, further increases in the number of false-crawls per nest occurring with a progressively lower probability.

To determine the timing of satellite overpasses over Cephalonia, I used satellite predictor software (Telonics Satellite Predictor, Telonics Inc., 932 E Impala Avenue, Mesa, AZ 85204-6699, USA), and ephemeris data from NASA Prediction Bulletins (NASA/Goddard Space Flight Center, Code 513, Greenbelt, MD 20771, USA). Following the procedure of Service Argos (1989) and Mate et al. (1986), I assumed that once the satellites were over 5° above the horizon they were able to receive signals from a PTT at sea level. As the number of messages received by the satellite on an overpass increases, so the accuracy of the location (location class (LC) specified by Service Argos) improves. LC 0 is the least accurate, with the reported position accurate to within only tens of kilometres (Keating et al. 1991, Hays et al. 1991). LCs 1–3 are progressively more accurate, but can only be obtained when ≥ 4 messages are received by a satellite on an overpass (Argos, 1989). I assumed that PTTs would be built with a pulse repetition only tens of kilometres (Keating range 8–12 overpasses per day; Fig. 3). These would be equally distributed between the satellites, so that if a satellite was overhead for ~ 315s while a turtle was on land then a high-quality location was expected. The number of satellite overpasses (NOAA 10 and 11) would occur per day over Cephalonia (Fig. 3B and C) (n = 30, range 8–12 overpasses per day; Fig. 3). These would be equally distributed between the two satellites (mean number of overpasses per day 4.9 for NOAA 10 and 5.0 for NOAA 11). However, NOAA 11 but not NOAA 10 would pass over at night when turtles would be on land.

I assumed an Ls value of 1, and having thus defined the components of the model I conducted a simulation of nesting events. I first randomly selected a day in June for a nesting emergence. From the known frequency distributions of nesting events (Figs 1–4), I then randomly selected:

1. the time the turtle left the water on a nesting emergence (Fig. 3A);
2. the length of time that the turtle spent on land while nesting (Fig. 1a);
3. the number of false-crawls preceding that nesting event (Fig. 4);
4. the length of those false-crawls (Fig. 1b);
5. the time interval between false-crawls associated with the nesting emergence (Fig. 2).

If a false-crawl had occurred on a different night to the nesting emergence, I calculated when it had occurred on that other night from Fig. 3A.

I then used the satellite predictor software to calculate whether the turtle would have been located while on the nesting emergence or the false-crawl preceding it, and hence the laying of a clutch identified. I simulated 100 nesting events (nesting emergences plus the associated false-crawls). NOAA 10 failed to locate any turtle that was on land. NOAA 11 located a turtle that was on a nesting emergence on 53 of the 100 nesting events, and on a false-crawl preceding a nesting emergence on 14 out of the 100 nesting events. Of the 100 nesting events, 62 were identified by a location on land, i.e. by either a location of a nesting emergence and/or a false-crawl.

The influence of various components in the model
To examine the relative importance of the components in the model, I varied the components to realistic limits (Fig. 5). Latitude was varied from 0 to 38°N (longitude was not altered), in line with the distribution of loggerhead nesting beaches (Dodd 1988); the proportion of false-crawls to nesting emergences was varied from 0.63 to 0.58 between 38°N and the equator (n = 4 different manipulations of the biological components; Fig. 5). Similarly the proportion of false-crawls had only a small effect; if no false-crawls occurred the mean probability of nest identification declined from 0.61 to 0.57 (n = 3 different latitudes). Of the components examined, the most important was the time that turtles spent on land while nesting; when the mean time to nest increased from 60 min to 150 min, the mean probability of nest identification increased from 0.43 to 0.78 (Fig. 5).

The importance of the probability of locating a nesting event
The probability of identifying a nesting event may not influence the mean estimate for the true number of clutches laid. For example, if this probability was 0.4, and 10 nests were identified, then the estimated true number of nests would be 10 × 0.4 = 25. If the probability was 0.8, and 20 nests were identified, then the estimated true number of nests would similarly be 20 × 0.8 = 16. However, although these mean estimates do not differ, they may have different confidence limits (CL) associated with them. To investigate this I used nest identification probabilities of 0.4 and 0.8. I assumed that each PTT was attached while the turtle laid its first clutch of the season and that one and two further nests for each turtle were identified when the nest location probabilities were 0.4 and 0.8, respectively. By binomial expansion I calculated the 95% CL for the mean estimate of clutch frequency. The estimated true clutch frequencies had the same mean (3.5 clutches per turtle), but the associated confidence limits were smaller when the location probability was higher (Fig. 6). For example, when nine PTTs were attached, the 95% CL was 0.77 clutches per turtle when the location probability was 0.8, but 1.88 clutches per turtle when location probability was 0.4.

DISCUSSION
There have been a number of studies in which the movements and diving behaviour of sea turtles have been examined by satellite (Timko & Kolz 1982, Stoneburner 1982, Byles & Keinath 1990, Hays et al. 1991), and satellite tracking during the nesting season has shown that sea turtles may be located while on land, i.e. while on nesting emergences or on false-crawls (Stoneburner 1982, Hays et al. 1991). However, the probability of locating turtles during such events has not been investigated.

The geographical position of nesting beaches would be expected to influence the probability of obtaining locations on land because the number of satellite overpasses per
day increases at higher latitudes (Argos 1989). However, I found that the length of time that turtles took to nest was a more important factor influencing the probability of a location (Fig. 5). This probability of location was important as it influenced the subsequent confidence limits for estimates of clutch frequency (Fig. 6).

By using only the satellite overpass predictions for a single location (Fig. 3B and C), I assumed that all the nests will be laid in approximately the same area. However, conventional tag/recapture studies with flipper tags have shown that the same turtle may occasionally nest on beaches many hundreds of kilometres apart (Stoneburner & Ehrhart 1981, Iwamoto et al. 1985, Le Gall & Hughes 1987). Therefore, the model may be modified to include the probability of locating tracked turtles if they nested in different geographical locations (Fig. 5).

I have assumed that a location will always be obtained when an overpass occurs when the turtle is emerged, i.e. that $L_s = 1.0$. However, Keating et al. (1991) found that $L_s$ averaged 0.561 for PTTs on mountain peaks and dropped to an average of 0.105 for PTTs in valley bottoms. Clearly $L_s$ would need to be tested by positioning PTTs on nesting beaches.

In conclusion, with the advent of small reliable PTTs that can function on sea turtles for prolonged periods (Hays et al. 1991, Byles & Keinath 1990), satellite tracking can be used to quantify the clutch frequency and nest site fidelity of sea turtles. This study demonstrates how the relationship between satellite overpass times and animal behaviour rhythms can influence results of tracking studies.

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