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Importance of modeling in sea turtle studies

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ABSTRACT

Sea turtles spend most of their life in the water where they are almost inaccessible. Therefore, monitoring of these species uses various kinds of statistical and mathematical tools to reveal their hidden life. In this paper I describe two models applied to marine turtles. The sex determination in marine turtles is dependent on eggs incubation temperature. A mechanistic model that mimics sex determination in loggerhead turtle *Caretta caretta* (Linnaeus, 1758) is described. It permits to illustrate the use of simulation in sea turtle ecology. The other model permits to describe and analyze nesting season of marine turtles. It permits to quantify the number of nests during a season but also to analyze the phenology of nesting season. The use of quantitative models is absolutely necessary in the context of marine turtle studies.

KEY WORDS: Marine turtles, model, nesting season, sex determination, temperature, simulation

RESUMEN

Las tortugas marinas pasan la mayor parte de sus vidas en el mar, donde son casi inaccesibles. Por esta razón, el seguimiento de estas especies se hace mediante distintos tipos de herramientas estadísticas y matemáticas para revelar su vida oculta. En este artículo describo dos modelos que se aplican en el estudio de las tortugas marinas. En las tortugas marinas el sexo de las crías lo determina la temperatura de incubación de los huevos. Aquí se describe el modelo mecánico que imita esta determinación en la tortuga boba *Caretta caretta* (Linnaeus, 1758). Este modelo permite ilustrar el uso de la simulación en la ecología de tortugas marinas. Un segundo modelo permite describir y analizar la época de anidación de las tortugas marinas. Permite cuantificar el número de nidos durante la época de anidación pero también analizar la fenología de la época reproductora. El uso de modelos cuantitativos es absolutamente necesario en el contexto de los estudios sobre tortugas marinas.

PALABRAS CLAVES: Tortugas marinas, modelo, época de anidación, determinación sexual, temperatura, simulación.

LABURPENA

Itsas dortokek uretan ematen dituzte bizitzako ordurik gehien, beraien inguruko ezagutza oztopatuz. Baina badira beren bizitza ezkutua ezagutzera emateko eta hauen jarraipena egiteko erabili ditzakegun zenbait tresna, hala nola estadistika eta matematika hain zuzen ere. Artikulu honetan itsas dortoketan erabili ohi diren bi modelo deskribatuko ditut. Sexu zehaztapena itsas dortoketan, arrautzek duten inkubazio tenperaturen baitan ematen da. Hemen modelo mekaniko batek, benetazko dortokaren *Caretta caretta* (Linnaeus, 1758) sexu zehaztapena nola imitatzen duen deskribatu da. Hala itsas dortoken ekologian simulazioak nola ematen diren ikusiz. Bigarren adibideak itsas dortoken errute garaia aztertzeko eta deskribatzeko aukera ematen du; habiak zenbatu eta era berean errute garaiaren fenología aztertzeko aukera. Modelo kuantitatiboen erabilera beharrezkoa da itsas dortoken ikerketen testuinguruan.

GAKO-HITZAK: Itsas dortokak, modelo, errute garaia, sexu zehaztapena, temperatura, simulazioa

INTRODUCTION

In multidisciplinary Universities, students in Ecology can be easily recognized, as they are often clothed to be ready for field trip, sometimes even with binocular as necklace to observe birds. These students are often frustrated when they realize that scientific ecology is probably the biology field, which uses the most statistics, mathematics and various kinds of modeling. For example, a search in GoogleScholar with the two words Model and Ecology gives 1,280,000 outputs (Model and "Cellular biology" give only 226,000 outputs). We will see in this short review why ecologists, and particularly those studying marine turtles, use models.

Ecology is the scientific study of the distributions, abundance, share affects, and relations of organisms and their interactions with each other in a common environment (Begon *et al.*, 2006). Contrary to other field of biology, where the individuals are maintain out of the experience of variability of external conditions, ecology has an interest in organisms experiencing complex situations and interactions. The uses of model in ecology is intractably linked with the high level of complexity of the studied situations.

Mathematical descriptions of ecological system may be made for two quite different purposes, one practical and the other theoretical (Smith, 1974). Description with a practical purpose, have been called 'simulations'. If, for example, one wished to know how temperature will affects sex ratio in marine turtles, we need a good description on the effect of temperature on the growth of embryos, how temperature will affect the sexual phenotype of individual but also time series of temperatures. Then simulations can be built to anticipate the changing condition of the environment. For example in the context of global change, meteorologists produce models of earth temperature in 100 years and how populations will answer such a change will require model. We will see how the effect of temperature will affect the sex ratio of marine turtles using such a simulation.

The value of such simulations is obvious, but their utility lies mainly in analyzing particular cases. A theory of ecology must make statements about ecosystems as a whole, as well as about particular species at particular times, and it must make statement which are, true for many different species and not just for one. Any actual ecosystem contains far too many species, which interact in far too many ways, for simulation to be a practicable approach. In analyzing any complex system, the crucial decision lies in the choice of relevant variables.

Different kinds of mathematical description, which may be called model, are called for. Whereas a good simulation should include as much detail as possible, a good model should include as little as possible. A model cannot be used to predict the future behavior of whole: ecosystems, or of any of the species composing it. In Ecology, a model can be used when only a fraction of the studied system is known. For marine turtles, this situation is the most frequent. For example, males, juveniles and subadults are rarely seen, females are seen easily when they come to nest but they do not nest each year. And even when they nest, they can decide to deposit their eggs in a remote non-monitored beach. Then, even if "saturation tagging" program is done for one nesting place (RICHARDSON *et al.*, 2006), it does not remove the necessity to the use of modeling to take decision. Furthermore, tagging individuals is not probably free of consequence for the tagged individuals (NICHOLS *et al.*, 1998; NICHOLS & SEMINOFF, 1998). Then, it could be safer to tag a fraction of the population and to infer the global status based on a model. We will see how the nester density can be estimated from only a sampling a nesting females.

Other authors have made different kinds of categories in the model or simulation used in ecology, for example taking into account the kind of mathematical tools that are used (statistical models, differential equations) or if the model is deterministic or stochastic (MCCALLUM, 2000). The exact way the model or the simulation is done could be also dependent on constraints exterior to the biological system studied: the knowledge or habit of the researcher, limitation in computing time, available data in literature to gather data.

MARINE TURTLES FACE A HOT WORLD

In this section, I will not make a list of recipes on how turtles have been cooked along the ages, but rather describe a simulation used to study the impact of temperature on sex ratio.

Many species of oviparous reptiles, including crocodilians, a majority of turtles including all marine turtles, some lizards and the two closely related species of *Sphenodon* have displayed temperature-dependent sex determination (TSD). In these species, the differentiation of gonads into ovaries or testes depends on the incubation temperature of the embryo during a critical period of embryonic development designated the thermosensitive period (TSP) (MROSOVSKY & PIEAU, 1991; YNTEMA & MROSOVSKY, 1982). This period begins with the appearance of gonad during embryogenesis and encompasses the middle third of embryo development. It is approximately the same embryonic stages for any TSD species (BULL, 1987; FERGUSON & JOANEN, 1983; LANG & ANDREWS, 1994; PIEAU & DORIZZI, 1981; WEBB *et al.*, 1987).

Most of the data about relationship between temperature and sex determination in reptiles with TSD has been obtained from artificial incubation at constant temperatures. Whereas it has been demonstrated long time ago that TSD occurs also in natural conditions (PIEAU, 1974), the relationship between a time series of changing temperatures and sex ratio has been rarely investigated and when it was, rather crude relationship between some proxies of nest temperature and sex ratio have been used (GIRONDOT *et al.*, 2010).

Ample information indicates that reptile embryo developmental rate is dependent on incubation temperature (BOOTH, 2006). The growth of internal organs is also dependent on incubation temperature as the mass of most organs in turtles scaled to body size (PACKARD *et al.*, 2000). The main difficulties were to integrate the variation of incubation temperatures during the 15 days when the temperature influence sex determination. It has been solved using exponential recurrence equation (GIRONDOT *et al.,* 2010). The simulation is synthesized on figure 1.

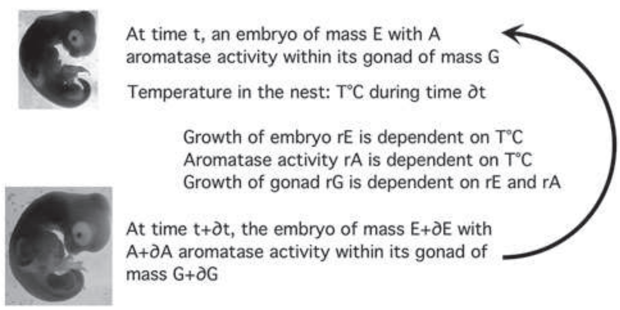

Fig. 1.- Recurrence used to simulate the growth of turtle embryos and the dependency of sex determination to temperature (adapted from DELMAS *et al.*, 2008).

The model fitted for the European pond turtle *Emys orbicularis* Linnaeus 1758 sex determination necessitates 36 parameters. It has been adapted to the slider turtle *Trachemys scripta* Schoepff 1792 to create a phenocopy of sex determination for this species (DELMAS, 2006). A phenocopy is an individual whose phenotype under a particular environmental condition is identical to the one of another individual whose phenotype is determined by the genotype (GOLDSCHMIDT, 1935).

Here I construct a new phenocopy of sex determination for *Caretta caretta* (Linnaeus, 1758) based on data from Greece in Mediterranean (MROSOVSKY *et al.*, 2002). In this study, 184 eggs incubated at 9 constant incubation temperatures were sexed. The best model describing these data is a symmetric logistic model (GODFREY *et al.*, 2003) with a pivotal temperature equal to 29.3°C (SE 0.1°C) and a slope describing the rate of change of sex ratio according to change of temperature equal to -0.26 (SE 0.06). The model cannot be rejected to fit the data (p= 0.94).

By manipulating the threshold of gonadal estrogen to feminize an embryo in the model and the variability of aromatase activation by temperature feminize (ra parameter in DELMAS *et al.*, 2008), it has possible to mimic the pattern of sex determination of Mediterranean *C. caretta* (Fig. 2). Using this phenocopy of *C. caretta* sex determinaton, it is thus possible to mimic change of incubation temperature and analyses the output on sex determination. Fluctuating regime of incubation temperatures has been computer-generated from a mean temperature of 23°C to 30°C. For each regime, the mean daily temperature was obtained randomly around the mean temperature (SD 5°C) and the nycthemer change of temperature was less than 1°C (KASKA *et al.*, 1998; MAXWELL *et al.*, 1988). Two examples of computer-generated traces of temperature are shown in figure 3A. Hundred regimes were generated for each mean temperature and 100 eggs were incubated for each simulated regime. The male proportion for these 10000 eggs is shown in figure 3B along with the male proportion if they were incubated at the same constant temperature. Clearly the introduction of variability in the nest temperatures feminizes the sex ratio. Such a conclusion is important because the future climate change will include both an enhancement of the variability of temperatures as well as increasing of temperatures. Both factors will contribute to feminization of marine turtle populations.

Finally, the comparison of both curves in figure 3B clearly shows that the curve of sex ratios obtained at constant temperatures must not be used as a guide when analyzing the incubation temperature from natural nest with changing temperatures (contray to IKARAN SOUVILLE, 2010 for example).

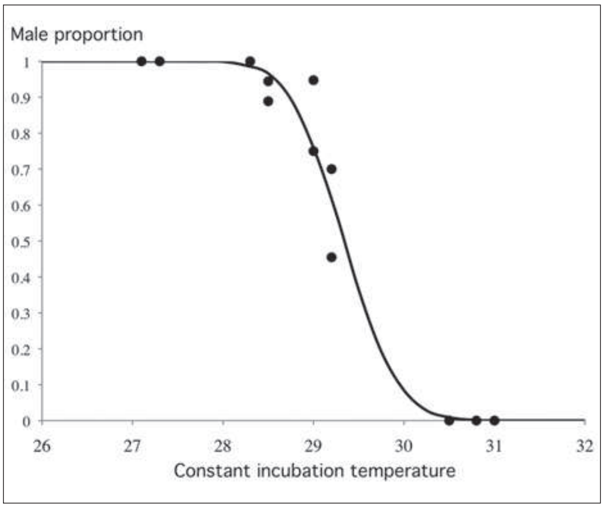

Fig. 2.- Male proportion in two nests of *Caretta caretta* from Greece incubated at various constant temperature (black points; MROSOVSKY *et al.*, 2002) and output of a mechanistic model of sex determination for *Caretta caretta* that reproduced these sex ratios (solid line).

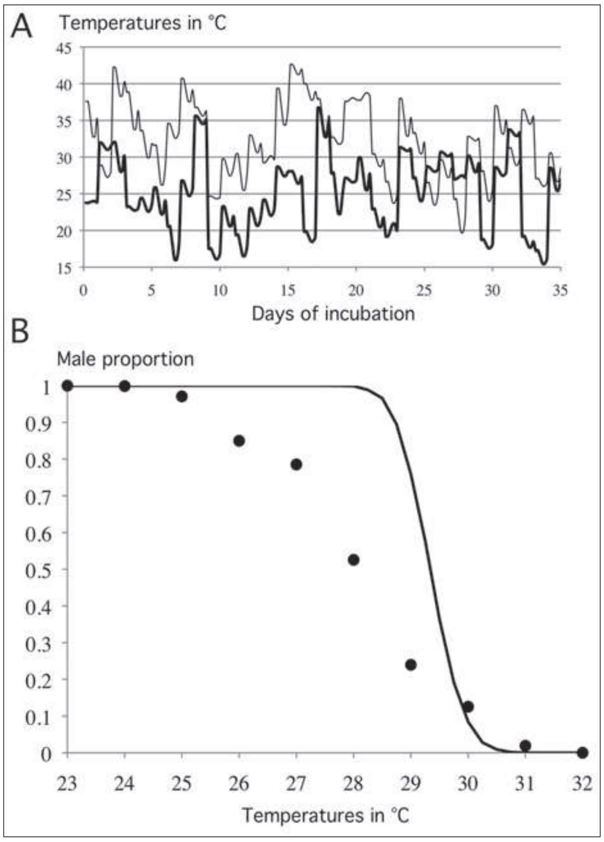

Fig. 3.- Two examples of computer-generated nest incubation temperature traces with mean temperature being 25°C (bold) or 32°C (faint). (B) Points represent the male proportion for 10000 eggs incubated in fluctuating temperatures regime with varying mean temperature (see A). The curve represents male proportion if the eggs were incubated at the same constant temperature.

FIELD WORKERS FACE A HUGE WORLD

To my knowledge, the number of beach kilometers used by marine turtles around the world has never been calculated, but it is huge for sure. Monitoring such a huge world is impossible whereas our knowledge of the status of marine turtles are directly linked to this monitoring (see for example SEMINOFF, 2002). This problem is usually solved, by taking a number of samples from around the habitat, making the necessary assumption that these samples are representative of the habitat in general. To better visualize this idea, imagine an 8x8 checkerboard. Put some pieces on the board and ask somebody else how many pieces are present. Various strategies can be used to answer the question. If you want an exact number, the observer has no other choice than explore entirely the board and count how many squares are occupied. Then you will obtain an answer free of error, but you will wait to get this answer. Alternatively, the observer can choose X squares, count how many pieces N are present on these X squares and then the best estimate of the number of pieces is 64.(N/X). Doing such a strategy, he will answer fast if X is not large but he will make an error especially if X is small relative to 64. Now imagine that the checkerboard is a beach and pieces are turtle nests: exactly the same strategy can be used. We can use also other strategies to estimate the abundance of turtles on nesting beaches. Indeed, the decision-making process in sampling must be viewed as a flexible exercise, dictated not by generalized recommendations but by specific objectives (KENKEL *et al.*, 1989). Generally for marine turtles, the specific objective is not to estimate the number of nests for one particular night but at the scale of the entire nesting season.

In most part of the world, the marine turtles are not present on nesting beach all along the year. The temporal distribution of nests during a season tends to be bell- shaped. This pattern permit to gain information because when the number of nests is known for a day D, the temporal autocorrelation can be used to get information on the number of nests for day D±x. Various authors have proposed solutions to estimate the number of nests for a nesting season based on sampling of night counts during the season (GIRONDOT *et al.*, 2006; GRATIOT *et al.*, 2006; WHITING *et al.*, 2008) but all these models suffer from weakness (reviewed in GIRONDOT, 2010). Recently, a new model has been proposed that solves these weaknesses (GIRONDOT, 2010). The bell-shape is rendered with a combination of two sinus functions and the distribution of nests around is modeled with a negative-binomial distribution.

To illustrate here the advantage of this model, data gathered for leatherback turtles *Dermochelys coriacea* (Vandelli, 1761) on Yalimapo beach (French Guiana) in 2003 are used. Two categories of patrols were done: seventy-eight 4-hours night patrols and seven 6-hours night patrols all centered on the peak of high-tide. These two categories of patrols were obtained from a same nesting season and then a single model to describe nesting season shape has been used. Only the scaling factor (Max) is fitted separately for the two categories. The fitted nesting season is shown on figure 4. The Max value for the 4-hours patrols is 40.61 (SE 2.49) and the Max value for 6-hours patrol is 52.56 (SE 6.58).

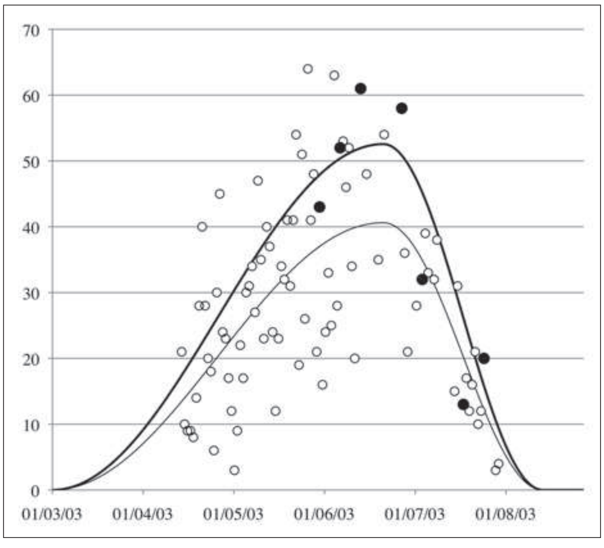

Fig. 4.- Male proportion in two nests of *Caretta caretta* from Greece incubated at various constant temperature (black points; MROSOVSKY *et al*, 2002) and output of a mechanistic model of sex determination for *Caretta caretta* that reproduced these sex ratios (solid line).

Thus we can conclude that the 4-hours patrols were missing 22% (confidence interval at 95%: 10-31%) of the nesting turtles as compared with the 6-hours patrols.

The software that implements this model can be downloaded freely here: http://www.ese.upsud.fr/epc/conservation/Girondot/Publications/Marine_Turtles_Nesting_Season.html.

It has been used to compare nesting season between two beaches (GIRONDOT, 2010) or between years and species (GODGENGER *et al.*, 2009).

CONCLUSION

The two examples used in this paper fit well the two categories defined by SMITH (1974): the simulation used to describe sex determination uses 36 parameters only for the biology part and complex time series of temperatures; on the other hand, the nesting season of marine turtles can be described with only 4 parameters. But many other models have been used in sea turtle studies. For example, a large number of papers have been published that use various population dynamic models, from very simple to very complicated ones (CHALOUPKA & BALAZS, 2007). Anyway, sea turtle ecologists must have a mathematical and statistical culture to solve more and more complex problems.

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