- Obtener abundante información biológica sobre los caimanes, sobre todo la distribución más acertada obtenida en base a la cosecha de nidos de ambas especies.

- Valorizar en términos económicos a la tierra que originalmente se consideraban improductivas

- Utilizar racionalmente a estas especies como propósito para la conservación.

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A PROLEGOMENA TO THE STUDY OF HARVEST-INDUCED ADAPTIVE CHANGE IN CROCODILIANS

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INTRODUCTION

Crocodilian populations are hunted non-randomly. For instance, regulations almost invariably specify a minimum harvest size, and preferentially harvest mature individuals (e.g., Gallego, H.C. 1973, Hofmann, R. 1968, and the Government of the Republic of Venezuela 1982). Moreover, in many geographic areas, hunting can be intense. These two processes combine to form potentially powerful selective pressures on some phenotypic traits. When these traits are heritable, hunting can induce evolutionary changes within the managed population. Depending on the particular organism under investigation, the ecological consequences of such

phenotypic evolution can range from insignificant to considerable (c.f. Darcole et al. 2002).

In recent years, there has been a burgeoning interest in understanding the effect harvesting can have on phenotypic evolution in marine fisheries. (c.f., Stokes et. al., 1993, Law 2000, Barot et al. 2005) Yet despite clear similarities, the natural resources management literature for other harvested taxa continues to largely ignore the challenges presented by phenotypic evolution in their respective systems (but see Tenhumberg et. al. 2004). This prolegomena proposes to narrow this gap by suggesting how many of the methods used in the fisheries and aquaculture literature are applicable to studying the effect of hunting on phenotypic evolution in caiman populations. Indeed, not only is the question of considerable interest to crocodilian management and husbandry programs, but raises exciting basic research problems. In particular, I argue that a judicious admixture of observational studies and computational modeling can provide a uniquely promising approach to tackle this question. A computational framework for examining a variety of questions is presented. Management and husbandry questions that are raised by this research project will be highlighted, and the limitations of this approach will be explained. Finally, I end with a brief discussion on potentially promising empirical investigations on caimans suggested by this approach.

THE CASE FOR MODELING

Crocodilians make dubious model organisms to investigate basic questions in population biology. They mature relatively late and are long-lived. Moreover, they are physically difficult to handle and are not easily subjected to enclosures or field perturbations. As such, crocodilian populations are difficult to experiment with. To overcome these difficulties, crocodilian biologists have often turned to quantitative models (c.f. Nichols 1989, Abercrombie 1989, Velasco et al. 1994, and Castro 2001). By using such models, investigators can generate concrete, testable hypotheses that could be analyzed with the corpus of modern statistics.

Modeling has a further advantage in that it can suggest a standardized framework that can be consistently referred to in order to handle particular situations an investigator may encounter. For example, managing a population of caimans in a wet forest often requires different assumptions about their spatial distribution than managing a population of caimans in a savannah. A well-constructed model should be able to present investigators in these different situations with enough flexibility to alter a few parameters to accommodate their particular situation. For instance, a savannah population may involve considerable panmixia, while a population in a wet forest may be more fragmented. Similarly, different populations can have different initial gene frequencies even if they are in comparable ecological habitats. By using a model flexible enough to accommodate these differences, we can establish a working framework that can allow meaningful generalizations to be made across crocodilians, as well as suggest localized management proscriptions.

Modeling also allows the investigator to explore the consequences of different management strategies without having to perturb a real ecosystem. For instance, if an investigator is interested in designing a hunting reserve, the investigator can refer to a model to explore the reserve's optimal size, its requisite ecological foundations, etc... without actually having to conduct these time-consuming, expensive, and occasionally environmentally problematic endeavors. Different harvesting strategies can be explored without having to kill more caimans or present confusing or vague

suggestions to stake-holders. Models therefore offer an "experimental vacuum" of sorts where mistakes can be made. When dealing with activities as permanent as changing gene frequencies, this aspect of modeling becomes invaluable. Moreover, models offer the promise of presenting a framework with which different parties can come to an agreement on how the implications of these investigations should be interpreted (Gaff et al. 2004).

OBJECTIVES OF THE MODEL

Criticisms of population biological models often come in two variations. Models are either too simple to the point of basically being useless, or they are too complex to be generalizable. Generally speaking, models exploring the dynamics of crocodilian populations have had to deal with the former critique. For example, Abercrombie (1989) highlights at least five possible shortcomings of stage-structured matrix models (c.f. Case 2000) as they are applied to crocodilian populations:

1. The models do not adequately account for demographic and environmental stochasticity.

2. The models are age, or, at best, cohort-based rather than size-based, thereby ignoring a fundamental fact about crocodilian biology.

3. The models fail to structure the population by sex, geography, etc...

4. To incorporate any of the above shortcomings, the new model's parameters cannot be reliably estimated.

5. The models ignore density-dependence.

While most of Abercrombie (1989)'s criticisms have traditionally been dealt with in other organisms using continuous-time ordinary or partial differential equations, crocodilian population biology typically follows seasonal patterns and is best modeled as a discrete, stochastic process. Moreover, as we are interested in exploring potential evolutionary outcomes, the model needs to be flexible enough to provide a unified setting in which one can investigate both population dynamics and the changes in gene frequencies within populations. Differential equations models are often limited in their capacities to deal with these complications. Thus, not only must our model accommodate most of the extant criticisms for purely ecological models, but it must also incorporate the formidable corpus of models of evolutionary dynamics.

Analytic formulations of such models in evolutionary ecology do exist. However, they have frequently met with mixed success when applied to empirical situations, even where the genetics or ecology are considerably simplified and intensive numerical examinations are conducted (c.f. Pierce and Ollason 1987, Stokes et. al., 1993, Childs 2004). At least in many long-lived organisms, there are few instances where we can gain a meaningful resolution of the underlying genetic architecture of the traits of interest (c.f. Law 1991, 2000). Moreover, few of these approaches have sought to incorporate ecological models at the level of complexity that has been suggested to adequately study crocodilian population dynamics.

To illustrate the advantage of the computational, individual-based approach as compared to the analytic approach in exploring the effect of harvesting on

phenotypic evolution, consider modeling the process of gamete formation in the parental generation. If we assume that there are l loci controlling a trait Z with corresponding fitness function $W(ij)$ for a diploid individual with genotype ij, then in a completely randomly mating population of hermaphrodites, where selfing is permitted, the population is at equilibrium size, and with no age structure and non-overlapping generations, if pi denotes the frequency of haplotype vector $\boldsymbol{i}$ = (allele at locus 1, allele at locus 2, ..., allele at locus l), and if $\{I,J\}$ are decompositions of L={1,2,…,l}, then the genotypic frequencies in the next generation are given by:

$$p_i(t+1) = p_i(t)\frac{\sum_j W(ij)p_j}{\sum_{i,j} W(ij)p_j p_i} - \frac{1}{\sum_{i,j} W(ij)p_j p_i}\sum_j W(ij)\sum_I r_I(p_j p_i - p_{i_I j_J} p_{j_I i_J})$$

However, even with these genetically restrictive assumptions, most of which don't apply to crocodilians, this formula is difficult to analyze analytically, and few general conclusions can be drawn from studying its dynamics (Bürger 2000, T. Nagylaki, pers. comm.). While ecological models present less of a problem under single-locus assumptions (c.f. Charlesworth 1980, Case 2000), few quantitative phenotypes of interest are controlled by only one locus. The analysis becomes essentially intractable in the multilocus case when the fitness function, $W(ij)$, is expressed in terms of even the simplest the single-species population dynamics.

By contrast, the same process of gamete formation in the proposed computational model is illustrated in Figure 1. Embedding this process in the context of an individual-based model (IBM) is straightforward. When individuals reproduce, they produce gametes according to the algorithm, and the gametes fuse. While under certain platforms the computation may be time consuming, the computational approach is sufficiently versatile to accommodate arbitrary ecological and genetic assumptions.

Indeed, computational models have the promise of being able to overcome many of the oversimplifications, while remaining generalizable and realistic. It is reasonable to begin with the following 6 features in a model:

1. Birth/Death Process (e.g., mean fecundity and mortality)

2. Age/Size Structure (e.g., how does mortality decrease with increased size?)

3. Spatial Structure (e.g., do the crocodilians constitute a homogeneous population or are they in a metapopulation?)

4. Stochasticity(e.g., how does somatic growth rate vary from year to year?)

5. Evolutionary mechanisms (e.g., are all loci in the crocodilian genome autosomal?)

6. The influence of other individuals, including conspecific and other species.

A cursory review of the literature in other organisms exploring the question of harvest-induced phenotypic evolution shows that these 6 features, or permutations thereof, are usually sufficient to explore the effects a range of management, ecological, and evolutionary scenarios (e.g. Stokes et. al., 1993, Claessen et al. 2000, Ernande et al. 2004). Increasingly, these studies employ a computational

approach as opposed to an analytic one. Indeed, both these conclusions can be
gleaned from a literature that covers a wide range of taxa of importance in fisheries
and aquaculture: taxa which often have fundamentally distinct biologies (c.f.
Wenighofer 2005). Moreover, many of these points address the aforementioned
shortcomings that left managers and biologists skeptical of using modeling when
studying their crocodilian population. Finally, the computational approach's
parameters are mechanistically linked to the underlying individual-level biology (for
example, conversion efficiency of food into body weight), thereby facilitating
estimation of these parameters. Indeed, a computational model incorporating these
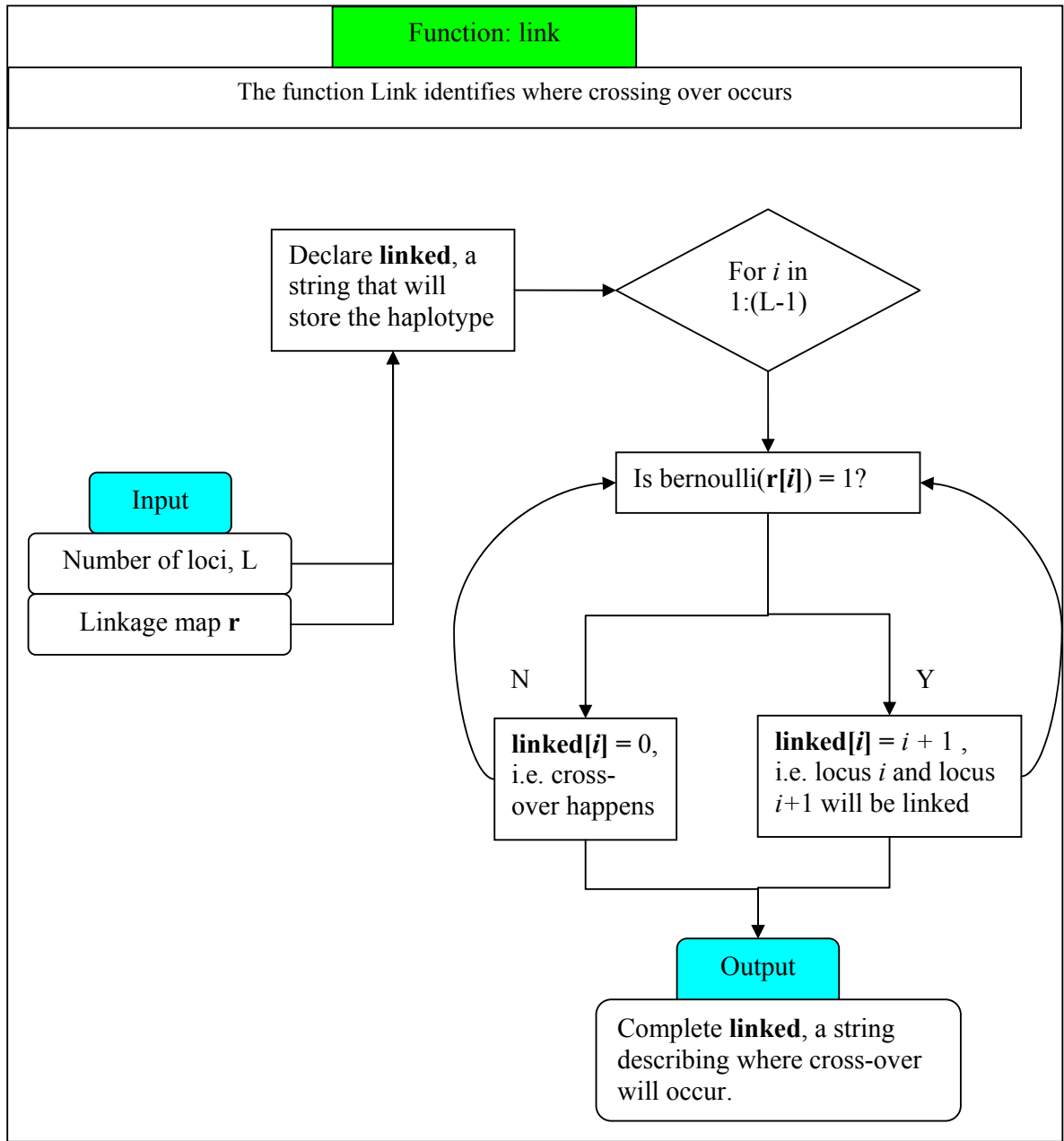6 elements can be of considerable utility to crocodilian biologists.

Figure 1.A. The function link, which identifies where the cross-over event occurs
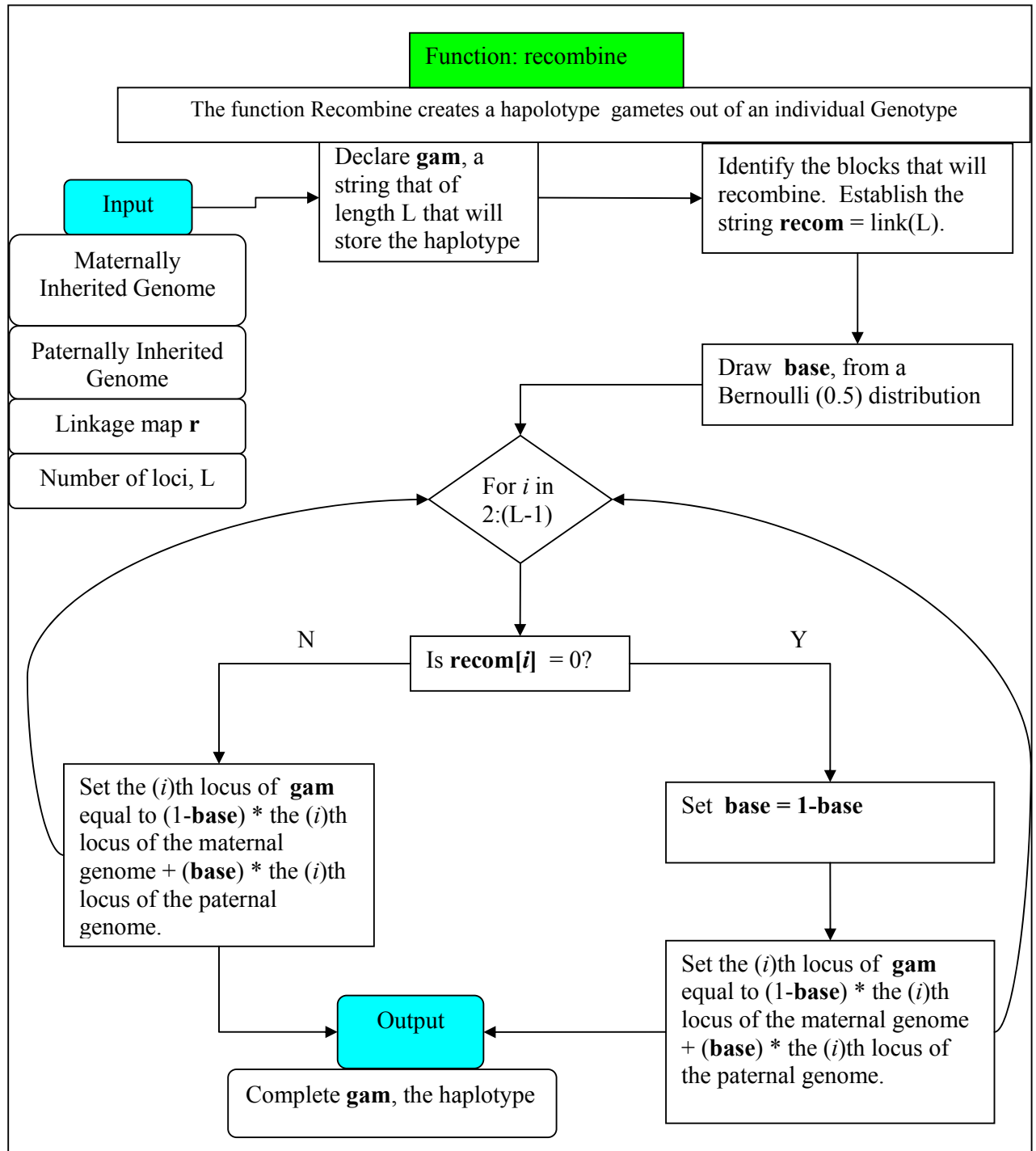during meiosis

Function: recombine

The function Recombine creates a hapolotype gametes out of an individual Genotype

Declare **gam**, a string that of length L that will store the haplotype

Identify the blocks that will recombine. Establish the string **recom** = link(L).

Input

Maternally Inherited Genome

Paternally Inherited Genome

Linkage map **r**

Number of loci, L

Draw **base**, from a Bernoulli (0.5) distribution

For *i* in 2:(L-1)

N

Is **recom[i]** = 0?

Y

Set the (*i*)th locus of **gam** equal to (1-**base**) * the (*i*)th locus of the maternal genome + (**base**) * the (*i*)th locus of the paternal genome.

Set **base = 1-base**

Set the (*i*)th locus of **gam** equal to (1-**base**) * the (*i*)th locus of the maternal genome + (**base**) * the (*i*)th locus of the paternal genome.

Output

Complete **gam**, the haplotype

Figure 1.B. The function Recombine, which creates a gamete from a diploid
individual

DESCRIPTION OF THE MODEL

Extant IBM's for caiman populations (c.f. Velasco et al. 1994) present the logical starting point for using computer simulations. An evolutionary component is imputed into the model by embedding a diploid genotype into the simulated individuals in the IBM. A function translating the genotype into the phenotype mediates the interaction between the genotype and the environmental context in which the individual finds itself. Genotypes are passed on to gametes after mutation and recombination. The gametes subsequently fuse to form new individuals. In this way, the model is quite similar to genetic algorithms with n-point recombination (c.f. Spears 2001), but differs from these by allowing linkage between the loci and arbitrary complex (or simple) ecological fitness functions. Such genetic processes as natural selection, drift interact with ecological processes such as harvest mortality and spatial structure, thereby acting on our individuals in the specified ecological context. Thus, our model proceeds in the spirit of Strand et al. (2001), who embedded a haploid genetic algorithm in an IBM to study life-history and behavioral evolution in the fish, Muller's pearlside (*Maurolicus muelleri*).

A flowchart of the over-all model, with maximum complexity for the single-species case and with arbitrary birth, death, movement and growth functions, is presented in Figure 2.

The model is designed to be generalizable. The investigator may multiply or remove most components as their situation may warrant. Such additions and removals are fairly straightforward. For instance, multiple species models can be accommodated by duplicating this flowchart for a prey (say, fish) or a predator (say, wading birds), but only considering their birth, death, and movement processes and constraining the phenotypic space in these taxa. The death, growth and birth functions for the focal species are then updated in the code to reflect the dependence of these demographic processes on other species in the ecosystem. Alternatively, an investigator may find their population is largely homogeneous, in which case s/he can do away with the movement stage altogether. This means that most classical, discrete-time IBMs are a special case of the model presented. Detailed flowcharts of the simulation program, as well as source code in S/R, are available at:

http://home.uchicago.edu/~kwokamot/software/

The flowcharts are designed with the life-history of an ectothermic vertebrate in mind. In particular, the parameter values have been taken from the fisheries literature (c.f. Claessen et al. 2000, 2002). The extension of these models to crocodilians is the subject of the next section.
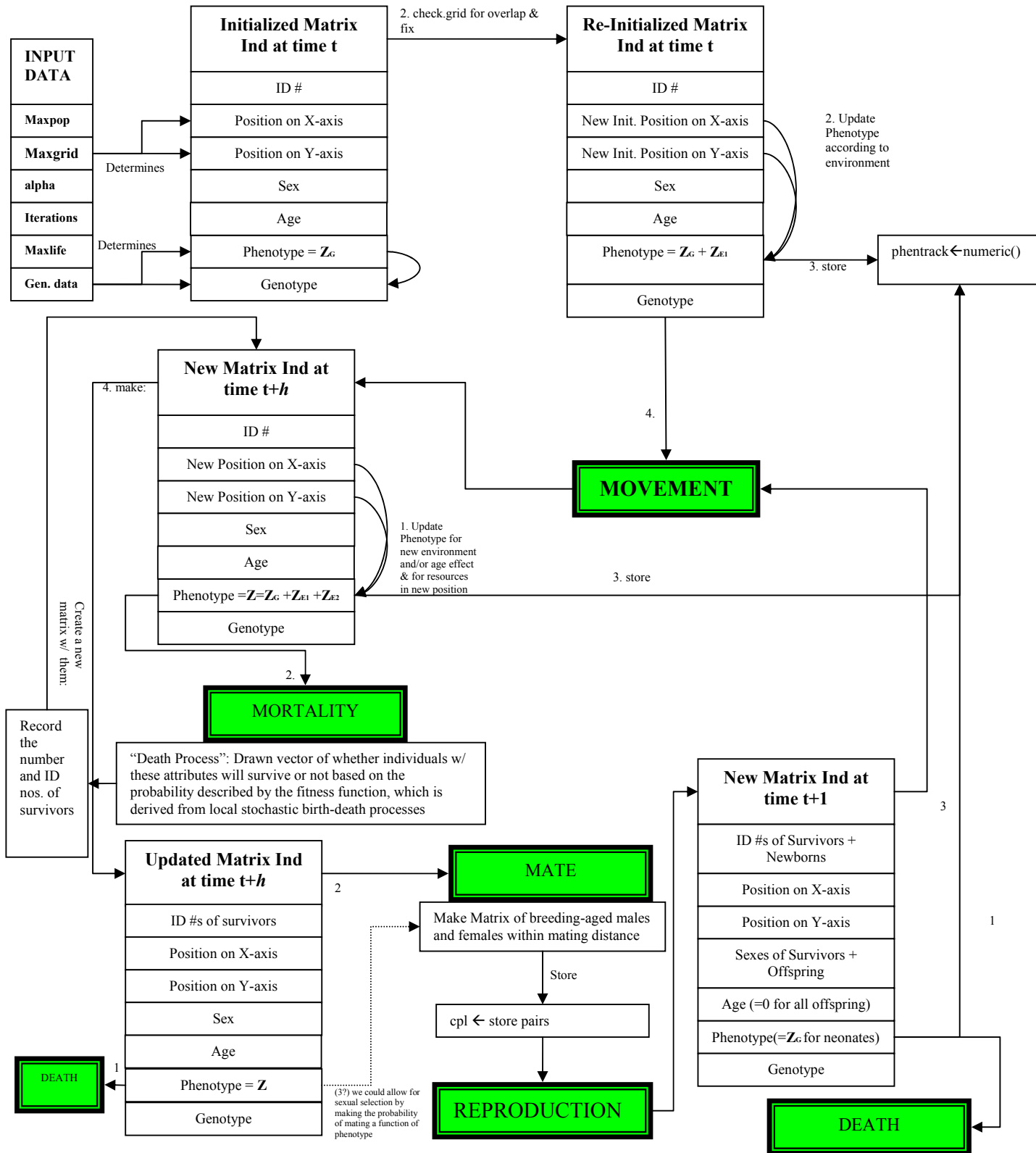
Figure 2. The model's main processes. In the full model, the phenotype will include energy reserves, reversible and irreversible mass, and any other phenotype(s) of interest.

EMPIRICAL DATA

One challenge of using a model is collecting the pertinent empirical data. At its most complex, the model requires some sense of the underlying genetic architecture for a range of phenotypes, ranging from relatively straightforward traits (e.g. clutch size) to rather complex behavioral parameters (e.g. the "steepness" of the ontogenetic shift in a crocodilian functional response). Even in well-studied model systems (e.g. Drosophilia *spp.*), obtaining this level of resolution could take years (c.f. Lynch and Walsh 1998). Ecological parameters will require some time to collect, and the reliability and veracity of the parameter values one obtains will always be a matter of uncertainty. A further difficulty, which will be discussed later on, involves the imperative of attempting to infer process from pattern in this approach.

Table 1. Parameters to be Used in the Full Model

Subject and Symbol	Unit	Interpretation	Reference
i-state variables			
x	g	Irreversible Mass	Claessen et al. 2000
$xrev$	g	Reversible Mass	Claessen et al. 2000
Π	…	Patch ID	…
Pch	…	Number of Patches	…
Time:			
t	t	Seasons	Claessen et al. 2000
Ontogeny:			
xf	g	Maturation bone mass	Claessen et al. 2000
qJ	…	Juvenile Maximum Condition	Claessen et al. 2000
qA	…	Adult Maximum Condition	Claessen et al. 2000
wB	g	Egg size (total weight)	Claessen et al.

			2000
kr	…	Fraction of *xrev* spent on reproductive tissue	Claessen et al. 2000
GT(·)	…	Statistical model relating size at time *t*+1 to size at time *t*	Childs et al. 2004
σ	…	Residual variance of GT	Childs et al. 2004
f(·)	…	Function specifying the amount of somatic growth that goes to *x*	Claessen et al. 2000
Consumption			
Ke(*x, xrev*)	…	Size-specific intake coefficient	Claessen et al. 2000
I(·)	…	Food intake rate	Claessen et al. 2000
Atti(*x, xrev*)	…	Size-specific attack rate for prey *i*	Claessen et al. 2000
$\xi i1$	$T g^{(1+\xi i2)}$	Allometric scalar for handling time of prey *i*	Claessen et al. 2000
$\xi i2$	…	Allometric exponent for handling time of prey *i*	Claessen et al. 2000
Hi(*x, xrev*)	…	$\xi i1 \, (x+xrev)^{\xi i2}$	Claessen et al. 2000
Metablism:			
$\rho 1$	$g^{(1-\rho 2) t-1}$	Allometric Scalar	Claessen et al. 2000
$\rho 2$	…	Allometric Exponent	Claessen et al. 2000
$\rho 1'$	$g^{(1-\rho 2')} t-1$	Allometric Scalar during migration	…
$\rho 2'$	…	Allometric exponent during migation	…
Mortality:			
P	…	All top predators	…
Ai(*x, xrev*)	…	Size-specific attack rate from predator *i*	…

$H_{j,k}(\cdot)$	…	Size-specific handling time of predator j on prey k	…
s	t^{-1}	Starvation coefficient	Claessen et al. 2000
q_s	…	Starvation Condition	Claessen et al. 2000
$\mu_{T,B}(x)$	…	Background mortality	…
Migration			
$\text{Im}\Pi \rightarrow \Pi'(y)$	…	Immigrants of size y from patch Π to Π'	…
$\text{E}\Pi' \rightarrow \Pi(y)$	…	Emigrants f size y from patch Π' to Π	…
η	…	Number of migration attempts	…

Many of these considerations suggest that *Caiman* spp. will be the best-suited crocodilian for exploring the consequences of harvest-induced changes in crocodilians. The genus is reasonably well studied, and perhaps most importantly is widespread across a large longitudinal gradient, and are, after all, común in a range of differing ecosystems. While in some cases locally extirpated, the species is in a healthier state over its range than most other crocodilians (c.f. Thorbjarnarson et al. 1995). *Caiman crocodilus* is popular in laboratory investigations, and there is a sizable husbandry industry for the species (c.f. Diefenbach 1975, Axelsson et al. 1989, Janke et al. 2001).

Indeed, many of the drawbacks presented by parameterization are hardly fatal. A consequence of focusing on *Caimans* is that many of the ecological parameters required by the model (Table 1) can be found in the literature. Where data on *Caiman* are lacking, an investigator can experiment by imputing parameters from closely related *Alligator spp*. Moreover, crocodilian biologists are in only marginally worse shape than most (though certainly not all) fisheries managers when it comes to the precision of our parameter estimates, and indeed in some cases we may have a better sense of their natural history (A. Shelton, pers. comm.). Yet the considerable success of fisheries managers in studying the impact of harvest-induced phenotypic evolution suggests that such a study is feasible given the present state of knowledge about at least some *Caiman* populations.

A second reason why the seemingly onerous task of parameter estimation, especially for some of the genetic models, is manageable is that data on the genetic architecture of some of these traits are available from a range of other animals, which can suggest some parameter combinations to start the simulations with. Moreover, the computational framework readily allows the investigator to explore whether and how different genetic assumptions affect their conclusions.

A more serious limitation presented by the study of crocodilian biology is the difficulty of conducting nice field experiments. As mentioned, crocodilians are long-lived and difficult to handle. Hence, the investigator will often have to conduct

"natural experiments" or observational and comparative studies in addition to their
modeling work to attempt to infer process from pattern. The limitations of such
approaches are well publicized (c.f. Diamond and Case 1985, Ito et al 2004). Thus,
validating model conclusions, by virtue of our study organism, becomes a serious
challenge.

One way to handle this difficulty would be to conduct well-designed comparative
studies. For instance, if we want to investigate whether hunting pressure lowers the
size at maturity, we can look at two separate populations in the same ecosystem,
where one had been the subject of intense hunting in the past while the other was
not. Using these computer simulations, we can test whether alternative processes
(e.g. drift, migration, phenotypic plasticity in response to microhabitat differences,
etc...) can explain the discrepancy in the size at maturity. If we find that alternative
processes do not account for our observation, then we can reasonably claim that
hunting pressure was responsible for the differences in the size at maturity. This in
turn will suggest alternative harvest strategies for the hunted population. While we
are still inferring process from pattern, our simulation may nevertheless help
elucidate which mechanisms can most effectively explain our observations with
reference to the underlying theory.

QUESTIONS FOR MANAGEMENT

Apart from helping design sustainable harvest programs of caimans and
crocodilians more generally, the modeling approach described above can be of
some use to other issues in crocodilian conservation. Indeed, we are often
interested not only in the sustainable harvest of crocodilians, but also in the
conservation of the local ecosystem as a whole, as well as the economic and social
impacts of harvesting policies. With regards to the latter, while the model does not
explicitly model human social phenomena, the consequences of other corollaries of
human activity such as land-use and introduced species can be explored in the
model. Additionally, if one was sufficiently interested, the model can allow for *ad hoc*
refinements. For instance, one could change the function describing hunting-
induced mortality to vary periodically in a fashion consistent with fluctuations in the
market price for caiman hides.

The framework is more useful for being applied to ecosystem management (c.f.
Miller 1996, Jennings et al. 2001). As already observed, the framework can be
generalized to allow for multitrophic interactions. This can also allow other natural
resource managers to understand the impact of, for example, caiman harvest
strategies on their own focal taxa. Indeed, investigators can simulate local
extirpation without having to carry out actual culling, and follow the resulting
dynamics of caiman predators and prey species. Such an approach can also help
answer questions about resource management priorities, for instance by providing
evidence for the assertion that crocodilians often form keystone species in their
habitat.

In recent years, the adaptive management paradigm has become widely accepted
(c.f. Comiskey et al. 2001). As better data become available, the model's behavior
may change. Consequently, there is a need to vigilantly re-evaluate our
management strategies in the face of consequences predicted by this new data. The
framework presented here is ideally suited for this process, especially as it allows
investigators in some cases to anticipate and simulate a wide range of potential
outcomes of a particular management strategy and its contingencies. Finally, it is my

hope that the model can be of some use to the crocodilian husbandry industry. Quantitative genetic studies on crocodilians have just begun, and given their success in other domesticated animals, QTL studies on traits that are important both commercially and ecologically are becoming possible (c.f. Isberg et al. 2004, Slate 2005). There is no reason why the computational evolutionary ecology model needs to be restricted to natural settings, and an individual-based simulation of a crocodilian farm or farming operations can be done to explore approaches to disease management and optimal breeding programs. Additionally, we can gain a more nuanced understanding of, for instance, the genetic effects of reintroductions and captive breeding programs in zoos.

DISCUSSION

Despite these promising prospects, computer simulations are not a panacea. Indeed, like any method used in empirical science, they have their inherent drawbacks that can be difficult to manage. Firstly, conclusions drawn from simulation studies might not be as clear as from analytical or even experimental studies; often, it is harder to elucidate and isolate mechanisms that drive the dynamical behavior that is simulated than in analytical models. Secondly, we may need to test a large range (i.e. run many simulations) of the parameter space before we can draw conclusions. Finally, summarizing parameter combinations that lead to specific dynamical outcomes becomes a serious challenge. Nevertheless, given the substantial difficulties and limitations of analytic models of crocodilian population biology, let alone evolutionary ecology more generally, simulations provide a tractable and workable alternative. Indeed, their success in the study of other taxa should not be minimized.

A lingering difficulty is the amount of computational time the simulation takes up. In principle, this can be improved through more efficient coding, language choice, and algorithm design. However, due to its inherent complexity, while the simulation may be able to address many questions in principle, in practice the computation time may prove prohibitive. Over the time-scale of concern to managers (~1000 years) this was usually not a problem using the model in Section VI; however, for biologists interested in understanding, for instance, macro-evolutionary trends in the Crocodylia over the scale of millions of generations, this could present a serious limitation of the approach advocated here.

Indeed, evolutionary, ecological and demographic processes in crocodilians are inherently stochastic and often complex. Nevertheless, by formulating an individual-based model and specifying a range of gene frequencies, investigators can hope to explore a range of plausible management scenarios that could induce selective pressures on crocodilian populations. *Caiman* spp. are a particularly fruitful taxa in which to explore these questions, and offer promising scientific, conservation, and husbandry grounds for future research.

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PROYECTO DE CONSERVACION DEL *Crocodylus acutus* (Cuvier, 1807) Y SU HABITAT NATURAL - BAHIA DE CISPATÁ DEPARTAMENTO DE CÓRDOBA-COLOMBIA

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Conservación Internacional Colombia

ZOBEN C.I.

GARBE C.I.

ANTECEDENTES

En el mundo, los *Crocodylia* actuales, comprenden 23 especies agrupadas en tres subfamilias: Crocodylinae (géneros: *Crocodylus* y *Osteolaemus*), Alligatorinae (*Alligator*, *Caiman*, *Paleosuchus* y *Melanosuchus*) y Gavialinae (*Gavialis* y *Tomistom*a). Colombia con 6 especies (4 subespecies de Caiman crocodilus), posee una alta diversidad. Además es uno de los mayores productor de pieles en el