No hay datos disponibles sobre el tamaño de la poblacional de *C. acutus* en Monte Cabaniguan en el sureste de Cuba. Sin embargo, la cantidad de nidos encontrados allí abarca 171 (promedio de los años 1992-96), 4.5 veces mas que el promedio de nidos en el Lago Enriquillo. Eso significa que en Monte Cabaniguan pueden estar fácilmente 2000 cocodrilos, sin contar los neonatos.

Densidad poblacional. La densidad poblacional se expresa en Individuos por km de orilla en ríos, lagos y lagunas y en individuos por km2 en zonas pantanosas. Para Etang Saumatre Thorbjarnarson (1988) distingue entre la densidad cruda, incluyendo todas las orillas disponibles y la densidad ecológica que excluye áreas que no son usadas por cocodrilos, por ser muy expuestas a oleajes fuertes. Él calcula una densidad cruda de 6.3 y ecológica de 9.6 Ind./ km. Aplicando su método en el Lago Enriquillo llega 4.5 Ind./km densidad cruda y 8.8 Ind./ km densidad ecológica. Si queremos comparar los datos de este estudio con los del Etang Saumatre tenemos que tomar en cuenta que el ultimo ha sufrido probablemente la misma o una peor disminución de la población, hace falta una nueva investigación de los cocodrilos en Haiti.

En otras areas donde abunda el cocodrilo americano las densidades son menores, el promedio para Venezuela es 1.57 Ind./km, con un máximo de 3.7 Ind./ km, según Sejas (1986). Para Belize se calcula 0.27 Ind./km, con un máximo de 3.4 Ind./ km (Platt & Thorbjarnarson 1997) y para Honduras 0.51 Ind./km con un máximo de 2.4 Ind./km (King et.al 1991).

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ZOOCRIA Y MANEJO DE POBLACIONES SILVESTRES DE *Crocodylus acutus*: ÍNDICES REPRODUCTIVOS Y COMPORTAMIENTO SOCIAL

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Siendo Panamá garante del Convenio de Diversidad Biológica, firmado en 1992 en Río, está obligado moralmente, entre otras cosas, a desarrollar proyectos que fomenten la protección y preservación de la vida silvestre, promoviendo ante todo el desarrollo sostenible de sus recursos naturales. Consientes de que en el Desarrollo Sostenible se deben involucrar todas las fuerzas vivas de la sociedad, la empresa Panama Gator S.A., desde hace diez decidió tomar parte activa en la generación de tecnologias que permitan una producción más acorde con nuestros tiempos.
La granja durante 8 años a logrado reproducir en cautiverio exitosamente la especie *Crocodylus acutus*.aquí. Desde 1990 la granja montó un proyecto de investigación con el objetivo de establecer un patrón sobre las actividades preanidatorias, anidatorias y postanidatorias, de mayor importancia para la zoocría del *Crocodylus acutus* en la granja Panagator S.A., de la República de Panamá Para ello, se realizó un análisis retrospectivo de datos colectados desde 1990 hasta 1998. Se determino que existe un comportamiento de ocurrencia regular en el tiempo y en el espacio, y establecieron pautas para predecir y manipular el ciclo reproductivo de la especie, con fines comerciales y ecológicos. El porcentaje de incubación por temporada fue de 60.3%, el porcentaje de incubación por nido fue de 79.7 y el de fertilidad por hembra fue de 74.9. El porcentaje de sobrevivencia de neonatos en la mayoría de las temporadas fue mayor del 80% y el periodo mínimo para alcanzar la edad adulta fue de 36 a 40 meses. Actualmente, mediante un convenio entre el Instituto Smithonian de Investigaciones Tropicales, La universidad Santa María la Antigua y la Granja Panagator S.A., se están realizando estudios de genética poblacional mediante la técnica de PCR. Apartes de es trabajo fueron presentados en el Congreso "Medio Ambiental Siglo 21''que se celebró en Santa Clara Cuba, en junio de 1999

Panama is dedicated to the preservation of its natural resources, including the treasure of biodiversity. Following the general structure laid out by the United Nations Convention on Biodiversity, one of the national goals is to develop projects that ensure that biological resources that are important for biodiversity are conserved and used in a sustainable manner. To get a sustainable development of any species or ecosystem, studies on population dynamics and social behavior in the open and controlled spaces must be conducted. With all the gathered data in those studies we can establish a methodology that allow us to use the resources and at the same time ensure a long life of the resources in the area and get economical benefits for the human population in the area.
The objective of this investigation was to establish a pattern about the most important pre-nesting, nesting and post-nesting activities that happen in the reproductive cycle of *Crocodylus acutus* at Panagator, S.A. an alligator farm in The Republic of Panama, Central America, using all data collected in the period between 1990 and 1998. The achievement of our objective allowed us to determine that a regular occurring behavior in time and area exists and establish guide lines to predict and manipulate the reproductive cycle of the species to get commercial and ecological benefits. The percentage of incubation per -season was 60.3%, the percentage of incubation per- nest was 79.7 and the fertility per female was 74.9. More than 80% of new born survive until adult state. They get adult state in 36 to 40 months.

INTRODUCCIÓN

Antecedentes y planteamiento general del problema

Desde que se describió por primera vez la anidación del *Crocodylus acutus* por Medem en 1958 y después de los trabajos realizados por el mismo investigador en el período comprendido entre 1962 y 1969 sobre la distribución de los Crocodylia en América, es poco lo que se encuentra en la literatura científica sobre esta especie y su distribución en Panamá.

Uno de los problemas en la mayoría de los países del Tercer Mundo es cómo alcanzar un desarrollo sostenible. Para alcanzar un desarrollo sostenible de cualquier especie o ecosistema deben hacerse estudios de dinámica de poblaciones y del comportamiento tanto en medio silvestre como en confinamiento. Usando los datos obtenidos en los estudios se podrán estandarizar metodologías que aseguren la perpetuidad del recurso y la obtención de beneficios.

Panamá no cuenta con información científica suficiente para elaborar una metodología que permita la producción de *Crocodylus acutus* en forma comercial y que a su vez, asegure la protección y preservación de este recurso y su hábitat. Aunque sí se cuenta con abundante información sobre el manejo en el país del *Caiman cocodrilus fuscus* en cautiverio.

Panamá es garante de muchos convenios internacionales relacionados con la protección y el manejo de la vida silvestre, esto obliga a todas la fuerzas vivas del país a desarrollar proyectos relacionados con el manejo sostenible de recursos naturales. La Universidad Santa María La Antigua con su Maestría en Ecología y Conservación y la empresa privada, han decidido tomar parte activa en el estudio y desarrollo de proyectos relacionados con este tópico.

Objetivos

Establecer un patrón sobre las actividades preanidatorias, anidatorias y post-anidatorias, de mayor importancia para la zoocría del *Crocodylus acutus* en la granja Panagator S.A. en la provincia de Panamá, República de Panamá, América Central, mediante un retrospectivo de los datos obtenidos desde 1990 a 1998.

Hipótesis

"Si existe un comportamiento reproductivo de ocurrencia regular en el tiempo y en el espacio, entonces este se puede patronizar en pro de obtener un modelo que permita predecir y manipular el ciclo reproductivo de la especie *Crocodylus acutus*, con fines ecológicos o comerciales".

FUNDAMENTACIÓN BIBLIOGRÁFICA

Los cocodrilos actuales, como los conocemos, son los sobrevivientes directos de la era predominante de los reptiles. En la era Mesozoica 260 millones de años atrás, un grupo de Anfibios se separó y en los inicios del Tríacico dio origen al los Pelycosarios y a los Archosaurios. Los Pelicosaurios dieron origen a los mamíferos actuales y los Archosaurios dieron origen a 17 ordenes de reptiles primitivos. Uno de estos ordenes fue el de los Decodontios, que posteriormente dio origen a las 22 especies de cocodrilos existentes actualemente.

Clasificación del lagarto blanco o aguja: Clase Reptilia; Orden Crododylia; Familia Crocodylidae; Género Crocodiles; Especie Crocodiles Acutus.

Esta especie se encuentra distribuida en los ríos, estuarios y manglares de las costas del Pacífico y del Atlántico, desde el sur de los Estados Unidos hasta el norte y centro de América del Sur.

Características reproductivas generales de la especie

Todos los cocodrilos se reproducen por medio de huevos. La madurez sexual está influencia por el tamaño y la edad del individuo. No hay dimorfismo sexual aparente, pero internamente los machos cuentan con un hemipene protruible.

Según Medem en 1981 y Alderton en 1991 se definen a los *C. acutus* como animales de reproducción altamente estacionaria, ya que sólo se reproducen en verano.

La época de reproducción se inicia con el cortejo, el cual ha sido ampliamente estudiado en el caso del *Alligator missisipiensis,* cuyo proceso es más o menos similar en todas las especies de cocodrilos. Los machos comienzan a secretar sustancias aceitosas altamente olorosas y facilmente detectables por las hembras de sus glándulas pericloacales y submandibulares.

Tanto los machos como las hembras de todas las especies de cocodrilos, vocalizan en tonos claramente audibles al tiempo que los machos sacuden su cuerpo con fuerza haciendo vibrar el agua y liberando el aceite, que se dispersa en la superficie. Todo esto se lleva a cabo en el territorio previamente señalado por el macho. Las hembras acuden al llamado del macho, y se introducen en su territorio cautelosamente. Aquí se produce el primer contacto físico, al chocar las narices suavemente, colocando sus cuellos uno alrededor del otro.

Son las hembras las que eligen, y al llamado del macho pueden acudir un número diverso de hembras, las cuales durante el período de reproducción viven juntas (Anaya 1991).

Alderton (1991) reporta que después de varios contactos, se lleva a cabo la copula, la cual tiene una duración corta. Existen diferencias interespecíficas en cuanto al lugar donde se realiza la copula. Algunas especies la realizan en la tierra, otras en aguas de poca profundidad, pero el *C. acutus* la realiza en aguas profundas.

Todos los Crocodylia construyen un nido para depositar sus huevos. Las condiciones ambientales parecen ejercer gran importancia en la forma de construir su nido y en la elección de la época de postura. Los *C. acutus* construyen su nido haciendo excavaciones en lugares cerca del agua, en suelos arenosos, de grava o suelos duros (Vegambre 1956, Huertas 1959 y Medem 1962).

Medem en 1962, Ramírez en 1977 y Alderton en 1991 describen que los *C. acutus* ocasionalmente construyen sus nidos haciendo pequeñas excavaciones y cubriéndolos con tierra y material vegetal.

Según Alderton , el período de incubación de los huevos de cocodrilo demora de 2 a 3 meses en general, a una temperatura de 33° C. Cuando los bebés cocodrilos están por nacer, uno de los polos del huevo se reblandece por acción del diente de eclosión del animal. Ellos emiten sonidos característicos que comunican a la hembra que ha llegado el momento de destapar el nido. Las crías permanecen con su madre alrededor de sus dos primeros años de vida, período después del cual se lanzan a la parte más honda del agua, donde suelen ser depredados por los machos adultos, especialmente.

MATERIALES Y MÉTODOS

1. Población en estudio

La población de *C. acutus* en estudio se encuentra establecida en el mismo lugar (un lago artificial) desde 1982. Se desconoce su origen, el tamaño y peso exacto de los individuos. Consta de 11 adultos, de los cuales 9 son hembras y 2 son machos. De estos 2 machos, uno es claramente el predominante, siendo el más grande en tamaño (aproximadamente 22 pies de largo), con un peso de alrededor de una tonelada, y es el más agresivo.

La proporción de hembras por macho fue estimada por el número de nidos, ya que no existen registros sobre la llegada de los animales al lugar. Desde agosto de 1990 hasta marzo de 1998 se han registrado datos sobre los eventos preanidatarios y anidatorios de este grupo de animales.

2. Área de estudio

Panagator S.A., es una empresa que se ha dedicado desde 1990 a la zoocría del *Caiman crocodylus fuscus* (babilla) y del *Crocodylus acutus* (lagarto blanco). Se encuentra ubicada en la milla 16.5 de la carretera Transístmica que conecta las ciudades de Panamá y Colón. La granja fue reconocida como criadero comercial de *C. crocodylus fuscus* bajo la resolución DG-DNADU 5-014-97 emitida por El Instituto de Recursos Naturales Renovables el 23 de julio de 1997 y se le asignó el número de registro CITES 022.

El hábitat está compuesto por un lago de 2 hectáreas de espejo de agua con una profundidad de 15 m, de forma irregular, con una porción de tierra-agua de 1:1. Posee además una playa, que recibe 12 horas de sol constante en la época de verano, y unas 11 en la temporada de invierno. El área total se encuentra cercada con malla de 2 pulgadas, enterrada a 2 pies de profundidad y con una altura de 5 pies.

El lago esta a 9° 7′ 50″ de latitud norte y a 79° 37′ 56″ longitud este. Se encuentra empotrado entre dos cerros de mediana altura, en una zona tropical húmeda altamente intervenida, a una altura aproximada de 125 m.s.n.m., y una precipitación media anual de 2,300 mm. La temperatura del aire es 27 ° C durante la temporada seca y de 25°C en el período de lluvias.

El área cercada cuenta con dos terceras partes de su superficie en árboles de Teca (*Tectona grandis*), Balo(*Glaricidia sepium*), Ficus (*Insipida sp*), Cholopelado (*Bursera simarouba*) y Paja canalera (*Saccharum spontaneum*). El sotobosque y el suelo de estas dos terceras partes no reciben luz solar durante todo el día debido a la sombra que proyectan los cerros que rodean el área y por los árboles. La tercera parte restante, que se encuentra expuesta a la luz solar durante todo el día, tiene Paja canalera y gramíneas pequeñas que se secan en verano, permitiendo que la luz del sol caliente directamente el suelo.

El área fuera del cercado se encuentra constituida en un 25% por potreros y en un 75% por un rastrojo de más de 10 años, en el cual se encuentran: Cedro Espino (*Bombacopsis quinatum*), Teca, Laurel (*Cordia alliodora*), Cholopelado, Balo, Guásimo (*Guazuma ulmifolia*), Paja canalera, y en su gran mayoría de Palmas de penca (*Roystonea elata*).

La fauna del lugar se encuentra representada por ranas, sapos, iguanas (*Iguana iguana*), culebras, borrigueros (*Ameiva ameiva*). La población de aves migratorias o que escogen el lugar para anidar son cada vez mayores. Por ejemplo: Garceta bueyera (*Bubulcus ibis*), Gallito de agua (*Jacana jacana*) y patos (*Phophyrula martinica*). Se ha encontrado estiércol de venado (*Odocoileus virginianus*), y familias completas de armadillos (*Dasypus novemsintus*) y monos Tití (*Saginus geoffroyi*). El lago se encuentra cubierto en un 25% por lirio acuático (*Euchornia crassipes*) y tiene Tilapias (*Sarotherodon sp*) sembradas, que pesan más de una libra.

En esta región hay una estación seca o verano y una estación lluviosa. La estación seca va de diciembre a marzo y se puede extender hasta finales de abril. La estación lluviosa va desde finales de abril a finales de noviembre. La mayor precipitación en la temporada lluviosa se da en los meses de octubre y noviembre y la menor en junio y julio.

Hay que recalcar que la falta de malla no ha producido la emigración de los cocodrilos hacia otras regiones, lo que indica que se encuentran ya establecidos en ese lugar, donde la población existente ha permanecido delimitando perfectamente sus territorios. Se reporta que en 1993 se intentaron introducir 2 hembras y 1 macho, los cuales fueron atacados expulsados del lugar por los cocodrilos residentes y capturados posteriormente para ser reubicados.

Aunque los 11 animales son alimentados una vez por semana con vísceras rojas de cerdo mezclados con un suplemento mineral y vitamínico, ellos varían esta dieta comiendo ocasionalmente aves que anidan en los árboles o en el lirio acuático, peces, ranas, etc.

Medem (1958) reporta que los Crocodylia son de ciclo reproductivo altamente estacional. Las 8 temporadas de postura estudiadas se han efectuado en el período de enero a marzo, durante la estación seca. Por comunicación verbal directa con antiguos cazadores en diferentes áreas del país se pudo establecer el hecho de que los *C. acutus* ponen en verano y las primeras crías se ven con los primeros aguaceros de la temporada de lluvias

3. Metodología

La observación de los animales se realiza una vez por semana durante los meses de abril a noviembre, y diariamente durante los meses de diciembre a marzo. Los estudios se realizaron por lo general durante todo el día y solo algunas veces se realizaron mediciones en las horas de la noche.

Las variables a medir se dividieron en Variables Subjetivas y Variables Objetivas. Las subjetivas se relacionan más con el comportamiento social e individual de los animales estudiados y son: Límites territoriales, comportamiento y relaciones dentro del grupo social, comportamiento de la hembra después de la postura y antes de la eclosión.

Las variables objetivas corresponden, en su mayoría a los índices rerpoductivos y son: proporción de hembras por macho, fecha y época de postura, características físicas del lugar de postura, porcentaje de eclosión, promedio de días de incubación, porcentaje de fertilidad del lote y por nido, porcentaje de muerte embrionaria, tamaño y peso de huevos y neonatos.

Los huevos recolectados son incubados en nidos artificiales, que consisten en recipientes de plástico de 5 galones previamente identificados con la fecha de la recolección, el número del nido y la cantidad de huevos recogidos. Los huevos se acomodan en el recipiente con material extraído del mismo nido. Dichos recipientes se colocan a una temperatura entre 30 a 33 °C, permaneciendo allí de 78 a 82 días.

PRESENTACIÓN Y DISCUSIÓN DE RESULTADOS

3.1. Etapa de preanidación

Cortejo y apareamiento:

A finales de la temporada lluviosa los machos comienzan a lucirse. Ellos nadan con la parte dorsal, de la punta de la nariz a la punta de la cola, en forma de flecha. El macho dominante nada en la parte más profunda del lago, en el área del centro, cruzándolo a lo largo y a lo ancho. El macho dominante tiene más de 22 pies (8 mts) de largo y debe pesar más de una tonelada, es de color gris ratón. El está siempre alerta y muy nervioso, especialmente ante la presencia humana. No se le ve pelear con el otro, sino a la hora de la comida. En esta temporada los machos producen sonidos, aunque con menor frecuencia de lo que lo hacen los *Alligatoridae*

Las hembras en esta época son menos agresivas, se ven nadando muy cerca unas de otras y al igual que el macho ellas conservan su lugar de descanso. En algunas horas se ven nadar y descansar en los territorios de los machos. El macho dominante tiene de 6 a 7 hembras muy cerca y el otro tiene 2 ó 3 hembras.

A medida que avanza el período se ve al macho mucho más tiempo en el centro del lago, en el área más profunda y de vez en cuando se ven algunas hembras dirigirse hacia él. La hembra nada diferente al macho, con la punta de la cola sumergida y el cuerpo completamente recto, y se encuentran nariz con nariz. Algunas veces se gruñen y otras hay un chapoteo y se separan. En la granja, ese momento es considerado como la cópula.

Post-apareamiento

Las hembras y machos comen con voracidad. Al inicio de la temporada seca las hembras, dependiendo de cada una, comienzan a disgregarse de los grupos que hacen con el macho y pasan la mayor parte del tiempo con la cabeza sobre la playa y el cuerpo en el agua. Siempre lo hacen en el mismo lugar. Las hembras se ponen nerviosas, pero con baja agresividad, el abdomen comienza a crecer y a veces les impide nadar, especialmente con las patas traseras, las cuales a medida que aumenta el tiempo de gravidez se alejan del cuerpo hasta quedar casi horizontales.

A medida que avanza la temporada seca, las hembras comen cada vez menos y con más dificultad. Siempre se llevan la comida a su playa; comen cada vez menos en el centro del lago. A finales de enero y principios de febrero las hembras pasan mucho tiempo afuera caminando, buscando los antiguos lugares de postura. Rascan el suelo en varios lugares, lo que es considerado como la señal del inicio del período de postura.

3. 2. Etapa de anidación

En esta etapa, cada hembra ha delimitado ya su territorio. Después de 2 ó 3 intentos de hacer el nido, por fin la hembra ha escogido el lugar perfecto. Saca tierra hasta formar un agujero de cierta profundidad. Las hembras jóvenes suelen hacer huecos poco profundos, e incluso poner en la superficie de la tierra. Una vez encontrado el lugar y hecho el hueco, en las 24 horas siguientes la hembra pone sus huevos. Pone todos los huevos de una sentada y los recubre posteriormente con la tierra que dejó al excavar el hueco. Los huevos son tapados de tal forma que los nidos son difícilmente encontrados. La presencia de hojarasca seca y ramitas en la parte superior del nido no se debe a una aportación de la hembra, sino que más bien son parte del suelo excavado.

Bremen (1946) hizo referencia a los nidos excavados en las orillas del Río Chucunaque, en la Provincia del Darién, los cuales tenían una profundidad de 45 cm. Vegambre (1956), Huertas (1959) y Medem (1962) también coincidieron al señalar que en sus estudios encontraron nidos de los cocodrilos de esta especie en excavaciones cerca del agua, en suelos arenosos, con cascajos o simplemente en suelos duros.

Medem en 1962, Ramírez en 1977 y Alderton en 1991, describen que ocasionalmente los *C. acutus* construyen sus nidos haciendo una pequeña excavación, cubriéndolos con tierra y material vegetal. Estos 3 autores sugieren que esto sucede por razones climáticas en áreas con estaciones o porque la vegetación dificulta la entrada de sol al área;en estas dos condiciones no se genera calor suficiente, requiriéndose entonces el calor producido por el fenómeno de putrefacción de la vegetación.

En algunas ocasiones una hembra saca los huevos del nido de otra y pone allí los de ella. Otras veces los ponen tan cerca que parecen una sola postura. Este comportamiento se observó sobre todo en el grupo de hembras que suelen permanecer juntas durante el período de reproducción. Las observaciones de las investigadoras no coinciden con lo expresado por Alvarez del Toro, quien sostiene que los nidos se encuentran situados a una distancia de 50 a 100 metros el uno del otro, y que una hembra no tolera la presencia de otra hembra en ese trecho.

Después de la postura la hembra pasa mucho tiempo cuidando su nido. Está nerviosa y pendiente, aunque cuando se manipulan los nidos ellas no atacan. Esto confirma el caso presentado por Vegambre en 1956, de una hembra que anidó en una huerta casera, y que nunca atacó a nadie, ni siquiera cuando se recogieron los huevos.

En algunas ocasiones en horas del medio día, las hembras salen del agua y se colocan sobre sus nidos. Es impresionante ver a las hembras de 3.5 a 4 metros de más de 500 libras posarse con suavidad sobre sus nidos. Este mismo fenómeno fue reportado por Vegambre de las observaciones realizadas por él sobre el caso del cocodrilo del huerto. La hembra después de 1 ó 2 horas o cuando escucha ruidos se tira al agua.

Para esta etapa y a medida que pasa el tiempo las hembras muestran más interés en la comida. Por lo general comen una vez por semana 2 pulmones o hígados en el centro del lago, y luego se llevan un pulmón a su playa o asoleadero donde, apoyándose con sus patas delanteras en la parte menos profunda, levantan las cabezas y tragan. El nadar se hace más placentero, con las patas traseras pegadas al cuerpo, y se sumergen en las áreas profundas del lago.

Las hembras constantemente revisan y acomodan el nido, incluso aunque se hayan recogido los huevos. Por lo general siempre ponen en el mismo lugar o a pocos metros de la postura anterior, no importando que haya habido intervención del hombre para acomodar los nidos (para liberarlos de la presencia de piedras y obstáculos). Los machos bajan su agresividad, incluso ante la presencia de humanos. Se repliegan a sus playas y sólo salen a comer.

La etapa de anidación dura hasta el mes de mayo cuando comienzan las lluvias y los huevos eclosionan. Esto lo confirman los estudios realizados por Vegambre (1956), Huertas (1959) y Medem (1962) respectivamente. También coinciden en el hecho de que las anidaciones se dan en la época de verano, cosa característica de la familia *Crocodylidae*.

A medida que pasa el tiempo y muy cerca de la época de eclosión, las hembras se tornan agresivas, se pelean entre ellas y casi nunca se encuentran con los machos. Después del cortejo y la cópula el macho es relegado a un segundo lugar y él continúa con su rutina habitual.

En la Tablas 1 se reportan el resumen de los resultados de la observación: Características del nido en cuanto: tamaño, temperatura, profundidad, humedad, número de huevos total, fértiles, rotos. También se reporta algunas características de los huevos, tales como: número de huevos fértiles, tamaño de la banda embrionaria, números de huevos rotos, presencia de moco y fecha de recolección. Usando a fecha de recolección, el tamaño dorsal del embrión y los días de incubación se calcula la fecha posible de la postura utilizando el tamaño dorsal del embrión, basados en los datos obtenidos por T. Johansen en 1981.

La recolección de los huevos se realizó, cuando fue posible, dentro de las primeras 48 horas de la postura, como lo recomienda Johanen en 1981 Se encontró alta correlación entre el tamaño dorsal del embrión y número de huevos sin desarrollo embrionario por nido.

Los huevos son colocados en nidos artificiales que son tanques plásticos de 5 galones, con orificios en el fondo, los cuales son llenados hasta un tercio de su capacidad con el material nidífico que rodea los huevos. Los huevos son incubados dentro del nido artificial en un cuarto con temperatura entre 30 y 33 ° C, y humedad a saturación.

3.3. Etapa de post-anidación

Si las crías nacen en el lugar de la postura, siempre se mantienen en la orilla dentro del territorio de la madre y especialmente donde hay más vegetación. Las hembras están tan violentas que es difícil navegar en un bote en el lago por que ellas tratan de voltearlo al chocarlo de frente con sus cabezas o acercándose para golpearlo con la cola. Cuando los neonetos lloran, ellas emiten ruidos ensordecedores y golpean el agua.

En esta etapa vemos que la hembra ha recuperado la facilidad de nadar, y su abdomen ha vuelto a su estado natural. Una hembra posee un ancho de entre 50 y 60 cm de barriga en este período. Si los huevos son recogidos antes de mayo, que es el mes cuando las hembras esperan que nazcan sus crías, se ponen agresivas y pelean entre ellas pero su actitud territorial va disminuyendo con el tiempo hasta que llega un punto en que la vida en el lago se torna tranquila y rutinaria en espera de la próxima estación de cortejo.

No se han dejado en el lago recién nacidos por miedo a que sean depredados o expulsados del lugar. Este miedo está fundamentado en el hecho de que la población sólo se encuentra formada por adultos desde su inicio hasta ahora y no se han escuchado reportes de que se hubieran visto prejuveniles.

3. 4 Etapa de descanso

La etapa de descanso se realiza en el período comprendido entre los meses de mayo y diciembre. Se presenta después de la recolección de los huevos o después de la eclosión de los mismos en el sitio natural. En este período se llevó a cabo un control del tipo observación y conteo de los animales una vez por semana.

En este período tanto hembras como machos permanecen la mayor parte del tiempo solos, nadando, comiendo y durmiendo. En este último año se pudo comprobar que los hábitos alimenticios de los cocodrilos han variado a causa del aumento en la nidación de la *Bubulcus ibis,* por que ellos han incorporar a los pichones de esta última a su dieta. En este año los cocodrilos prefieren descansar bajo los árboles ocupados por estas garzetas y sus nidos, en espera de que algún polluelo caiga al agua

CONCLUSIONES

1. Basados en los resultados de este estudio se obtuvo que existen cambios en el comportamiento de los animales en cuanto a las siguientes variables subjetivas: distribución en el área, grado de agregación y territorialidad, orden social y agresividad, y respuesta al ofrecimiento de alimento, lo que permitió el establecimiento de cuatro diferentes etapas en el proceso de reproducción de los *Crocodylus acutus* mantenidos en condiciones de semicautiverio: Preanidación, anidación, post-anidación y descanso.
2. Las variables objetivas como: Días probables de postura, pre-recolección, tamaño del nido, temperatura interna del nido, número de huevos por postura y por hembra, tamaño y peso promedio de un huevo, número de huevos fértiles y días promedios de incubación se concideraron como variables independientes. El número de neonatos por nido fue conciderada como variable dependiente. Podemos decir que existe una alta correlaciónmúltiple entre las variables independientes y la variable dependiente. El Indice de correlación múltiple es de 0.9993 con un error estandar de 0.43 y con una probabilidad de 1 de que esto ocurra por causas directas del experimento y no por casualidad.
3. La variabilidad de la variable dependiente puede explicarse estadísticamente en un 31.71%, en un 47.26% y en un 91.13% por el efecto causado por las variables independientes número de huevos fértiles por nido, número de huevos sin desarrollo embrionario por nido y número de huevos con mortalidad embionaria por nido, respectivamente.
4. Aplicando la correlación simple encontramos que hay una alta relación para los pares de variables número de huevos fértiles por nido versus número de neonatos por nido y, peso promedio de huevos versus número de neonatos por nido. Por otro lado, se encontró correlación media entre peso promedio de huevos versus peso promedio de neonatos y profundidad del primer huevo versus temperatura del nido.
5. El grado de dispersión de los datos fue muy alto para las variables mortalidad embrionaria (121.6), huevos sin desarrollo embrionario (91.4), tamaño dorsal del embrión (52.2) y número de huevos rotos (73.7) debido a las condiciones rudimentarias de manejo e incubación de los huevos.
6. Se determinó que la forma de transporte y la época de recolección sí afectan el desarrollo embrionario y el porcentaje de eclosión.
7. En contraposición con lo reportado por Alvarez del Toro, se pudo comprobar que las hembras hacen grupos en el período de reproducción, y las integrantes del grupo anidan cerca una de las otras.
8. No se pudo afirmar o rechazar lo reportado por Medem en 1981 con respecto a la forma y materiales utilizados por las hembras para construir sus nidos, ya que la población estudiada sólo anida en tierra, y la materia orgánica que aparece en el nido no es aportada por ellas, sino que son parte accidental producto del sitio de excavación.
9. Desde 1991 a 1997 se han recogido 38 nidos, con un total de 1,116 huevos, de los cuales 958 fueron fértiles y produjeron 776 nacimientos exitosos. El porcentaje de fertilidad por temporada fue de 86%; el porcentaje de incubación por temporada fue de 72.8; el porcentaje de anidación por temporada fue 60.3; el porcentaje de incubación por nido fue de 79.7 y el porcentaje de fertilidad por hembra de 74.9.

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TABLA 1

RESUMEN DE VARIABLES DE LOS PERIODOS DE ANIDACION DEL C. ACUTUS DE 1991 A 1997

FECHA DE RECOLECCIÓN DIAS	TAMAÑO DEL NIDO (cm)	PROFUNDIDAD AL PRIMER HUEVO (cm)	TEMPERATURA INTERNA DEL NIDO (F)	No DE HUEVOS	No HUEVOS ROTOS	TAMAÑO PROMEDIO DE LOS HUEVOS (cm)	PESO PROMEDIO DE LOS HUEVOS (g)
9	53.4X41.6X29.2	15.3	83	29.8	4.0	20.04X12.66	82.3
9.3	39.5X28.8X28.5	10.0	82	27.0	2.8	19.2X12.8	88.5
4.4	36X31X23	10.4	83	29.9	3.3	20.2X13.5	85.2
5	58X58X29	10.7	83	32.3	3.0	18.4X15.4	89.0
1.2	41X29X31	11.8	83	28.8	2.5	20.7X13.2	86.7
1.6	29.7X22X25	12.7	83	27.0	10.4	20.2X13.8	85.6
1.4	55X38X31	12.8	82	30.0	1.8	18.8X13	*
		13.1	83	35.5	1.3		83.7
	44.7X35.5X28.1	12.0	82.6	29.3	4.0	22.9X13.5	86.2
		1.8	0.4	1.9	2.9		2.4
		15.2	0.5	6.4	73.7		2.8

Tabla 1 Continued

No DE HUEVOS FÉRTILES	TAMAÑO DORSAL PROMEDIO DEL EMBRIÓN (cm)	DIAS DE INCUBACIÓN	No DE HUEVOS SIN DESARROLLO EMBRIONARIO	No DE HUEVOS CON MORTALIDAD EMBRIONARIA	No DE NEONATOS	PESO PROMEDIO DE NEONATOS (g)	TAMAÑO PROMEDIO DE NEONATOS (cm)
26.6	3.0	84.6	1	10.4	15.2	49.1	24.8
24.3	2.8	84.3	5.8	0.0	18.5	51.8	24.0
26.6	1.6	85.2	2.3	1.1	23.1	48.4	23.9
27.7	2.0	81.7	2.7	0.3	24.7	48.9	27.2
26.3	0.8	88.8	1	3.3	22.2	49.9	25.6
16.6	1.1	87.3	0.7	4.3	11.6	44.6	21.8
28.2	0.8	90.4	0.6	1.4	26.2	*	25.9
34.2	1.4						
25.2	1.7	86.0	2.0	3.0	20.2	48.8	24.8
4.0	0.9	3.0	1.8	3.6	5.3	2.4	1.7
15.9	52.2	3.5	91.4	121.6	26.4	4.9	7.1

CORRE LACIÓN

PROFUNDIDAD/No DE HUEVOS	0.012163
PROFUNDIDAD/No HUEVOS FÉRTILES	-0.06668
NÚMERO HUEVOS/HUEVOS FÉRTILES	0.726003
PESO HUEVO/HUEVOS FÉRTILES	0.081337
POSTURA/FERTILIDAD HUEVOS	0.12478
POSTURA/No NEONATOS	-0.3269

Sustainable Use of Large Reptiles - An Introduction to Issues

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INTRODUCTION

The most critically endangered species of crocodilian in the world is the Chinese Alligator (*Alligator sinensis*). There is a large captive population, but the current wild population may be as low as 150 individuals, mostly restricted to 10 small ponds surrounded by lands used for intensive agriculture (Thorbjarnarson *et al.* 2000). Some of the local people living around these ponds are proud of "their" alligators and welcome visitors. Others see no value in the alligators at all because they eat their ducks. Visitors simply increase their anger about the whole affair. The latter group clearly do not consider themselves benefiting in any tangible way from a "conservation" effort in which they are an unwilling partner.

In conservation generally, the issue of "sustainable use" receives an equally diverse reception. Specialists with crocodilians have tended to embrace the concept. Chelonian specialists have tended to reject it. Amongst those working with snakes and lizards, there is a diversity of opinion. In most cases it is claimed that acceptance or rejection is based on scientific evidence, but it is by no means clear whether this is the case. Evidence from different taxonomic groups is seldom examined from the same perspective, by the same people.

The Crocodile Specialist Group (CSG) of the IUCN can point to numerous examples where conservation has benefited through sustainable use programs, yet when these examples are discussed in the context of principles that may be applied to other species, the response is often: "*but crocodiles are different*". The symposium "Sustainable Use of Large Reptiles" within the 15th Working Meeting of the CSG gives experts from a range of different taxonomic groups of reptiles the opportunity to discuss parallels and differences. My goal in this introductory paper is to raise a series of general issues about sustainable use which I think are important to developing a better understanding of the issue so that its strengths, weaknesses and potentials can be evaluated more objectively.

CONSERVATION AND SUSTAINABLE USE

It is hard to expect people to agree on the strengths and weaknesses of different approaches to the conservation if they do not share a common vision about what conservation is. The critical elements as I have come to see them over time are embodied in a simple definition:

Conservation is the sum total of actions taken to preserve and maintain items to which we attribute a positive value.

This definition is not restricted to wildlife conservation, neither is it controversial. It allows "value" to be expressed in terms of intrinsic or use (instrumental) values and assumes people should be willing partners. It accepts that people are unlikely to expend resources conserving items to which they attribute no value, or items which to them have only a negative value, as in the Chinese Alligator example. If you wish to conserve the last remaining wild Chinese Alligator populations, their value to the community must be increased to whatever level is required to change the current perception. Whatever is most likely to work, on site, in China, at the local community level, should not be unduly constrained by what people in different countries with different cultures decide is "acceptable".

If we can accept that "use" gives "benefits", which increase "values", which in turn create additional incentives to "preserve and maintain" a species or resource, then I would argue that the motivation is secondary. If people are prepared to conserve a species so that it can be used, it is a small price to pay. Nor do these links between conservation and value mean that the income earning base of people needs to be changed completely for conservation to benefit. A cattle station engaged in some use of crocodiles for commercial purposes does not need to manage his property like a national park. Relatively small economic advantages can change the perception of a wildlife species from liability (or irrelevant), to asset.

Loss of habitat over time is not necessarily restricted to rapid, large scale land-clearing. It involves many small and minor land use decisions, made daily, all over the world. This is what dictates whether small patches of habitat and the species they contain are retained or converted to other uses. Governments struggle with competing demands for financial resources, and funds allocated to wildlife are funds taken away from education, health, roads, communications, etc. It is far easier for governments to justify the allocation of resources to the conservation of species generating economic benefits than those not generating income.

The relationship described above is fundamentally one between "use" and "conservation". The "sustainability" element is quite different. To sustain uses of anything, from televisions to marriages to wildlife, requires the same ongoing process of monitoring, assessment and adjustment. It is misleading to talk of "sustainable use" as some different form of use: the "use" part is the same and it is only the management and control of use that varies. In terms of definitions for "sustainable use", I favour something like:

Sustainable use of a species is use associated with a process aimed at ensuring the use can continue and that its impacts are maintained within acceptable or defined limits.

Whether a use is sustained or not can only be determined by hindsight: *was the use kept going*? One cannot design a management program and prove in advance that it will be sustainable, although the probability that it will be sustainable can perhaps be judged as high or low on available information. Regardless, there is a very clear distinction between "predicted sustainability" (what I think might happen) and "measured sustainability" (what happened).

Thus the work of Congdon *et al.* (1993) has often been interpreted as indicating freshwater turtles cannot sustain uses because of their life history strategy. Yet we know Aboriginal people in northern Australia have been harvesting long-necked turtles (*Chelodina rugosa*), in large numbers each year, for over 20,000 years. Sea turtles have sustained massive harvests and their use for food stems back to the first humans. Their densities may have been greatly reduced over time and they may have various other problems, but there is no doubt that they are well equipped biologically to sustain some levels of use, regardless of predictions.

REPTILIAN CONSERVATION EFFORTS AND THEIR LEGACY

It is now globally recognised that the effective conservation of any species, in any part of the world, will ultimately depend on resolving problems that involve biological, social-cultural and economic variables (Hutton and Dickson 2000). This generalisation stands regardless of whether conservation is directed at preservation or sustainable use.

The idea that biological variables may often be the least important ones to consider may seem bold to some, but it is obvious. Vast numbers of species have been conserved without even knowing their taxonomy, within areas of habitat retained for other purposes. In contrast, species in the wild whose biology is particularly well known (eg tigers, Chinese alligators, rhinoceros), often face major conservation problems because social/cultural and economic variables have tended to be ignored.

So regardless of how important we consider "biological evidence", it is important to recognise that it is only one small part of solving conservation problems. Knowing the biology in great depth may contribute little to conservation if we ignore the other key variables. People generally "hate" snakes, because they can kill or threaten people. This socio-cultural element is far more important to snake conservation than most other issues, and if our problem is "snake conservation", we may need to look well beyond biological research to solve it.

In the case of reptilian conservation generally, the 1960's saw an upsurge of academic interest in herpetological research around the world that had little to do with conservation. However, this coincided in the late 1960's and early 1970's with an explosion of global interest in wildlife conservation generally, and herpetologists often ended up taking the lead in reptile issues. But most were zoologists and relatively few had wildlife management credentials. Indeed, at that time "wildlife management" was often viewed academically as a less challenging career than zoological research *per se*.

But because herpetologists did hold the intrinsic value of reptiles highly, and did benefit directly by conservation funding, they did become active in reptile conservation. In terms of pertinent experience, the herpetological literature of the day was paying great attention to life history parameters linked to population dynamics, but contained virtually nothing about dynamic populations (see below). Simple population models highlighted the relative importance of different parameters (eg Nichols *et al.* 1976), but were a long way short of being able to predict how populations would respond to say a 50% reduction in size. Sea turtle models today suffer from this same problem (Chaloupka and Musick 1997), because research on wild populations subject to harvest is rare (Carrillo *et al.* 1999). With the benefit of hindsight, some of the main reptile harvesters of the 1960's and 1970's were herpetologists themselves: it was a period in which museum collections increased exponentially!

Early conservation efforts with reptiles accepted that some species were used by people, and tried to accommodate that use to varying degrees when advancing conservation. Thus Schroeder (1962) labelled Green Sea Turtles the "buffalo of the sea" and Archie Carr (1967) recognised "a way to accomplish the dual aim of feeding people and saving natural turtle populations is to set up turtle farms". When the CSG was formed, Budowski (1971) advised: "not only should we emphasize the economic aspects, which are self evident, but we can also bring out eloquently the educational, aesthetic and cultural advantages that a sound programme of crocodile conservation, including wise utilization, can yield". Cott (1971) advised: "In many cases it will therefore favour the quota system rather than total prohibition as the best means of achieving its objective of species survival".

But during the late 1970's and early 1980's, the willingness to accommodate sustainable utilisation changed in favour of a highly protectionist focus. Although often claimed to be based on "science", there was still a paucity of information available on just how dynamic reptile populations could be when faced with harvests and reductions in density. With crocodilians, this information was starting to emerge (eg Webb *et al.* 1984). By the late 1980's the CSG was again supporting sustainable use programs and through the 1990's endorsed more and more programs involving the commercial, consumptive use of crocodilians. The extra values created by economic use generated increased investment in conservation. In contrast, the Marine Turtle Specialist Group (MTSG) never seems to have recovered its initial preparedness to accept commercial utilisation as part of any conservation package. This reluctance is sometimes justified on the basis of supposedly unique life history traits, particularly long ages to maturity (eg Mortimer 1995; Bjorndal 1999). But crocodilians, marine turtles and freshwater turtles have remarkably similar life history traits and population dynamics (Webb 1997), which suggests that the justification may be spurious. With lizards, important studies on harvests (Tinkel 1982; Tinkel *et al.* 1993; Fitzgerald 1994) and compensatory responses did not establish the research leadership that was needed.

In reality, the fundamental difference between crocodiles and sea turtles may have little if anything to do with science. Crocodiles eat people and domestic stock, whereas sea turtles do not. When crocodile numbers start to increase, negative values increase. This erodes total values to the community, and impacts on the commitment and allocation of resources to conservation. Those committed to conserving crocodiles, who mostly hold the intrinsic value of crocodiles very highly, experimented with economic values and soon found that they provided powerful tools for conservation.

It can be argued that crocodilians "are different" in that their predatory nature causes negative values, which do not exist for species such as marine turtles. But this would miss the point. No species today receives the optimum resources for their conservation. If new values can increase conservation resources, then such increases will benefit all species.

In overview, the knowledge base for the conservation and sustainable use of large reptiles varies amongst taxonomic groups. With crocodilians there has been a long history of harvest experimentation, some of which we have heard about in other talks here (Webb *et al.* 2000; Woodward *et al* 2000), and further experimentation is viewed positively and encouraged. Similar efforts with other reptile groups (Carrillo *et al.* 1999; Fitzgerald 2000) tend to be scarce, and there often appears to be a reluctance to engage in experiments that may challenge the preservation paradigm. As emphasized by Scott and Seigal (1992):

"Wildlife managers and herpetologists need to work together for the good of the resource: herpetologists must seriously consider the requirements of wildlife managers, and managers must approach management and conservation of reptiles and amphibians in the same rigorous fashion as birds and mammals."

LEVELS OF RESOLUTION

In solving any problem, it is important that the level of resolution of the problem is matched with the level of resolution of the solution. For conservation problems, the key variables are socio-cultural, economic and biological, and potential solutions need to look at all three.

When sub-problems are identified within the biological sphere, it is again important that solutions are found at a compatible level of resolution. If the problem involves unknown responses of populations to possibly excessive use, the optimum solutions probably lie at the dynamic population level of resolution: finding out how they do respond (Tinkle 1982). But the most common approach seems to be to initiate very thorough research at a fine level of resolution, quantifying individual life history parameters to the maximum degree possible. This is a long, costly and indirect approach to solving the problem, with no guarantee of success: *"decades are required to collect accurate data on these highly migratory and slowly maturing species"* (Crouse 1999). Indeed, with sea turtles I suspect that many of the data required are beyond our technical capability to collect no matter how much time we take!

But the problem does not stop there. Once decades of research have been done and models are created with all the measured parameters, they can still not predict what will happen when the population density is reduced. Harvesting experiments will eventually need to be done, because no model can predict the way variables interact. And then it can be argued that decades of further work are needed to ensure the impacts, through all life stages, are known and quantified (Mortimer 1995; Crouse 1999).

In essence, the time scale of the reductionist approach is totally out of alignment with the time scale at which conservation and resource use problems are arising today. It has led resource specialists to encourage experimental harvests and adaptive management approaches, rather than the collection of basic species-specific life history data (Walters 1986).

By way of analogy, we have the technology to measure bricks to many decimals places, but if our object is to design or construct a building, we only need to measure the bricks to the level of resolution required to solve that problem. We apply such commonsense judgement to problems we solve every day, but when it comes to wildlife the lessons seem to be forgotten.

HOUSE OF CARDS?

There are many reasons why some reptile specialists are particularly cautious about embracing sustainable use as an option, and the view that all wildlife populations are "fragile" is amongst them. This view is encouraged by reference to the precautionary principle, which is fundamentally flawed when it comes to wildlife conservation. In the 1960's and 1970's, the ecological paradigm of the day emphasised the often complex biological environment in which species and populations survive, with intricate food webs and interlinked energy cycles. The general impression created was that biological systems were like a house built of playing cards that would collapse if one of the supporting cards was removed. Yet in reality a more useful analogy may be a rubber glove full of water. Changes in one part of the glove (squeezing a finger) are absorbed by the system, which has an amazing ability to adapt and retain its fundamental structure, unless the primary energy flow through it (draining the water) is greatly compromised.

The concept of "fragility" with all wildlife populations contrasts markedly with our inability to make animal populations go extinct when we try. For example, we spend vast resources each year - billions of dollars - trying to control agricultural pests and eradicate feral animals. Attempts to eradicate feral Brown Tree Snakes (*Boiga irregularis*) from Guam (Rodda and Fritts 1992a, 1992b; Fritz and Rodda 1996, 1998) have not succeeded. The long history of uncontrolled utilisation and eradication of crocodilians around the world, makes it clear that if habitats are retained, crocodilians are not fragile but rather tenacious survivors (Webb *et al.* 1987). The same is surely well demonstrated with sea turtles, which have probably been under continual harvest since the first humanoids reached the first beach. The animals which survived the extinction of dinosaurs are still with us.

Species such as the Western Swamp Turtle (*Psuedemydura umbrina*) are represented by a few remaining individuals in one small area (Kuchling 1998), and the species can rightly be considered endangered (Webb and Carrillo 2000). In this case, realistic scenarios that could lead to extinction can be easily derived, and their management should perhaps be approached with a perception of "fragility". But with globally distributed species such as Hawksbill Turtles (*Eretmochelys imbricata*), which are abundant and secure in many areas, there simply are no scenarios that could lead to global extinction

(Mrosovsky, 2000; Webb and Carrillo 2000). To prevent research into the impacts of use, which can provide much of the missing information needed to model populations realistically (Chaloupka and Musick 1997), is counterproductive to conservation.

CAUGHLEY'S SPRING

The late Graeme Caughley likened wildlife populations to a spring. When they are reduced, but their environment and resources are still intact, it's like compressing the spring. The more they are reduced, the greater their potential to recover rapidly if given the opportunity. There is clearly a degree of compression (population reduction) which can break the spring, preventing recovery and causing extinction. But most wildlife problems are ones in which the biological ability to recover has not been compromised, although they are not being given the opportunity to recover.

For example we know intensive harvesting in Mexico over many years reduced sea turtle populations. But when harvest pressures were reduced, it resulted in exponential increases in the population size of Hawksbill Turtles (*E. imbricata*), Olive Ridley Turtles (*Lepidochelys olivacea*) and Green Turtles (*Chelonia mydas*) (Garduño-Andrade *et al.* 1999; Marquez 2000). Long-lived species which withstood intense harvesting for decades, had their populations greatly reduced, but did not lose their ability to recover. Saltwater Crocodiles (*Crocodylus porosus*) in Australia had their populations reduced to less than 5% of original numbers, but were able to recover when given the opportunity (Webb *et al.* 2000).

Harvest theory for all species basically says that there is maximum species-specific rate at which a compressed spring (reduced population) can recover (rate of recovery of the population). So all harvest models which try to maximise offtake must first reduce the population (compress the spring) to a level where the rate of recovery is maximised. If the recovering section of the population is then harvested each year, so the harvest can be sustained and the reduced population conserved (eg Caughley and Sinclair 1994; Erdelen 1998; Choquenot *et al.* 1998; Butterworth 1999).

POPULATION DYNAMICS VERSUS DYNAMIC POPULATIONS

If reptile conservation is to advance today, in the face of habitat loss and wildlife being used legally and illegally, inside and outside of programs aimed at achieving sustainability, it is imperative that we learn to drive research at the dynamic population level of resolution.

All populations are fundamentally similar in that they have dynamics which increase the population (reproduction, immigration), dynamics which decrease it (mortality, emigration), and lots of unpredictable interactions. But a vast gulf exists between research directed at population dynamics and research directed at dynamic populations. Populations respond to changed circumstances and these responses can be measured, quantified and used for prediction, even though we may have only have a very superficial view of how or why a particular response is generated (Tinkle 1982; Tinkle *et al.* 1993). For many management problems we need to know "what" will happen, and cannot afford the time or resources to work out "why" it is happening.

But once we learn to operate at the dynamic population level, and appreciate the capacities of wildlife populations to adapt to change, we can readily move between taxonomic groups, despite biopolitical barriers to such movements: *"What's he working on lizards for? He's a crocodile expert!"*

The car we need to learn to drive is clearly the dynamic population car. And just as we can rapidly extend skills with driving from a Ford sedan to other brands of car, and then to trucks, buses, tractors or bikes, once we learn to work with dynamic populations we can rapidly transfer those skills to other species and groups. To argue that we cannot work at the dynamic population level until we understand all the component parts of each vehicle we drive, is to totally lose sight of the problem we're trying to solve. It is simply not necessary to know the inner workings of a sparkplug to drive a car.

MODELS AND MODELS

As pointed out by Carrillo *et al.* (1999), when the life history traits are measured in a population at carrying capacity (stable or fluctuating around a stable mean), the dynamics which are expanding the population are matched to those reducing the population. So the population remains in balance. Simple models which rely on parameter estimates derived in this way (eg Smith and Webb 1985; Congdon *et al.* 1993; Congdon and Dunham 1994) do not have much utility in predicting the impacts of harvest, because the population is given no capacity to recover. A harvest reduces the population, and the population stays there. The impact of harvesting adults will automatically be predicted as being much greater than that of harvesting hatchlings. But in reality, harvests of adult American Alligators (*A. mississippiensis*)(Joanen and McNease 1987; Woodward *et al.* 1991, 2000) demonstrate wild populations have been expanding while harvests take place!

Another prediction from such parameter models will be that the population structure will be constant: the proportion of juveniles life stages to adults will be constant. For the US Loggerhead Turtle (*Caretta caretta*) population, 498,000 eggs and juveniles are estimated to be needed to support a stable adult population of 1277 individuals (Crouse *et al.* 1987). By extrapolation, 996,000 eggs and juveniles would be needed to support an adult population twice that size. But in reality, there is no constant or fixed relationship in the ratio of juveniles to adults. It is well known from the earliest studies (Cott 1961) with crocodiles that juveniles make up a high proportion of the population in a depleted or recovering population of crocodiles, but a very low proportion in a recovered population at or near carrying capacity. Despite the predictions of such simple models, the impact of harvesting crocodile eggs can seldom be detected (Woodward *et al.* 1991, 2000; Webb *et al.* 2000; Temsiripong *et al* 2000).

A further problem with simple models, is the tendency to use parameter estimates quantified outside the population being studied if they have been quantified with more accuracy and precision. Yet this can introduce remarkable biases, because reptilian life history traits show tremendous geographic variation. For example, the maximum size of Australian Freshwater Crocodiles (*Crocodylus johnstoni*) may be 1.2 m and 7 kg in some populations, and 2.5 m and 60 kg in others (Webb 1979): the relationship between growth rate and size is simply not transferable. Hawksbill turtles in Cuba grow at 2-4 times the rate of Hawksbill turtles in southeastern Australia and Puerto Rico (CCMA 2000). Nesting Hawksbill Turtles in Antigua are large animals which nest 4 times in a season: those in Mexico and Cuba are small and nest 2.5 times in a season. Clutch size for Saltwater Crocodiles in PNG averages 59 eggs (Cox 1985) whereas in Australia it averages 50 eggs (Webb and Cooper Preston 1989). Models which ignore such geographic variation (Heppel *et al.* 1995, 1996) can give highly misleading predictions.

In overview, the central problem with simple modelling is a failure to appreciate the many and varied ways in which population parameters respond to density: density-dependence or compensatory response. Indeed, Crouse (1997) criticised Cuba for even suggesting density-dependent mechanisms would apply to sea turtles. In a later paper (Crouse 1999), she acknowledges that now that people have looked (eg Bjorndal *et al.* 1998) density-dependent effects on growth rates are a reality.

MONITORING POPULATIONS

Scott and Seigal (1992) drew attention to the fact that reptile populations were generally difficult to estimate and monitor over time, which reflects the cryptic nature of most of them. They are not as "visible" as many birds and mammals. Fish populations can rarely be seen and most monitoring is linked to data derived from harvest samples (Butterworth 1999). The same problem applies to sea snakes (Heatwole 1997) in most areas. Information on sea turtle populations can be gathered through harvest statistics, but when no harvests occur, monitoring is largely restricted to nests and/or nesting females (Meylan 1997, 1999). Like sea turtles, crocodilians in heavily vegetated habitats can rarely be seen and nest counts are often the only index of the population available for counting (Hollands 1987; Joanen and McNease 1987). But in other areas, for example tidal rivers with large rises and falls in the tide, 60-70% of Saltwater Crocodiles (*Crocodylus porosus*) in a population can be seen in spotlight counts (Messel *et al.* 1981; Webb *et al.* 1986). Lizards and snakes are often particularly difficult to survey (eg. Scott and Seigal 1992; Abel 1998; Riquier 1998; Erdelen 1998), and information drawn from harvested specimens (Shine *et al.* 1995, 1996; Webb *et al.* 1996) may offer the only cost-effective and practical solution in areas where harvests take place. But snakes may clearly be much more abundant than is indicated by the number seen at any one time. Whitaker and Andrews (1996) introduced a program in India through which indigenous people could catch snakes, get paid for the venom extracted from them, and then mark and release the snakes. Some 15,000 snakes have been marked and released to date, but only 20 recaptures recorded!

How we interpret monitoring results depends in part on how we think the indices we measure relate to the population as a whole. But we seldom know a great deal about this, and when we do, the need for caution is clear. Saltwater Crocodiles (*C. porosus*) in the Northern Territory of Australia (Webb *et al.* 1999, 2000) provide a good example.

The wild population was greatly depleted by hunting (95%+) for skins between 1945 and 1971. Populations began to recover immediately after protection (1971), because the remaining small nucleus of wary adult nested, and in a greatly depleted population the hatchlings, then one-year-olds, then two-year-olds and so on, demonstrated high survival rates (Webb and Manolis 1992). By the mid-1970's, when more serious monitoring efforts were initiated, populations were heavily biased towards juveniles. But as recovery continued the population structure changed (Fig. 1) and juvenile numbers either stabilised or declined (Fig. 2). An analysis of trends (Webb and Manolis 1992) indicated survival rates of hatchlings over time were unrelated to crocodile density, whereas the survival of one-year-olds was highly correlated with the numbers of large crocodiles. With older juveniles, social exclusion limits the numbers in any one area and it is assumed many of the excluded animals die. Over time, the population structure became dominated by adults, and relatively few juveniles now survive.

With relatively comprehensive data now available, a series of basic questions can be asked:

1. What was the relationship between numbers of nests and available habitat?

In the mid 1970's, Magnusson (1980) predicted that there were potentially 933 suitable nest sites for Saltwater Crocodiles (*C. porosus*) in the Liverpool and Tomkinson Rivers, and the population of nesting females could increase by a factor of 18 before nest sites became limiting. But no such increase occurred. The adult population in these rivers increased by a factor of around 1.5 between the mid-1970's and 1998 and now appears stable (Webb *et al.* 1999). Nest numbers changed little. As demonstrated in American Alligators (*A. mississippiensis*) (Hines and Abercrombie 1987), a bottleneck occurs in adult-sized females. They are potentially mature but do not nest, regardless of available habitat. If these females are removed from the wild they are rapidly replaced by other nesting females, and if the females removed are

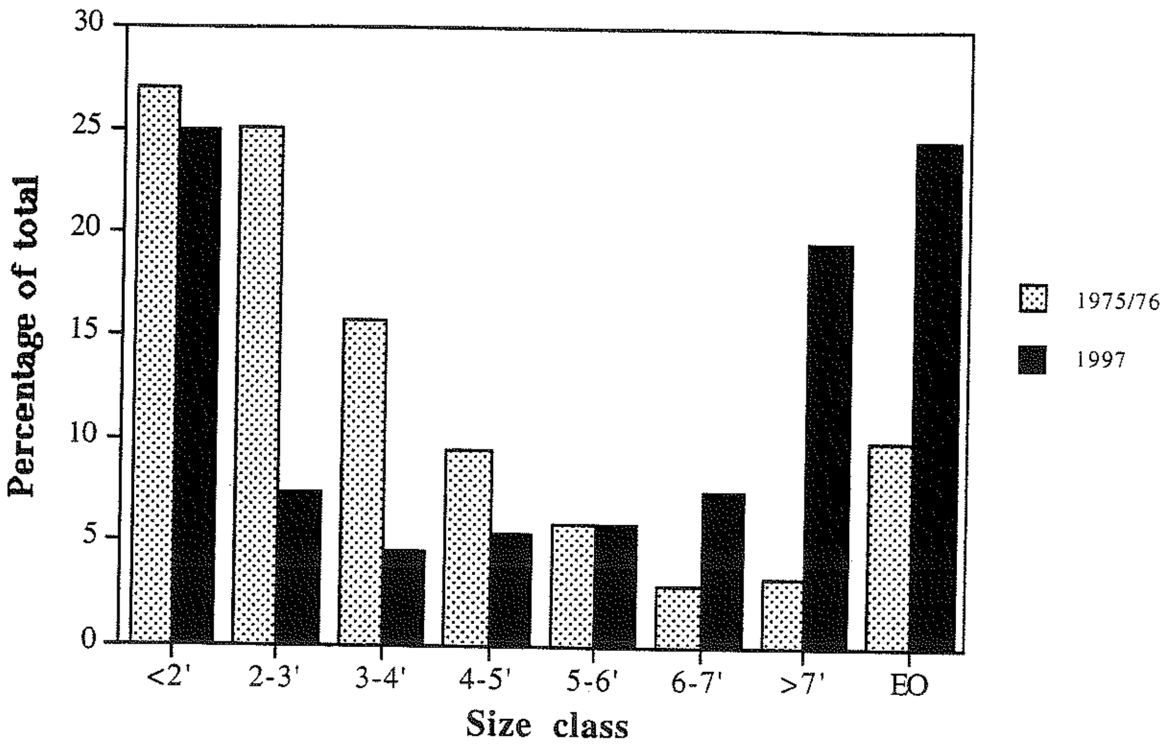

Figure 1. Histogram comparing the population size structure of *C. porosus* recorded in spotlight surveys in a 35 rivers in the Northern Territory in 1975/76 (shaded bars) and 11 rivers in 1997 (solid bars). EO represents eyeshines only: crocodiles where no size estimate could be obtained, most of which are large, wary adults.

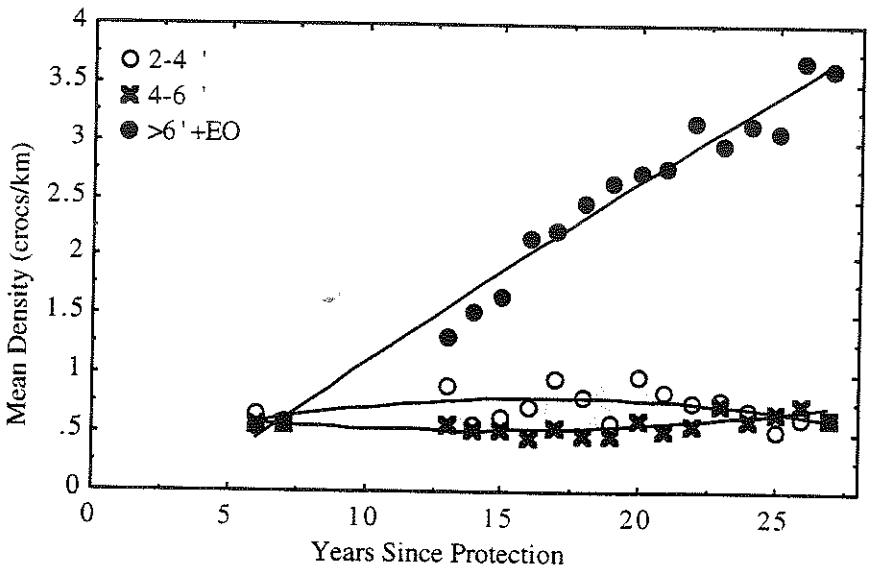

Figure 2. Mean density of different sized *C. porosus* sighted in spotlight surveys in 11 rivers (1977-98) as a function of years since protection (1971= year 1; 1998= year 27). Lines are linear and second order polynomial regressions indicating general trends. EO represent eyeshines only: crocodiles where no size estimate could be obtained (wary adults) and so are combined with >6' animals.

placed in captivity, they all begin nesting within a year. In short, the percentage of females that nest is itself density-dependent.

2. Do trends in nest numbers reflect the general pattern of population recovery?

In some areas they do and in others they do not. For example, in the Adelaide River mainstream (Fig. 3) nest numbers did not start to increase until 9-10 years after protection and were thus not correlated with the general increase in numbers of crocodiles. After this time the increase in nest numbers was correlated with the general recovering trend in the population. But in the major nesting area associated with the Adelaide River (Melacca Swamp), nest numbers fluctuated around a stable mean between 1979 and 1995 (Fig. 3) and did not in any way reflect the general population trends. That they increased dramatically in a step-like fashion after 1995 was equally not correlated with any obvious trend in the wild population.

3. Did nesting remain "patchy".

In the 1970's it was apparent that nesting was patchy in terms of nest locations and the density of nests (Magnusson *et al.* 1978, 1980). This same patchiness was retained, with increases in nesting density in some patches but not in others. Any argument that the patchiness reflected an artefact of depleted populations was wrong; it was a totally natural situation.

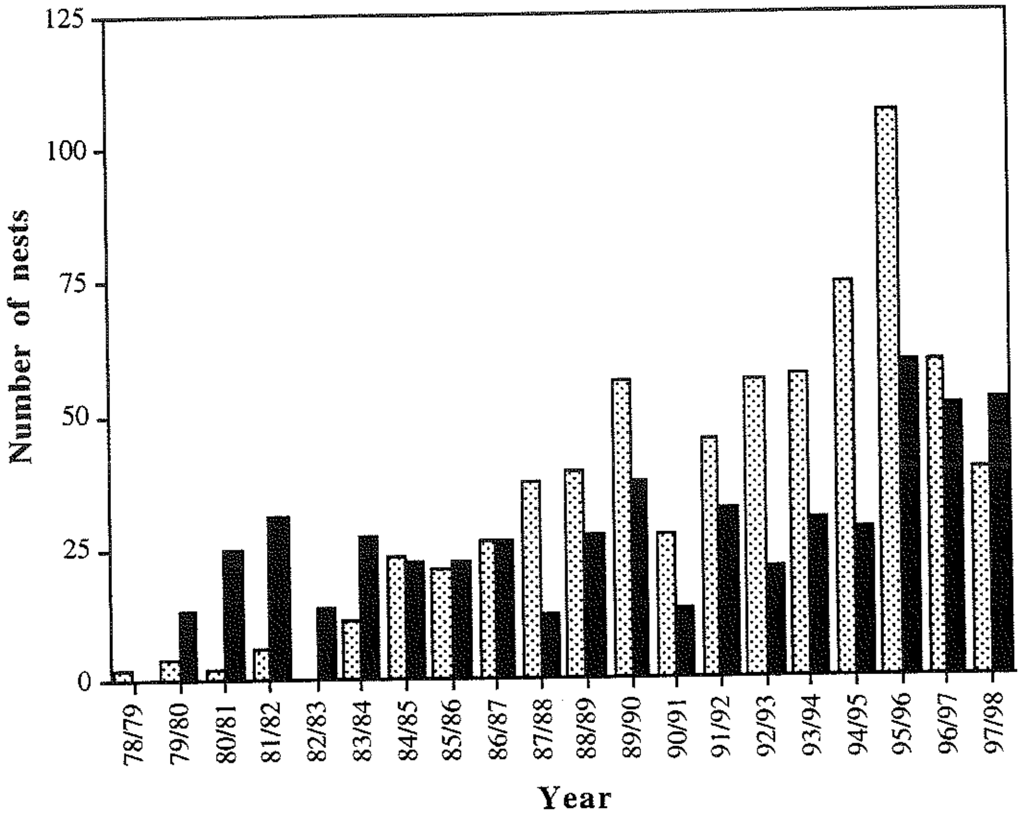

Figure 3. Chart showing the number of nests (excluding false nests) located in the Adelaide River system (shaded bars) and Melacca Swamp (solid bars). Nesting area was reduced on the Adelaide River in 1996/97 due to extensive flooding. Data for 1997/98 are incomplete.

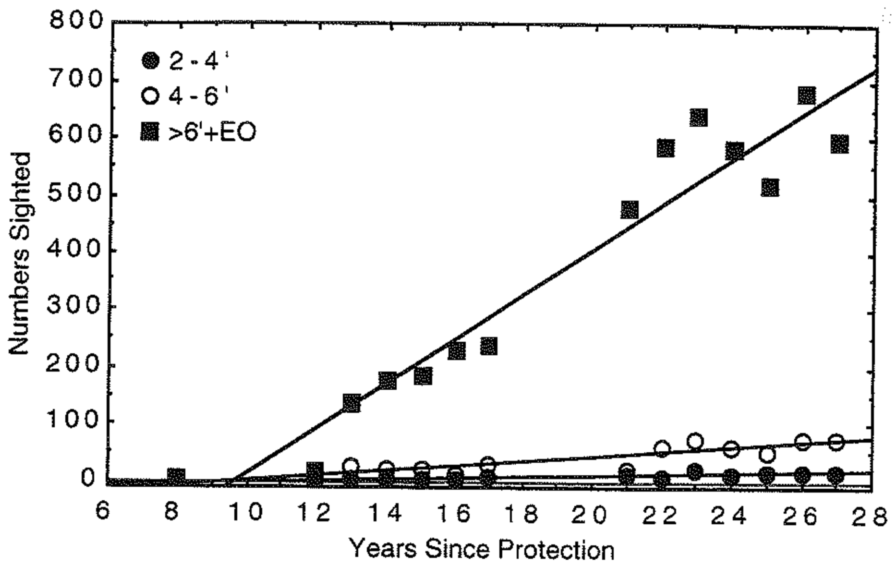

Figure 4. Numbers of *C. porosus* in major size classes sighted in spotlight surveys in the Mary River System against years since protection (0= 1971, ... 26= 1997). Lines are significant linear regressions. EO represent eyeshines only: crocodiles where no size estimate could be obtained (wary adults) and so are combined with >6' animals.

4. Did trends in nesting adequately reflect trends in the population?

In the first 5-6 years of protection, *C. porosus* numbers increased dramatically, and by 1980 the populations were around 50% of "pristine" abundance. Yet there were few nests because insufficient time had passed for animals to reach maturity (12-16 years). But many management decisions were implemented in the early 1980's based on the obvious recovery. It was not until the mid-1980's that the recovery would have been apparent from an increase in nest numbers, and in the case of Melacca Swamp, no significant recovery in the population would have been apparent by nest counts until 1995; 24 years after protection and well after a dramatic increase in the population had taken place. In the case of the Mary River (Fig. 4) the density of large adult crocodiles increased dramatically relative to other rivers, but virtually no nesting occurred (even by 1990 only 9 nests were sighted in the whole river system). If one was restricted to assessing population status based on nests, the wrong conclusions would have been drawn time and again.

In any overview, one must use whatever indices of abundance are available, but it is critically important that the limitations of those indices are appreciated.

HISTORICAL REFERENCE POINTS

Status is a relative measure which usually requires the distribution and abundance of a species today to be compared with that at some time in the distant past (Webb 1986). However, historical reference points are often vague statements made by early explorers or surveyors, and if not thoroughly researched can dramatically affect the perception of how conservation efforts are proceeding. For example, with Kemp Ridley's (*L. kempi*), a 1947 film of an arribada at Rancho Nuevo (Mexico) was interpreted as suggesting 40,000 turtles were nesting, yet by 1965 only 5000 were nesting (Pritchard 1997). Although this is probably the case with this species, it is equally clear that critical review of that

1947 piece of film is needed to establish this reference point so that later conservation goals are biologically attainable.

With *C. porosus* in Australia, it was once thought that the original wild population was well in excess of one million individuals. This figure seemed consistent with a cursory review of skin export figures and statements from early explorers and hunters about rivers "teeming with crocodiles". Thus by 1980, 9 years after protection, it was considered that the wild population was still only 1-2% of its former abundance (Messel *et al.* 1981). It was recognised that it may take decades for many of the rivers with low densities of crocodiles to repopulate. That is, that the conservation efforts being made at great expense were producing marginal results.

When the issue of historical abundance was thoroughly researched (Webb *et al.* 1984) it became clear that the wild population had never been so abundant, and that the numbers of skins exported was far more modest. Indeed, it even became clear that most rivers containing low densities of crocodiles by 1984 had always contained low densities, and that the rivers "teeming with crocodiles" were a handful of high density rivers that visitors in the 1980's were also reporting as "teeming with crocodiles". Thumbnail assessments indicated that the population by the early 1980's was conservatively 30-40% of what had existed historically, rather than 1-2%. With later research it now seems likely that it was 50%. In terms of conservation achievement, this historical research changed perceptions on the effectiveness of conservation efforts from 1-2% recovery to 50% recovery!

When we see statements that the waters around the Cayman Islands were teeming with Green Turtles when Colombus arrived (Fosdick and Fosdick 1994), it begs the question about how many turtles Colombus may have interpreted as "teeming". When Meylan and Donnelly (1999) extrapolate information to suggest that over 900 Hawksbill Turtles were nesting each night on a beach in Panama, when no such nesting densities have ever been reported elsewhere, even in areas with a long history of protection, it is immediately suspect. When it is implied that the low density nesting recorded in most areas where Hawksbills nest is a derived state, without any information to suggest it was ever any different, the alarm bells calling for some thorough and objective historical research ring loudly.

SUSTAINING USES IN A RECOVERING POPULATION

In many commercial harvest programs, the aim is to maximise the harvest and achieve Maximum Sustainable Yield (Tucker 1995; Butterworth 1999). However, when the aim of a harvest program is specifically to increase the value of a species in the eyes of the community, a harvest of much less intensity may be all that is needed. For example the recovery of Saltwater Crocodiles (*C. porosus*) in the Northern Territory occurred while a ranching program harvesting eggs was also occurring. The harvest program implemented in Louisiana for American Alligators (*A. mississippiensis*) did not stop the wild population continuing to expand. In both cases the rate of harvest was less that the rate of population increase. Indeed, the harvest may well have broken down social hierarchies constraining a population: a harvested population may contain more individuals than one not harvested. In any overview, there seems little to be gained by waiting until a recovering population is fully recovered before initiating a harvest program, in which the first step may be to reduce the population by 30% to stimulate a faster rate of increase. Similarly, it is rarely possible to define "when" a population has "recovered".

LONG-LIVED VERSUS SHORT-LIVED SPECIES

The question about whether longevity in large reptiles is an asset or a liability is confused within the literature. On the one hand it is argued that species which take long periods of time to reach maturity, and then survive for long periods of time after maturity is reached, are difficult to manage (Mortimer 1995). However, this is a totally different issue than "fragility". Short-lived species cannot withstand adverse impacts for long periods of time, because all adults in the population are affected. In contrast, long-lived species can withstand adverse impacts for long periods of time and still retain the ability to stimulate a population recovery. They are thus far more robust in terms of surviving adverse environmental situations with the potential to cause extinction. It is often implied that marine species such as sea turtles are particularly vulnerable because of their marine mode of existence and migratory habits. Yet relative to a terrestrial chelonian of similar size, both the marine life style and ability to move are major buffers against extinction.

CONCLUSIONS

Whether we support "sustainable use" as a conservation tool, whether we understand it, whether we are sceptical of its potential, or oppose its introduction vehemently - it is now impossible to walk away from the conclusion that it deserves to be investigated closely. There is no doubt it ruffles the feathers of some conservationists, but then so do many other things. If as I've argued here it can be an effective way of increasing the value of wild species to the community, so it has the potential to increase the resources which can be allocated to conservation. We should be able to look at this issue with the same objectivity we apply to other aspects of reptilian research.

It has become customary to think of those who promote sustainable use thinking as being insensitive beings who favour big business over aesthetic values. There's little that can be done about this: shooting the messenger is often easier than heeding the message. With Saltwater Crocodiles in the Northern Territory the calls for culling became loud in 1980 when it became obvious crocodiles were reinstating themselves across the complete Northern Territory coastline. Introducing programs with economic incentives proved extremely effective in winning general public support for crocodiles. This is not a hypothesis, it is fact.

When examining the application of sustainable use thinking to other reptile groups, I've tried to highlight issues where I think lessons from one group of reptiles may have application to others. Reptiles generally do not win a lot of public sympathy, and so to achieve conservation, innovation is often necessary. Even where they do have public sympathy (eg sea turtles) increasing the total values of a species to the community increases the resources made available for conservation, which are seldom considered adequate.

If there is a single message I would like to leave you with, it is that we will never be able to understand reptile conservation problems unless we concentrate research on dynamic populations rather than population dynamics. This is the car we must learn to drive. The results of research in this area will give a remarkable appreciation of just how adaptable many reptile populations really are. To ignore such adaptability at the population level, may well be to ignore the very processes that have allowed reptile populations to survive over time.

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