

**UNIFYING ECOLOGICAL AND SOCIAL SCIENCES INTO
A MANAGEMENT FRAMEWORK FOR WILDLIFE-BASED
TOURISM: A CASE STUDY OF FEEDING STINGRAYS AS
A MARINE TOURISM ATTRACTION IN THE CAYMAN
ISLANDS**

by

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ABSTRACT

As marine wildlife tourism attractions increase in popularity, the integration of natural and social sciences is required to ascertain and then assimilate strategies to effectively address the undesirable ecological and social conditions of the wildlife tourism setting. The overarching objective of my doctoral research was to develop and employ a framework for mitigating human-wildlife conflict in the management of wildlife tourism. Using the feeding of stingrays at 'Stingray City Sandbar' (SCS), Cayman Islands, as a model for marine tourism attractions, I examined ecological and social indicators that could lead to detractions from the tourist experience, or negative impacts on stingray fitness. Using quantitative social indicators, I assessed tourist preferences for certain proposed visitor management options at SCS, and tourists' expectations and satisfaction with SCS and their level of concern with the potential impacts of wildlife tourism. Results suggest tourists are heterogeneous in their degree of support for alternative management scenarios, and are furthermore not a homogeneous group as they possess differing expectations and divergent wildlife conservation values. The ecological indicators assessed - general, physiological and immunological health, were chosen to reflect the potential outcome of tourist activities such as feeding and handling stingrays. Findings reveal stingrays are receiving unbalanced lipid nutrition; they display grouping costs in the form of increased parasite loads, conspecific bite marks, and injuries; and they exhibit

parameters indicative of chronic stress. To unify the results, I incorporated the ecological and social findings into an integrated system dynamics model designed to simulate potential management policies and model the resultant outcome on tourist numbers/year, stingray population trajectories, and stingray life expectancy. A lack of SCS management is predicted to yield the lowest tourist- and stingray population and stingray life-expectancy over a 25-year time span, and the most effective management strategy in comparison is a reduction in visitor density, restriction of stingray interactions to the tour operator only, and an imposition of a 5\$ conservation access fee. The findings of this research have been formatted as a decision-support tool and are currently being used by Caymanian stakeholders in the development of a visitor management plan.

Keywords: human-wildlife conflict, conservation biology, human dimensions of wildlife, wildlife tourism management, ecological traps, tourist life-cycle model, *Dasyatis americana*

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GLOSSARY

The physiological chapters in the thesis are succinct as they are intended for publication. Consequently, this section provides definitions of and more detailed information on the physiological parameters analyzed.

Non-esterified fatty acids (NEFA)	<p>Non-esterified fatty acids are free fatty acids in the blood, as opposed to fatty acids that are bound to either triacylglycerols or phospholipids. Types of fatty acids are: saturated and unsaturated (mono- and poly-).</p> <p><u>Function:</u></p> <p>Free fatty acids is the portion of the total fatty acid pool that circulates in immediate readiness for metabolic needs. NEFA can be absorbed readily by muscle, heart, brain, and other organs as an energy source whenever insufficient quantities of glucose limit the usual carbohydrate energy source. In elasmobranchs (sharks and rays), NEFA are the main source of energy. They also play a roll in cell membrane stability, regulation of immune function, stress and disease resistance, and gamete quality.</p>
Saturated fatty acids	<p>Saturated fatty acids do not contain any double bonds or other functional groups along the chain. The term "saturated" refers to hydrogen, in that all carbons (apart from terminus [-COOH] group) contain as many hydrogens as possible. Saturated fatty acids form straight chains and, as a result, can be packed together very tightly, allowing living organisms to store chemical energy very densely. e.g. Butyric saturated FA's chemical structure is: $\text{CH}_3\text{-CH}_2\text{-COOH}$.</p>
Unsaturated fatty acids	<p>Unsaturated fatty acids are of similar form, except that a single-bonded " $\text{-CH}_2\text{-CH}_2\text{-}$" part of the chain is substituted with a double-bonded " -CH=CH-" portion. In cellular metabolism hydrogen-carbon bonds are broken down - or oxidized - to produce energy, thus an unsaturated fat molecule contains somewhat less energy than a comparable sized saturated fat. The greater the degree of unsaturation in a fatty acid (i.e., the more double bonds in the fatty acid), the more vulnerable it is</p>

to lipid peroxidation (rancidity). Antioxidants can protect unsaturated fat from lipid peroxidation.

Hematocrit (Hct)	Hematocrit or packed cell volume (PCV), is the proportion of blood volume that is occupied by red blood cells. When collected blood is spun at very high speeds, this process separates the blood into layers: packed red blood cells, packed white blood cells (leukocrit) and plasma, the liquid component of the blood in which the cells are suspended. The volume of packed red blood cells, divided by the total volume of the blood sample gives the Hct. Because a tube is used this can be calculated by measuring the lengths of the layers.
Leukocrit (Lct)	Leukocrit or packed white cell volume, is the proportion of blood volume that is occupied by white blood cells (including thrombocytes). It is measured with the same technique as for hematocrit.
Serum proteins	Serum proteins are the proteins found in the liquid portion (serum or plasma) of the blood and include transport proteins of minerals, fatty acids, and ions; immune proteins, and enzymes.
Reactive oxygen species (ROS)	Reactive oxygen species are ions or very small molecules that include oxygen ions, free radicals, and peroxides, both inorganic and organic. These molecules are characterized by having odd, unpaired electrons in their outer shell, or destabilizing oxygen-to-oxygen bonds. They are highly unstable as most molecules want to be in a stable state (of having paired electrons), and ROS will therefore 'steal' the electrons from other molecules, resulting in cellular damage.
Anti-oxidants	Antioxidants neutralize free radicals by donating one of their own electrons, ending the electron-"stealing" reaction. The antioxidant nutrients themselves do not become ROS by donating an electron because they are stable in either form. They act as scavengers, helping to prevent cell and tissue injury that could lead to cellular damage and disease.

CHAPTER 1: INTRODUCTION - THE ROLE OF CONSERVATION BIOLOGISTS IN HUMAN-WILDLIFE CONFLICT ISSUES

This thesis is arranged as a series of separate journal article manuscripts presented as independent, stand-alone chapters. The layout of the thesis therefore differs from the traditional approach. Each chapter has its own introduction and discussion sections, as well as a list of references, figures, and tables. The format of chapters two through six each differ somewhat from one another as they have been formatted for publication in different journals. The Introduction provides the rationale for my research in terms of my overarching objective: to find and employ a framework for mitigating human-wildlife conflict in the management of wildlife tourism from the perspective of a global conservation biologist.

1. The Role of Conservation Biologists in Human-Wildlife Conflict Issues

Human-wildlife conflict (HWC) is an escalating global concern as human activities continue to intensify and increasingly demand natural resources and access to land and water. It occurs when the needs and behaviour of wildlife impact negatively on the goals of humans, or when the goals of humans negatively impact the needs of wildlife (IUCN 2004). These impacts arise from events involving: (a) wildlife individuals, populations, habitats and communities;

(b) wildlife-management interventions; and (c) stakeholder interactions (Riley et al. 2003). Distefano (2005) lists a set of global trends which have contributed to the escalation of human-animal conflicts world wide and includes land-use transformations, increased livestock populations, species habitat loss, degradation and fragmentation, and growing interest in ecotourism and increased access to nature reserves (figure 1). Human-wildlife conflict can occur under many circumstances: for instance, when wildlife threaten human lives and livelihood, people can respond by culling wildlife. In the quest for land development and usage, people often endanger wildlife populations through interference competition over shared resources. And through the desire to maximize satisfaction, recreationists can unwittingly negatively impact the fitness of wildlife with which they seek to interact. Conservation biologists investigate the effects of human impacts on wildlife, regardless of whether they arise from humans acting as predators, competitors, or parasites (Low and Heinen 1993) since the outcomes all produce similar results – the endangerment of the species' survival. However, despite the diversity of situations and species that conduce HWC, the one common thread is that the thoughts and actions of humans ultimately determine the course and resolution of the conflict (Manfredo and Dayer 2004). Indeed, HWC frequently involves an equally important conflict between people who possess different goals, attitudes, values, feelings, levels of empowerment, and wealth (Madden 2004). Therefore, successful management of HWC without destroying wildlife or deteriorating human welfare requires a delicate balance between the ecological and social needs of the system (Treves

et al. 2006), and typically involves the research input of social scientists, resource managers, and of course, conservation biologists.

Conservation biology was formalized in the mid 1980's as a 'crisis discipline' (Soulé 1985). Its main objectives have been to help conserve biodiversity and the natural world through analyses relevant to the design and management of protected areas, the restoration and conservation of habitats and ecosystems, and the protection and augmentation of threatened and endangered species populations. Despite best intentions, Robinson (2006) has nevertheless observed that although conservation biology has hugely influenced the practice of conservation, it has had less of an impact outside the profession itself in terms of influencing national and international policy priorities. For conservation to become a societal concern, Robinson (2006) reasons that conservation biology must move beyond the original tenets of rigorous experimental design, tightly controlled variables and manageable scales and become more engaged with the societies in which we live. In essence, a conservation biologist should don the mantle of an interdisciplinary conservationist and (1) address conservation in a human-dominated landscape by including the human dimensions of wildlife; (2) go beyond the insights of biology and ecology by incorporating analyses from the social sciences and humanities; and (3) suggest conservation measures based on limited knowledge that recognize effects on humans (Jacobson and McDuff 1998, Haag and Kaupenjohaana 2001, Mascia et al. 2003, Robinson 2006).

2. Mitigating Conflict in Wildlife Tourism

The directions above are particularly relevant in the area of wildlife tourism, a human-animal activity that itself can be a source of human-wildlife conflict. In recent years, a growing worldwide demand to interact with wildlife has given rise to a wide range of wildlife tourism products (Reynolds and Braithwaite 2001). The ultimate benefit of wildlife tourism is its potential to create a positive feedback between resource persistence and tourism demand that results in a common incentive to protect the natural environment (Wilson and Tisdell 2003). Despite benefits, wildlife tourism is not a panacea for conservation that can unfailingly both protect the environment and support economic activity (Walpole and Thouless 2005). Instead, wildlife tourism can be prone to unmitigated development that is progressed at the cost of ecological integrity (Green and Higgenbottom 2000). This development can be attributed to the needs and expectations of tourists to directly interact with wildlife without consideration of the needs of wildlife which may not be adapted to the changes in their habitat. Studies have demonstrated that in the presence of tourists, animals exhibit increased predator-avoidance energy expenditure, augmented circulating stress hormones, compromised immune function, reduced body condition, and decreased reproduction and survival (Knight & Cole, 1995; Ikuta & Blumstein, 2003; Lusseau, 2003; Müllner et al., 2004; Amo et al., 2006; Ellenberg et al. 2007). Wildlife tourism activities, therefore, satisfy the prerequisites of HWC, as the needs of tourists are in conflict with those of the animals. Stakeholders involved in this type of nature-based tourism can themselves be embroiled in conflicts between those possessing divergent values and attitudes for

conservation and animal welfare, visitor satisfaction, and economic profitability (Reynolds & Braithwaite, 2001). Indeed, in the absence of deliberate management intervention, wildlife tourism attractions can evolve over time to the detriment of both the visitor experience and the focal wildlife species (Duffus & Dearden 1990; Higham, 1998). Accordingly, the directions suggested for conservation biologists for becoming enmeshed in society and affecting policy-level change in HWC apply equally well for when studying wildlife-tourism conflicts.

2.1. Human Dimensions of Wildlife

Conservation biology is shifting its research agenda from natural ecosystems into the human dominated landscape (Robinson 2006). The structure and function of modified ecosystems and the adaptations of wildlife to these altered habitats are a prominent area of focus, as one goal of conservation biologists is the protection and recovery of species populations. A research perspective that nonetheless additionally incorporates human activities as integral components in these altered systems, as well as focuses on how to maintain ecosystem services while meeting the needs of humans is just as essential (Palmer et al. 2004).

Conservation biologists can accomplish these dual goals through the consideration of the human dimensions of wildlife. Human dimensions is characterized by a variety of people-oriented management considerations and a cross-disciplinary range of inquiry (Jaconson and McDuff, 1998). The human dimensions of wildlife considers the attitudinal and behavioural elements of

people and their relationship to wildlife and its management (Manfredo 1989). Manfredo et al. (1995) suggest four areas in recreation-wildlife interactions to be examined in a human-dimensions context that can readily be extended to all human-wildlife engagements. The first area to pursue is the understanding of factors that lead to human-wildlife interactions; for instance, why do people use the resource in the way they do (i.e., the underlying political, economic, cultural, and social processes; Saberwal and Kothari 1996). A second area of investigation deals with the factors that dictate the flow and nature of interactions, such as the norms of behaviours and beliefs about wildlife associated with people's responses during specific types of wildlife encounters (Treves et al. 2006). A third area concerns the types of short- and long-term effects resulting from the interactions, both in terms of wildlife fitness values, and on people's attitudes and values towards wildlife uses. Lastly, the fourth area should address the ways and extent to which human-wildlife interactions can be influenced and controlled.

An awareness of this relationship by the conservation biologist can benefit many conservation-oriented research by providing insights into how decision-making arrangements, resource-use rights, non-market values of ecological goods and services, and conflict resolution can shape individual impact of – and hence state of – wildlife populations designated for management and protection (Mascia *et al.* 2003). Accordingly, through an understanding of the elements of wildlife management related to people, appropriate ecological-research questions can be

developed to provide invaluable perception into the ways HWC can be effectively managed. Human dimensions research has subsequently enhanced the capability for improved decision- making by wildlife managers by providing a more suitable balance between impacts on wildlife and provision of benefits (and reduction of costs) from wildlife (Enck & Decker 1997). Undeniably then, ecological and social impacts are often interrelated.

2.1.1. The Human Dimensions of Wildlife Tourism

Wildlife tourism lends itself well to the study of human dimensions. As urbanization, mobility, affluence, education and recognition of growing ecological crises have increased over the past sixty years, there has been a gradual rise in the incidence of protection- and appreciation-oriented values with respect to wildlife in North America and Western Europe (Fulton *et al.* 1996, Manfredo *et al.* 2003). An outcome of this adjustment of wildlife values and realized benefits is a rise in the participation and offering of wildlife-interaction activities. Today, wildlife tourism is one of the fastest growing tourism sectors worldwide, and demand for opportunities to interact with animals has been increasing rapidly (Rodger *et al.* 2007). Many tourists nowadays prefer to see and interact with wildlife species in their habitats and experience a much more intimate closeness to authentic habitats (Shackley 1996). As a consequence of these preferences, wildlife tourism, especially in the marine environment, has become one of the leading

sources of economic earnings for countries with coastlines (Garrod and Wilson 2004).

In a wildlife-tourism context, how people view wildlife is considered an expression of their value orientations (Bentrupperbäumer 2005). The four key determinants of the views of tourists and of other tourism-industry stakeholders towards wildlife are dominionistic values (the mastery, control and dominance of wildlife), utilitarian values (economic and psychophysiological benefits of wildlife), moralistic values (welfare rights and responsibilities for wildlife), and protectionist views (conservation and preservation of wildlife; Reynolds and Braithwaite 2001). Moreover, Hughes (2001) argues that animals are more often objects than subjects in tourism; they are more usually manipulated than recognized as purposive agents or actors in their own right. As such, they could best be described as having instrumental rather than intrinsic value within tourism processes; they are recognized for the value which they provide for people rather than that which they might possess for their own sake. These values have important implications across all levels of the tourism industry, influencing the representation of wildlife in a promotional context, the preparedness of the industry to take on a regulatory role, the adoption of codes-of-conduct by tourism operators, and the capacity of the nature and quality of the tourist interaction with wildlife to be affected (Bentrupperbäumer 2005). Consequently, values of conservation, animal welfare, visitor satisfaction, and economic profitability are often in conflict in wildlife tourism and tradeoffs are necessary (Reynolds and

Braithwaite 2001). Even amongst tourists themselves, research into the human dimensions of wildlife has found that within and across attractions, wildlife-tourists differ by ethics, values, motivations, levels of specialization, and desired wildlife experiences. All of these aspects affect their expectations of and experiences with their respective wildlife interaction (Martin, 1997; Moscardo, 2000; Higham and Carr, 2002; Scott and Thigpen, 2003; Curtin and Wilkes, 2005; Dearden *et al.* 2006). Mitigating negative impacts on wildlife and preserving or even enhancing the tourist experience therefore relies on the understanding of the tourist's relationship with wildlife.

2.2. Integration of Social Sciences with Ecological Data

Biological, geographical, political, economic, social, institutional, financial, cultural, and historical features make each conflict or coexistence situation between people and wildlife unique (Madden 2004). Consequently, biological science alone does not provide a complete understanding of or solutions to the conflict. There has long been a call for the integration of social sciences into conservation biology (Jacobson 1990). However, this amalgamation of disciplines with respect to human-wildlife interactions has been slow in realization as there has been a general lack of acknowledgement in the natural sciences that conservation is as much about people as it is about species and/or ecosystems (Bradshaw and Bekoff 2001). Secondly, when both natural and social scientists are called upon, researchers from different disciplines follow a

common research agenda, but then work independently and according to the tenets of their own disciplines, with the results of their work being amalgamated post hoc, and not necessarily effectively (Quinlan and Scogings 2004). Equally, natural scientists often only involve social scientists at the end of a project, inhibiting worthwhile collaboration (Fox et al. 2006). As a result, recommendations made by each 'end' of the research-discipline spectrum can be at odds with the interpreted data.

Creating interdisciplinary research frameworks is therefore not simply a matter of juxtaposing disciplines, nor of forcing a continuous interaction, but rather a dynamic operating mode (Deconchat et al. 2007). To achieve the level of conceptual and practical progress needed to improve human-wildlife interactions, collaborative research must transcend individual disciplinary perspectives and develop a new process of collaboration. Transdisciplinary research can be described as researchers working jointly and using a shared conceptual framework, drawing together disciplinary-specific theories, concepts, and approaches to address a common problem (Rosenfield 1992). Conservation biologists do consider the social sciences to play an important role in the policy processes involved in environmental decision-making. For instance, policy analysis, participatory planning processes, and decision support tools are some of the areas in which the contribution of the social sciences is substantial. However, the social sciences can equally enhance ecological data (and vice versa) by contributing its own data in both quantitative and qualitative forms in

the data-collecting phase. For example, recreational hunters and fishers play a direct role in the ecological system as predators of their target species. Unlike other predators, however, the humans engaging in these activities do so to satisfy psychological outcomes rather than purely physical needs (Manfredo *et al.*, 1983). Understanding their motivations and preferences regarding these activities allows managers to then balance the psychological objectives of the recreationists with ecologically driven goals such as maintaining viable populations of the targeted species. In a wildlife-tourism example, the relationship between people and wildlife can be likened to a parasitic relationship, in that tourists cannot entirely 'consume' their 'prey' resource without succumbing themselves; however, they can seriously weaken the system before they switch hosts. Discovering ways to strengthen the resource base without equally jeopardizing the needs of tourists can only be accomplished by finding relevant and interlinked ecological and social research directions when addressing the relationship between wildlife and tourists.

2.2.1. Integration of Social and Ecological Sciences in a Wildlife Tourism Context

Wildlife tourism includes aspects of ecology, biology, physiology, psychology and other aspects of social-science research including tourism (Rodger 2007). As wildlife tourism is not the domain of either ecologists/biologists or social scientists, research into the effects of wildlife tourism must instead transcend multiple disciplines (Braithwaite and Reynolds 2002). Any management plan for

wildlife tourism should therefore examine the relationship between wildlife fitness and human activities. One way to think of the link between the natural and social science disciplines in a wildlife-tourism context is the notion of ‘traps’ – both ecological and social. In an ecological context a trap occurs when human-driven environmental change decouples the cues that animals use to assess habitat quality from the true quality of the environment (Schlaepfer *et al.* 2002). An ecological trap occurs when animals mistakenly rely on false or altered environmental cues to maximize their fitness, but do not immediately receive the necessary feedback to inform them that their choices are wrong – i.e., no longer adaptive. Consequently, this maladaptive habitat selection leads to reduced survival or reproduction, compared to the probable outcome if the true high-quality habitat had been selected or remained unchanged (Battin 2004). In a wildlife-tourism setting, ecological traps can arise when: birds using historic breeding grounds are physiologically stressed by the arrival of tourists who affect the birds’ reproductive success; marine food sources are driven away from whale traditional foraging grounds by whale-watchers in boats; and marine wildlife are attracted to artificial food sources and receive an unnatural diet from tourists. In these circumstances, wildlife are making choices of where to breed and forage using cues which no longer relate to optimal conditions.

In a social context a trap occurs when tourists, in their quest to maximize satisfaction with their wildlife experience, possess values, motivations and actions that unwittingly cause impacts to the wildlife system (Higginbottom *et al.*,

2003). Similar to their wildlife counterparts, these tourists do not receive the immediate feedback necessary to inform them their actions and desires can cause negative impacts, and through the resultant repercussions on wildlife, a social trap transpires when the resource base deteriorates to such a point that tourist satisfaction becomes negatively affected, or equally, does not reach the maximum it could have under more favourable conditions. Consequently, tourist populations too, may decline. In a social trap, tourists - via their effects on wildlife – affect their own satisfaction (should they be return visitors, or affect the satisfaction of the same user group since they share similar expectations). Indeed, the evolution of the tourist product – a theoretically and empirically represented S-shaped growth pattern of tourist volume over time (Butler 1980, based on the economic product life-cycle concept), culminates in a fatigue of the site due to excess capacity, socio-economic factors, the appearance of other competitors, and the reduction of environmental quality, all of which lead to a decrease in tourist satisfaction (see Patullo 1996, Akama 1997 and Holden 2003 for examples). The fundamental relationship between the two traps is that a social trap can drive an ecological one (figure 2), and they are analogous to one another since both wildlife and tourists engage in activities that fail to provide the necessary feedback information that their actions are ultimately detrimental to their own and each other's goal: the maximization of fitness and satisfaction, respectively. In essence, in the absence of deliberate management intervention, wildlife tourism attractions can evolve over time to the detriment of both the

visitor experience and the focal wildlife species (Duffus & Dearden 1990; Higham, 1998).

The trap theory has the advantage of outlining the appropriate types of questions to ask, and guiding the inventory of suitable indicators which in turn can then be translated into effective management strategies. For instance, the following questions can be researched: what attributes of the wildlife tourism activity have the potential to affect animal fitness (i.e., what activities can cause an ecological trap)? What measures of fitness should then be used and investigated? Similarly, what attributes of the wildlife activity can both influence tourist satisfaction and impact wildlife fitness (i.e., what activities can cause a social trap)? What measures of tourism satisfaction should be used? More specifically, with respect to natural science indicators, attributes measured by the conservation practitioner should demonstrate the health, survival or reproductive impacts of the wildlife species that are directly attributed to the presence and actions of tourists. Equally, social-science indicators should reveal the tourist expectations, conservation ethics, and management tolerance of the wildlife interaction that contribute both to a satisfactory experience but can also negatively impact wildlife fitness. As a result of these investigations, strategies effective in managing visitors and wildlife will be deduced much more readily. However, a framework is still needed to guide these components into a cohesive model.

2.3. Suggesting Conservation Measures in a Socio-Ecological Context

For conservation biologists, the negative impacts on wildlife resulting from interactions with people can be notoriously difficult to detect: research findings can be mixed, and the diversity of potential impacts can pose problems for identifying their source (Tarlow and Blumstein 1997). Accordingly, conservation biologists have a limited ability to detect adverse effects and may have to reach conclusions and propose management options in the absence of complete knowledge (Robinson 2006). A widely adopted approach in the management of biological information-scarcity in human-wildlife conflicts is the development of predictive simulation models in which conservation scientists are required to specify their assumptions in reaching their conservation targets. These models vary in type and typically involve animal-population and habitat-suitability projections which can additionally enable the assessment of parameter uncertainties. However, socio-economic aspects of human-wildlife conflicts can also affect ecological outcomes, and this knowledge can be inherently incomplete or uncertain as well. For instance, there can be uncertainty in the benefits and costs associated with different wildlife population levels, and these tend to vary randomly over time (Bakshi and Saphores 2004). Also, purely ecological policy models ignore essential human behaviours such as forward-looking expectational behaviours which can impact the resource in unplanned ways (Westley et al. 2002). Therefore, in addition to the methods that enable conservation biologists to synthesize limited biological information and translate it

into predictive outcomes, there is the need for the capacity to evaluate alternative conservation management actions in a socio-ecological context, and to mediate the conflicts between conservation, ecological and socio-economic goals (Drechsler 2004).

The ability to inform policy decisions cannot be performed without an integrated model of natural and human systems (Costanza and Voinov, 2001). Integrative modeling attempts to capture the essence of a system well enough to address specific questions about the system; and models are useful because of the necessity to solve problems despite the lack of knowledge and understanding of the system (Grimm and Railsback 2005). In a resource-management context, integrative models are used to collectively assess the impacts of policy actions from both biological and social perspectives, and can assess the importance of precaution in decision-making, acceptable levels of additional risk, estimates of how long it may take for mitigating measures to take effect, whether effects are reversible, and efficient allocation of conservation resources (Thompson et al. 2000, Faust et al. 2003). Most notably, modelling can be used to build consensus between science, policy and the public by building mutual understanding and maintaining a substantive dialogue between members of these groups (van den Belt et al. 1998).

I believe there remains a significant capacity in which conservation biologists can still act to ensure the mitigation of human-wildlife conflicts. According to Haag

and Kaupenjohann (2001), the definition and delimitation of environmental issues should be driven by “real-life/real world” problems instead of isolated disciplines. Indeed, the most promising scientific endeavors come from areas at the edges of disciplines or, even more so, from areas where various disciplines co-operate and forge into new approaches (Gibbons et al. 1994). By studying and acknowledging how social and ecological systems are interlinked, and then designing research programs around the transdisciplinary impacts of people-animal interactions, the successes of conservation ‘biologists’ can be greatly enhanced (Rodger 2007).

2.3.1. Suggesting Wildlife Tourism Management Measures in a Socio-Ecological Context

Once wildlife and tourist indicators have been chosen and researched, findings need to be assimilated into management strategies that will affect both the resource base and the tourism experience as these two systems are interlinked. Conceptual frameworks describing the interactions between tourists and animals exist (Reynolds and Braithwaite 2001), along with frameworks guiding how wildlife tourism should be managed integratively (Higginbottom et al. 2003). Commonly absent in studies of wildlife tourism is a quantitative model that integrates social and ecological data into a cohesive system in which to investigate various management plans. A suggested reason for this absence is the increasing evidence that many scientists do not find researching the interactions between tourists and wildlife and the associated potential impacts of

tourists on wildlife intrinsically or professionally appealing as there are few professional rewards and recognition (Rodger and Calver, 2005; Rodger and Moore, 2004).

Instead, biologists studying the impacts of wildlife tourism typically model the biological outcome of tourist activities, such as population projections, energetics, and habitat suitability (see Bejder et al. 2006, Williams et al. 2006, Lusseau et al. 2007). There have been attempts by general conservation practitioners, however, to model both the socio-economic and ecological impacts of wildlife tourism. For instance, in a study of tourism development strategies in Dominica, a system dynamics model was used to integrate societal norms and networks with ecological habitat attributes, land use, and tourism-industry and gross-national product development to illustrate the interdependence of all these domains (Patterson et al. 2004). With particular reference to wildlife, the model demonstrated that Dominica's economy depends on the health of the environment, principally as a tourist draw (i.e., coral reefs); and that ecology impacts social capital through 'pride of place' as well as through resource extraction (including tourism). In another study on the management of the Patagonia coastal zone, a scoping exercise was created to assess important ecological and economic interlinkages (van den Belt et al. 1998). The system dynamics model predicted that the importance of the wildlife-tourism sector could in future greatly exceed the value of the fishing industry, provided impacts of oil spills and the dumping of tanker ballast water on penguin populations (the focal

tourism species) were kept to a minimum. Lastly, a simulation study by Anwar et al. (2007) used an agent-based model to predict how the behaviours of whale-watching tour operators affected the quality of the tourist experiences and the risk of injury to whales. The model predicted that information sharing and cooperation among tour operators resulted in a higher return since the 'happiness factor' increased for the tourists (measured as the ratio of whale observation time over the trip duration). However, these behaviours also boosted traffic congestion around an individual whale, exposing the animal to increased risk of boat collision, and collateral effects of noise disturbance and energetic expenditure in avoidance behaviours.

3. CASE STUDY: Stingray Tourism in the Cayman Islands

My doctoral research investigates the human-animal conflict of wildlife tourism in a human-dimensions and conservation-biology context. I apply the theory of social and ecological traps to a case study of feeding stingrays as a marine tourism attraction to explore the relationship between tourists and stingrays for the purposes of mitigating and managing the conflict. I attempt to accomplish these goals by following the directions introduced at the beginning of this chapter intended for the interdisciplinary conservationist. I begin this section with a brief introduction of the main players of the case study, followed by the conflict that exists between the multiple stakeholders in the system, as well as between the

wildlife and tourists themselves. Next, I describe the human dimensions of the stingray-feeding tourism attraction, how I immersed myself into the system, and used the theory of social and ecological traps to choose indicators to investigate. Lastly, I demonstrate how I have attempted to collate the social and ecological data into a unified system in which to simulate the outcome of various management plans intended for the site in terms of tourist numbers, stingray population size, and stingray life expectancy.

3.1 The Tourist Experience

The most popular tourist site in the Cayman Islands (CI) is Stingray City Sandbar (SCS), a warm, shallow water (1.6 m maximum depth) sandbar in the North Sound, approximately 7,740 m² in area and located roughly 300 metres inside the fringing reef (figure 3A). It is here that stingrays congregate to be fed frozen squid by tourists and tour-boat operators. Due to its massive popularity, SCS supports over 50 local snorkel and dive tourism operations and hosts approximately one million visitors a year, almost half of all visitors to the Islands. The numbers have more than doubled since 2000 (CI MoT, 2002). A day-long activity which first began in the mid 1980's (Shackley, 1998), a maximum of 2500 tourists can now be present at a given time at the shallow sandbar, engaged in unsupervised feeding, touching, and holding of stingrays as part of their marine tourism experience. Some tour operators provide only the most rudimentary information, while others provide an informative session in-water. The organized

trip also provides photo opportunities, with some tour operators holding the ray in or out of the water, or placing it on people's backs and heads while the picture is taken.

3.2 The Wildlife

The southern stingray (*Dasyatis americana*) is a long-lived (26 years; Henningsen 2002), common inshore ray frequenting tropical and subtropical shallow bays of the Southern Atlantic Ocean, Caribbean and the Gulf of Mexico. It is a continuous forager, feeding opportunistically on a varied diet of crustaceans and teleosts, and to a lesser extent, on molluscs and annelids (Gilliam & Sullivan 1993). Although southern stingrays inhabit all shallow bays around the Cayman Islands, it is only in the vicinity of SCS that these rays can be found year-round in a dense aggregation of individuals of both sexes. This amassment results from the unregulated quantity of provisioned squid (*Illex* and *Loligo* spp.), a non-natural diet item shipped in from the North Atlantic and North Pacific (Semeniuk pers. obs., Gina Ebanks-Petrie Director, Cayman Islands Department of Environment pers. comm.). The feeding routine (daily, except during the summer months when weekends are excluded) lasts from early morning until mid afternoon as tour boats continuously deliver tourists (mainly cruise line passengers) for an average forty-five minute visit to SCS. As a result of this regime, the fed rays have become diurnal (as compared to their non fed counterparts around the Island), and have reduced their activity space to the

shallow waters immediately surrounding the feeding area (Corcoran 2006). Nearly 170 individuals from the fed group have been tagged since 2002. The rays have a mean yearly recapture rate of 92.5% (0.03 S.D.; C.A.D.S. unpublished data, Corcoran 2006), indicating a very strong temporal and spatial fidelity to the feeding site. As such, there is a risk that SCS, which has produced and introduced change in the stingrays' environment, is attracting the rays to prefer a habitat which may not be suitable in the long-run, and may therefore be an ecological trap.

3.3 Conflicts

3.3.1 Human-Human Conflict

Without any management or codes of practice since the site's inception in 1984, SCS has become congested, and stakeholders (government officials, tour operators, tourists and locals) express concern about the long-term sustainability of the attraction (Gina Ebanks-Petrie, CI Director of the Environment, pers. comm.; C.A.D.S., pers. obs.). The Department of Environment (DoE) has distributed a press release regarding its misgivings with stingray feeding, fearing ray fitness consequences ([http://www.divecayman.ky/divemaster/press 01.asp](http://www.divecayman.ky/divemaster/press%2001.asp)). Residents have vocalized their discontent (in local newspapers) with regards to the number of tourists visiting SCS and subsequent negative effects upon the rays. Tourists have begun expressing dissatisfaction with site overcrowding and lack of safety measures (DoE pers. comm.). Additionally, tour boat operators are

concerned that if visitor flow is reduced as a form of strategic management, lost revenue may not be recouped due to either decreased tourist demand, and/or resistance (in the form of boycotting) from the cruiseline industry, which is responsible for over 80% of all SCS tour bookings (DoE, pers. comm.). Indeed, these circumstances are suggestive of a social trap in progress as tourists, in their quest to maximize satisfaction, possess values, motivations and actions which may unwittingly be causing their own experiences or that of other user groups, to deteriorate. In response to these issues, Cayman Island stakeholders convened a committee in 2003 to agree upon a set of detailed rules for crowding alleviation and stingray protection for Stingray City Sandbar. Regulations included limits of a maximum of 100 people per boat, a 20-boat maximum at any one time, and 1500 people in the water at any one time; restrictions on feeding of the stingrays (details are undetermined at this point); prohibitions on taking of marine life of any kind, including the removal of stingrays from the water; and the nature and collection mechanisms for a proposed access fee. Issues that needed to be addressed, however, were the acceptability of the proposed management plan to tourists, the pricing structure for trips to SCS (although a 0.25\$ to 1\$ fee per visitor has been discussed), and the effect, if any, these plans would have on stingray fitness.

3.3.2 Human-Wildlife Conflict

The resultant ecological plan (in addition to social and economic ones) which suggests the control of the quantity of food (squid) provided to the stingrays is intended to reduce their habituation to the constant supply of squid. This action would also serve to encourage stingrays to increase their foraging in their own natural habitat thus ensuring a more balanced diet in terms of nutritional composition. However, the panel was hesitant regarding the appropriateness or adequacy of the feeding restrictions, owing to the uncertainty of the extent to which the provisioned squid makes up the fed stingrays' diet, and whether it has a dissimilar nutritional composition as one obtained naturally in the wild. The panel could not, therefore, predict whether management including food restrictions would prove effective in terms of their concern over stingray well-being. With regards to the handling restrictions, a subset of tour operators felt that directly interacting with stingrays enhances the experience, and photo opportunities with rays are integral to the satisfaction of their customers. One other commonly expressed opinion by tour operators was that "if the stingrays weren't healthy or didn't like the sandbar, they wouldn't still be here year after year" (pers. comm.). This belief led to sentiments that management for the sake of the rays' benefit was unnecessary. Aside from the intrinsic value of protecting stingrays, animal welfare issues are also a serious concern; and from a genetic diversity point of view, the Cayman Island population of Southern stingrays is

restricted in gene flow from other Caribbean populations and should thus be managed as distinct evolutionary units as well (Richards and Shivji 2005).

3.4 Mitigating Conflict at SCS

3.4.1 Human Dimensions of SCS

During the course of my investigations in which I spent over six months in the Cayman Islands over a three-year period, I had discussions with many of the Caymanian stakeholders, which included the Director of the Department of Environment, the Assistant Director of DoE, and its Marine Researchers and Enforcement officers. I equally had exchanges with the Director of the Department of Tourism (DoT), the Public Relations Officer - DoT, the Marine Conservation Board Stakeholder Group, the SCS tour operators, the Rotary Clubs of the Cayman Islands, the Finance Minister, and the Governor General. I also attended a town hall meeting in which tour operators were invited to express their concerns and questions about the management proposed for Stingray City Sandbar. Through these exposures I feel that I was able to understand the nature of the conflict, and the attitudes each stakeholder group possessed. Fortunately, we were all working towards a common goal of sustainability, and I was accepted into the community (for the most part; there was a very small minority of older tour operators who were steadfastly adamant that no management was necessary and refused to allow me to survey their customers). From the initial stages I expressed my own objectives of maintaining and even improving the tourism experience while safeguarding the stingray population

which I stressed I did not believe to be mutually exclusive goals. The one stakeholder group of which I did not have any insight was the tourists themselves, and I believed that for any management to be truly effective, it was essential that the tourists and their relationship with the stingrays be understood, first. For this reason, I concentrated my efforts on this stakeholder group exclusively (with the exception of the stingrays), and conducted research (in the form of surveys) on a sample of visiting cruiseship passengers.

3.4.2 Unifying Ecological and Social Sciences for SCS Management

Based on the theory of traps – i.e., maladaptive decisions that result in lowered fitness and satisfaction - indicators should reflect the communal impacts between the stingrays and tourists so as to guide conservation practitioners with management efforts that would prove most effective for the SCS attraction. At SCS there are two human activities which have the potential to cause traps (i.e., affect wildlife fitness and tourist satisfaction): ‘handling’ stingrays (either through direct interaction or indirectly through collisions with boats); and feeding stingrays.

With regards to the social-science component of the research, I conducted intercept surveys on cruise ship passengers upon their immediate return from SCS at Safehaven Dock (figure 3B). I targeted this sample population as they comprise over 85% of tourists (in comparison to stay-over visitors) at SCS (Gina

Ebanks-Petrie, pers. comm.). The social indicators investigated reflect tourist expectations, wildlife-tourism values, and tourist preferences for the activities at SCS (Table 1). Specifically, the indicators, in the form of a questionnaire, comprised: a) tourist preferences for certain proposed visitor management options at SCS, b) tourists' expectations (met or not) with various attributes of Stingray City Sandbar, c) the contribution of specific activities towards a satisfying wildlife-tourism experience in general, and d) tourists' level of concern with the potential impacts of wildlife tourism. These indices would consequently provide me information on the conditions at SCS that would have the greatest potential to add to or detract from tourist experiences, including direct activities with the stingrays. They would also help establish whether and what type of information would be required in promoting wildlife stewardship and awareness amongst tourists of the types of interactions that affect wildlife fitness; and be able to determine which managerial options for SCS could potentially garner the most (or least) support by visitors (Chapter 2).

The ecological outcomes of tourist activities at SCS over the past two decades are that stingrays: a) are including non-natural food in their diet; b) are forming groups when previously solitary; and c) are interacting with a new species (i.e., humans) and in a new environment. Because of the non-natural diet fed to the stingrays, indicators in this category should reflect whether squid is indeed a major item in the diet, and if so, then whether nutritional requirements of stingrays are being met (Chapters 3 and 5). Indicators reflecting the

consequences of novel grouping behaviour should be able to quantify parasites loads (to identify facilitated parasite transmission), conspecific injuries (as evidence of aggression), predator injuries (suggesting increased conspicuousness to predators), and boat injuries (signifying the hazardousness of the environment; Chapter 4). Lastly, indicators chosen to reveal the impacts of direct interactions with tourists on stingray wellbeing should be associated with injury rates (from boats), or stress levels (from the novel environment – all factors combined; Chapters 4 and 5) and are listed in Table 2 of this chapter. In order to establish whether the parameters measured are within the limits of what naturally occurs in the environment, the biological indicators of tourist stingrays were compared to those collected from stingrays at three non-visited sites about Grand Cayman (figure 3C-E). Although SCS stingrays are sampled from one site only, this is not an instance of pseudo-replication or having a sample size of one; instead, one can consider this research design as a natural experiment, having a treatment versus a control group. Furthermore, the effects investigated are from the direct cause of tourism and not from environmental features inherent to North Sound, as this treatment group was artificially created when tourism began in 1984.

3.4.3 Suggesting Conservation Measures in a Socio-Ecological Context

The types of indicators chosen for this study allow for the integration of the findings into a simulation model to predict the ecological and social outcomes of varying managerial and policy directives (Chapter 6). Using STELLA (Systems

Thinking Experiential Learning Laboratory), a systems dynamics model, the wildlife and tourist indicators can be combined into a stochastic and dynamic management model to simulate the outcome of various management policies and predict the state of the marine tourism attraction, specifically, tourist population numbers, stingray population size, and stingray life expectancy, over time (figure 4). The null model of no management can be contrasted against five differing management scenarios which consist of varying levels of congestion control, stingray interaction regulations, ecological outcomes, and a conservation access fee. Social data to incorporate in the model include utility preferences of latent tourist segments for the different management options as well as for stingray- and tourist- densities (from Chapter 2), which can be assumed to link with behavioural intentions regarding future visitation rates; and actual data on tourist population trends, arrival and departure rates. Ecological data to use are stingray population growth rates and annual survival estimates (from mark-recapture data) and estimates of mortality rates caused by the chronic nature of tourism (Chapters 3 to 5) under the divergent management scenarios. There exists uncertainty as well as incomplete knowledge in the system pertaining to the specific contributions of tourist activities on stingray mortality rates and tourist arrival rates. However, through sensitivity analyses and comparing the relative (not absolute) differences in model predictions of different management plans, the results will nonetheless demonstrate management actions which can lessen the occurrence of social and ecological traps. Moreover, modelling of this wildlife-tourism system can also present an analysis of alternative socio-ecological

outcomes for policy makers to choose from in a transparent fashion, which can then feed into the policy-process and, ultimately, become part of institutional analysis and iterative public dialogue.

4. Conclusion

Suggestions on ways to improve the practice of conservation biology are widespread and multifarious. With particular reference to human-wildlife conflict issues, biologists are counselled to be more holistic and become immersed in the human dimensions of the system, to integrate their work with the social sciences, be selective in the choice of indicators, and to suggest alternatives of conservation measures in a socio-ecological context even though knowledge may be incomplete or uncertain. My research attempts to reconcile these proposals into a cohesive framework by thinking of tourists and wildlife as an integrated, non-separable system. This direction is facilitated by using the social and ecological trap theories presented here, and serves as a means by which the ecological and social sciences can be unified with the goals of mitigating negative impacts on wildlife while simultaneously providing quality experiences to tourists.

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Table 1.1 List of social indicators researched.

Social Science Indicator Category (Chapter 2)	Indicators Based on Wildlife Interactions
Support for Proposed Management	Preferences for hypothetical management scenarios planned for SCS
Tourist Experience	Expectations met or not at SCS
Conservation Values	Importance of general wildlife-tourism activities to overall satisfaction
	Concern with potential impacts at SCS

Table 1.2. List of biological indicators researched.

Wildlife Fitness Indicator Category	Indicator	Ecological Condition
<u>General Health</u>		
(Chapter 4)	Parasite load (virulence transmission)	Atypical grouping
	Conspecific bite marks (aggression)	Atypical grouping, Non-natural diet
	Collision injuries	Human contact
	Predator injuries	Atypical grouping
<u>Physiological Health</u>		
(Chapters 3, 5)	Serum essential fatty acids	Unnatural diet
	Hematocrit	Unnatural diet
	Serum protein	Unnatural diet, Human contact
	Total anti-oxidant capacity	Unnatural diet, Human contact
<u>Immunological Health</u>		
(Chapter 5)	Leukocrit	Human contact, Atypical grouping
	White blood cells	Human contact, Atypical grouping
	Total oxidative status	Human contact, Atypical grouping

Figure 1.1 Human wildlife conflict in the context of human relations with animals.

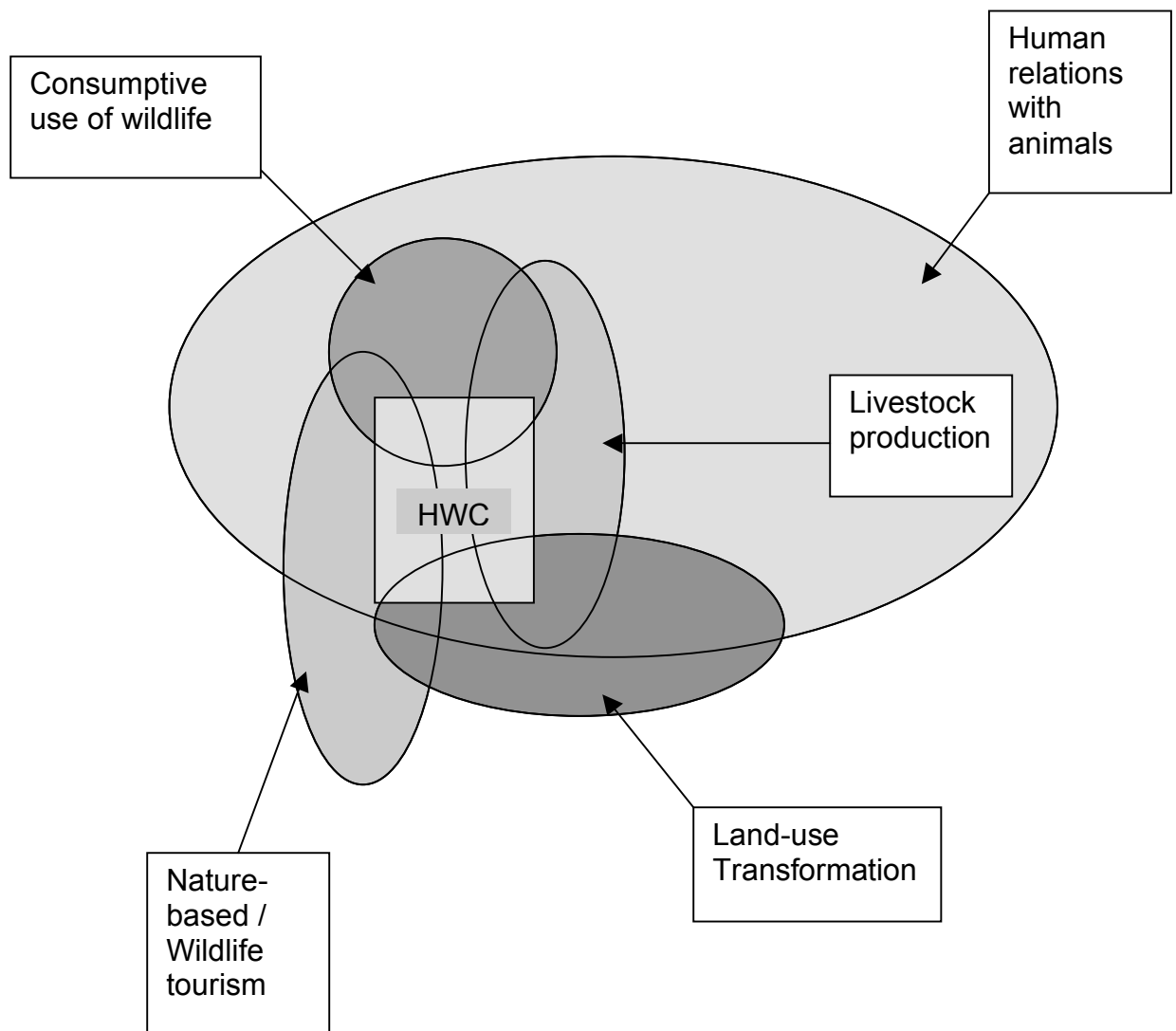


Figure 1.2 Conceptual schematic of the unifying theory of ecological and social traps in a wildlife-based tourism setting.

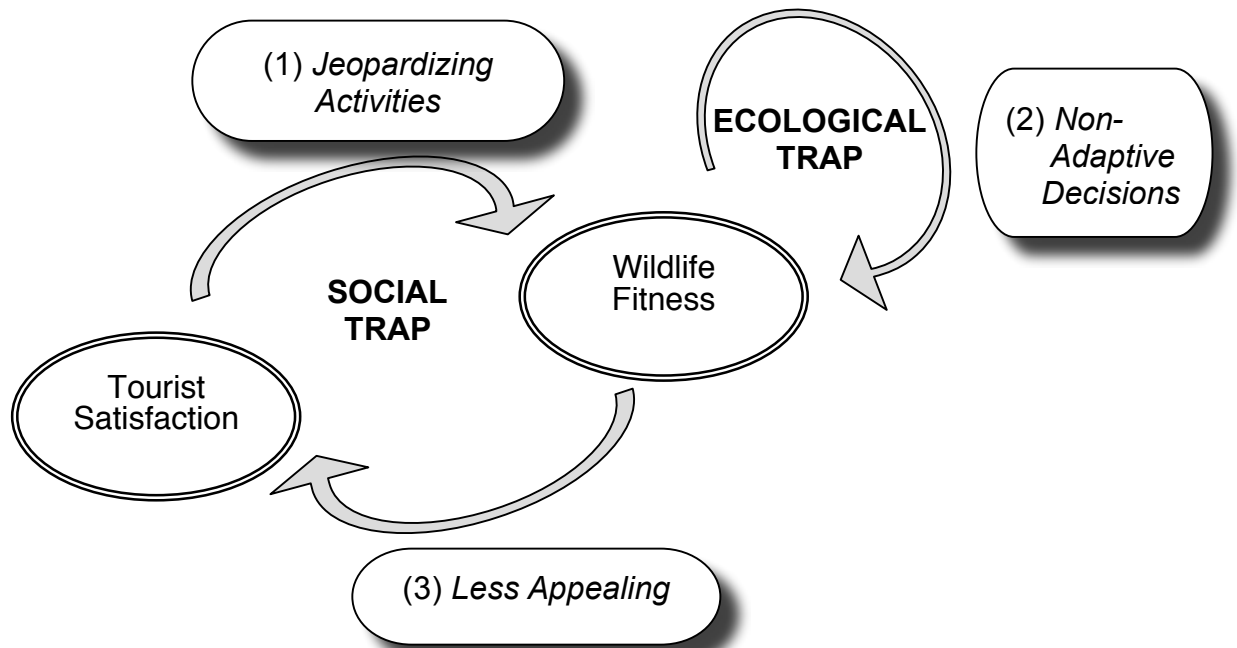
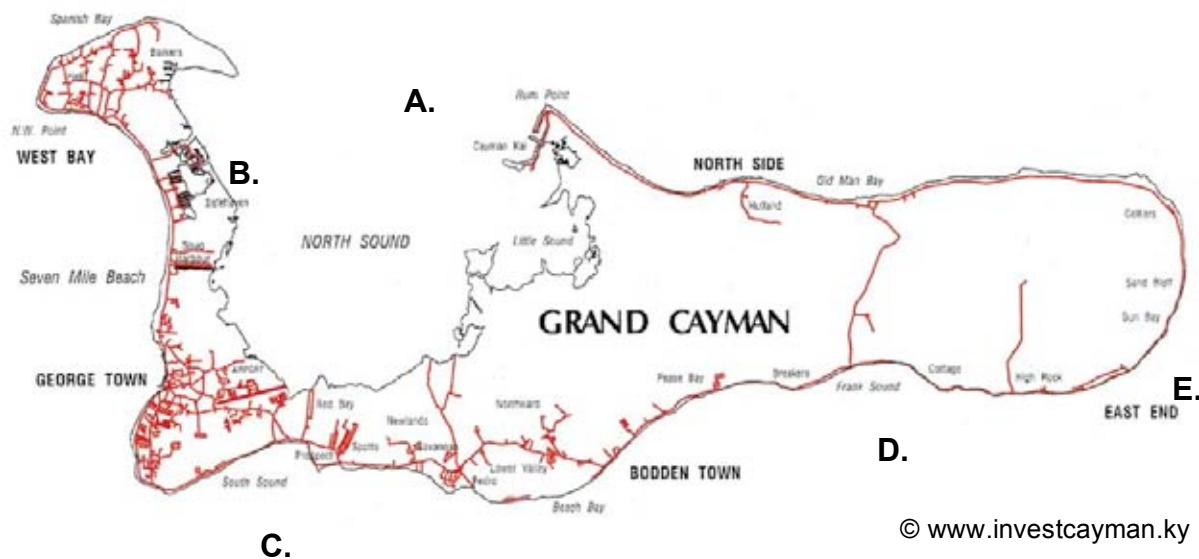
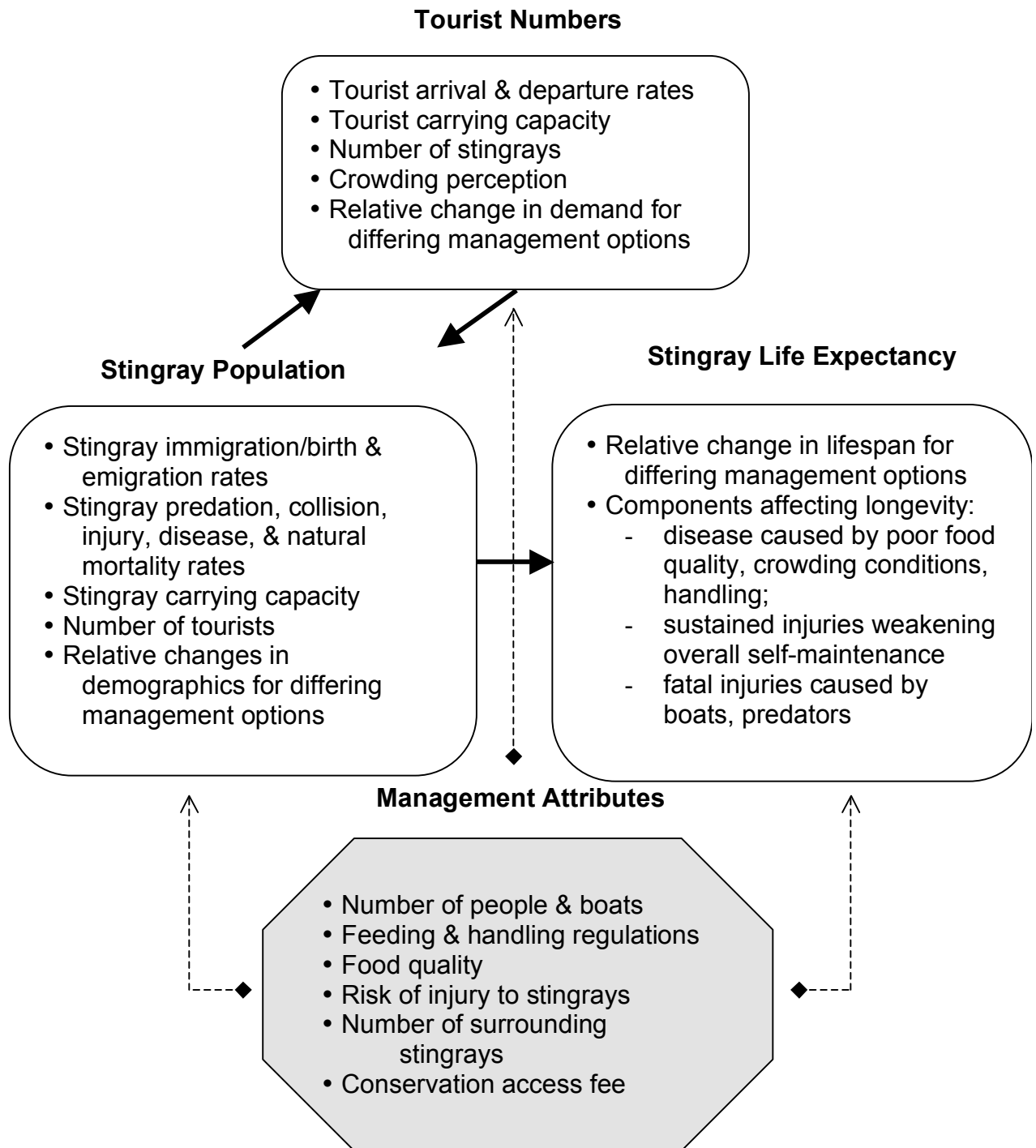


Figure 1.3 Map of Grand Cayman showing: A. Stingray City Sandbar (SCS), the tourism attraction; B. Safehaven, the dock at which cruise ship passengers were intercepted upon their return from SCS; and the three control, non-visited sites: C. South Sound, D. Frank Sound, and E. East End.



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Figure 1.4 Tourist-stingray system demonstrating the relationship between tourist numbers, stingray population size and stingray life expectancy, and the factors affecting each system component.



CHAPTER 2: A multi-attribute trade-off approach for advancing the management of marine wildlife tourism: a quantitative assessment of heterogeneous visitor preferences

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Running Head: Heterogeneous management preferences for marine wildlife tourism

Key Words: marine wildlife tourism, marine-tourism management, stated preference choice model, latent class analysis, human dimensions of wildlife, stingray

ABSTRACT

Wildlife tourism can be prone to unmitigated development to promote visitor satisfaction that is all too often progressed at the cost of ecological integrity. A manager is thus faced with the dual task of enhancing the tourist experience and protecting the wildlife species. Accordingly, this mandate requires research into how tourists would respond to proposed wildlife-management plans. This study examines the heterogeneity of tourist preferences for wildlife management at a stingray-feeding attraction in the Cayman Islands, using a latent class stated preference choice model. A sample of visitors to Stingray City Sandbar (SCS) evaluated hypothetical wildlife viewing experiences in a discrete choice experiment. Its scenarios were characterized by seven attributes such as animal-feeding and handling rules, ecological outcomes, social crowding, and management cost (defined as a conservation access fee). The latent class segmentation identified two groups in the population: approximately 68% preferred the implementation of fairly strict management rules, while the other 32% valued more the maintenance of status quo with its intensive human-wildlife interactions. Despite the differences between the 'pro-management' and the 'pro-current' segments, both exhibited a preference for the continuation of feeding and handling the stingrays (albeit at different levels of intensity) suggesting that one effective way to implement any management actions is to alter the promotional and marketing strategies for SCS. Other survey questions on trip experience, conservation values, and socio-demographics were used to define these classes further, with the main distinguishing trait being the level of

concern for potential impacts occurring at SCS. The discrepancies between the two segments became most obvious when calculating their respective market shares of support for alternative management strategies. This approach to determining visitor preferences can help explain how the various segments will be affected by management options, and therefore can provide the basis for developing feasible strategies that will assist wildlife managers in maximizing tourist satisfaction while achieving wildlife-protection goals.

INTRODUCTION

Wildlife tourism, as one particular form of non-consumptive tourism, can be embroiled in conflicts between conservation, animal welfare, visitor satisfaction, and economic profitability (Reynolds and Braithwaite, 2001). Wildlife tourism can also be considered a type of 'soft' ecotourism (Weaver, 2001); it is characterized by being a short-length component of a multipurpose trip in which travellers, reliant on interpretation, expect a high level of comfort and services. The wildlife tourist is typically part of a larger group that is physically passive, and usually leaves the area in the same, or somewhat degraded condition. Given the similar characteristics in terms of volume, purpose of travel, and reliance on infrastructure of services, wildlife tourism can be regarded as a form of mass tourism (Weaver, 2001). As a type of mass tourism, wildlife tourism is of special concern in the Caribbean, a region of unique flora and fauna and with a large cruise-tourism industry. In 1998 the Caribbean received 50% of total world capacity of cruise tourism placement, and many established Caribbean destinations now receive more cruise ship passengers than stopover tourists (Johnson, 2002). However, cruise tourism may lead to congestion at traditional destination venues and specifically at 'soft' eco-tourism attractions. Indeed, in the absence of deliberate management intervention, wildlife tourism attractions can evolve over time to the detriment of both the visitor experience and the focal wildlife species (Duffus and Dearden, 1990; Higham, 1998; Garrod and Fennell, 2004). Consequently, managers of wildlife tourism face the dual mandate of catering to the needs of the visitor and of conservation of the natural resource

base. When balancing these conflicting objectives it can be very useful to understand the tourist's relationship with the wildlife resource (Duffus and Deardon, 1990). Among the many possible research directions in the human dimensions of wildlife management, the investigation of user preferences for any proposed management alternative of the wildlife-tourism attraction is one option with direct management implications.

While wildlife tourists may all be participating in a common activity - i.e. photographing, touching, feeding or experiencing wildlife, they may not necessarily be one homogeneous group in terms of their beliefs, values or expectations (Duffus and Dearden, 1990), and may not fit one rather generic typology/description as proposed in some ecotourism typologies (Lemelin and Smale, 2005). Instead of characterizing a single user type, research into the human dimensions of wildlife has found that within and across attractions, wildlife-tourists differ by ethics, values, motivations, levels of specialization, and desired wildlife experiences. All of these aspects affect their expectations of and experiences with their respective wildlife interaction (Martin, 1997; Moscardo, 2000; Higham and Carr, 2002; Scott and Thigpen, 2003; Curtin and Wilkes, 2005; Dearden et al., 2006). Consequently, it is not unreasonable to assume that wildlife tourists may also be heterogeneous in their preferences for the intensity and type of site management proposed.

Research in other areas of tourism and recreation has indeed demonstrated divergent visitor preferences for the management of recreation activities in parks (Borrie et al., 2002; Kempermann and Timmermans, 2006), the management of congestion in wilderness areas (Michael and Reiling, 1997; Boxall et al., 2003), and recreational fisheries (Oh and Ditton, 2006). Although tourist preferences for the management of non-consumptive, or appreciative, wildlife tourism attractions have been investigated (Davis et al., 1997; Birtles et al., 2002a; Lewis and Newsome, 2003; Parsons, 2003), to date no study has explored heterogeneous preferences for the management of wildlife viewing and/or interaction. However, such information would be essential to develop and adapt products and facilities, as well as to make decisions about permitted activities, levels and types of use (Moscardo, 2000). Such detailed information would allow managers to more accurately anticipate how the various tourist profiles might react to new strategies or management policies (Davenport et al., 2002), and to establish whether each respective tourist type is compatible with the resource capabilities (Wall, 1993). Without such an understanding, inappropriate products or services may be offered, resulting in reduced visitor satisfaction, or in possible detrimental impacts on the natural resource base. As such, implementing a management plan that can satisfy the desires and expectations of a heterogeneous tourist demand and can simultaneously maintain ecological integrity is a challenging, yet crucial task.

Lately, multivariate methods have been introduced to human dimensions research which are especially well suited to uncover the preferences for management options in more detail (Aas et al., 2000; Hunt, 2005). Stated preference research in the form of discrete choice experiments constitutes a significant alternative to the traditional approach of investigating single-item questions. In a stated choice survey, respondents choose between two or several hypothetical management scenarios that are composed of various attributes of differing levels. Heterogeneity of preferences can be tested on individual visitor segments that have been defined *a priori* by the researcher (i.e. segments may be predefined or determined by cluster/factor analysis) and then followed by a between-segment statistical comparison. For this purpose, segmentation criteria may be socio-demographic characteristics, or behavioural traits and antecedents as proposed by social psychological theory (e.g. crowd-tolerance, recreation specialization, activity commitment, etc.) (Arnberger and Haider, 2005; Oh and Ditton, 2006). An alternative method is to uncover segments directly from the stated choice responses in underlying (latent) classes and test if these groupings differ in their management support. For this purpose latent class models are the most commonly applied types (Greene and Hensher, 2003; Train, 2003), which have also found application in recreation and human dimensions research (see Hunt et al. (2005) for a random parameters logit approach; and Oh and Ditton (2006) and Boxall and Adamowicz (2002) for latent class applications). These latent typologies can then be further described using

numerous exogenous psychographic and socio-economic variables (Boxall and Adamowicz, 2002). A latent class approach will be the focus of this paper.

This study differs from previous research of wildlife-tourism management in two ways. First, existing studies asked management-preference questions to tourists either in single-item format or in a ranking format, but they did not allow tourists to consider tradeoffs they might make between alternatives. As such, these studies are unable to conclusively determine the manner in which the tourist's experience would be affected, or whether management actions would change tourist behaviour. Second, these studies have not explored at all whether the sampled population possessed heterogeneous preferences for the various management options.

The overall purpose of this study was to understand and predict preferences and degree of support for management options of feeding marine life in the Cayman Islands. The most popular tourist site in the Cayman Islands (CI) is Stingray City Sandbar (SCS), a warm, shallow water (1.6 m maximum depth) sandbar in the North Sound, approximately 7740 m² in area and located roughly 300 m inside the fringing reef. It is here that stingrays congregate to be fed frozen squid by tourists and tour-boat operators. Due to its massive popularity, SCS supports over 50 local snorkel and dive tourism operations and hosts approximately one million visitors a year, almost half of all visitors to the Islands. The numbers have more than doubled since 2000 (CI MoT, 2002). A day-long

activity which first began in the mid-1980s (Shackley, 1996), a maximum of 2500 tourists can now be present at a given time at the shallow sandbar, engaged in unsupervised feeding, touching, and holding of stingrays as part of their marine tourism experience. Some tour operators provide only the most rudimentary information, while others provide an informative session in-water. The organized trip also provides photo opportunities, with some tour operators holding the ray in or out of the water, or placing it on people's backs and heads while the picture is taken. Without any management or codes of practice, the site has become congested, and all stakeholders (government officials, tour operators, tourists and locals) express concern about the long-term sustainability of the attraction (Gina Ebanks-Petrie, CI Director of the Environment, pers. commun.; C.A.D.S., pers. obs.). Since 2003, a management plan has been drafted for the site, but without any information on tourist acceptance or confirmed ecological necessity, stakeholders are unsure of its utility.

This study sought to ascertain whether any management of the human - wildlife interaction would significantly impact visitor preferences. The specific objectives were to: (1) determine tourist preferences for proposed management actions using stated-preference choice modelling and testing for latent heterogeneity in management choices; (2) investigate visitor profiles around trip experience, motivations, and conservation values; (3) identify and describe the latent classes using these visitor-profiles as explanatory variables, and lastly; (4) demonstrate the value of elucidating heterogeneous preferences by examining

their differences in supporting alternative management policies with a decision-support tool.

METHODS

The latent class choice model

A stated-preference method, the discrete choice experiment (DCE) was used to determine hypothetical management preferences for SCS. A DCE attempts to estimate the utility associated with individuals' evaluations of a designed set of multi-attribute management scenarios (McFadden, 1974; Ben-Akiva and Lerman, 1985). The analysis of DCEs is based on the assumptions of the general discrete choice model (McFadden (1974) - also referred to as the random utility model), and assumes consumers seek to maximize utility when they make choices (Hunt et al., 2005). The random utility theory suggests that each individual holds a deterministic (observable) component, and a random (unobservable, or error) component of utility:

$$U_i = V_i + \varepsilon_i, \quad (\text{eq. 1})$$

where U_i is the overall utility of an attribute i , and is composed of V_i , a deterministic parameter vector of attributes, and ε_i , the random component for the non-deterministic component of a respondent's choice. An individual will choose alternative i if $U_i > U_j$ for all $j \neq i$. Although it is assumed that this type of choice

behaviour is deterministic on the individual level, modeling is conducted as an aggregate stochastic process, in which the probability of choosing alternative i is:

$$Prob \{i \text{ chosen}\} = prob \{V_i + \varepsilon_i > V_j + \varepsilon_j; \forall j \in C\}, \quad (\text{eq. 2})$$

where C is the set of all possible alternatives. Choice models are typically analysed with a multinomial logit model (MNL) to produce regression estimates, known as part-worth utility (PWU) parameters for each attribute, the sum of which represents respondent preferences as a whole:

$$P(i | i \in M) = \frac{\exp(X_i, \beta)}{\sum_{j \in M} \exp(X_j, \beta)}, \quad (\text{eq. 3})$$

where the probability of choosing alternative i from all scenarios included (M) equals the exponent of all the measurable elements of alternative i (i.e. X , the vector of explanatory variables, and β , the parameter vector to be estimated) over the sum of the exponent of all measurable elements of all alternatives, j .

To account for preference heterogeneity in respondent choice the basic MNL form can be expanded to a mixed logit form, such as a latent class formulation. In the latent class model (LCM), the population is assumed to consist of a finite number of heterogeneous groups of individuals (i.e. segments) that are each characterized by relatively homogeneous preferences that differ substantially in their preference structure from each other (Birol et al., 2006). Class membership depends on the unobserved social, attitudinal and motivational characteristics of the respondents, and therefore the number of

segments is determined endogenously by the data. The latent class choice model assumes that respondent characteristics affect choice indirectly through their impact on segment membership, and thus accordingly combines a choice model with a probabilistic approach for determining the unobserved (i.e. latent) class membership of individuals (Boxall and Adamowicz, 2002; Vermunt and Magidson, 2005).

Latent class models assume discrete changes in parameters across different classes that are distinguished by individual heterogeneity (Brefle et al., 2005). For each class, the model estimates a separate set of choice model parameters (PWUs), and it is these different parameter estimates for each class that account for preference heterogeneity in the choice model. Within a class the choice probabilities for all scenarios included (M) are assumed to be generated by the mixture conditional logit model:

$$P(\text{choice } j \text{ by individual } i \text{ in choice situation } t \mid \text{class } c) = \frac{\exp(X_{it,j}\beta_c)}{\sum_{j=M} \exp(X_{it,j}\beta_c)}, \quad (\text{eq. 4})$$

where β is the class-specific vector j^{th} alternative, and j and X are defined as above (see Greene and Hensher, 2003 and Morey *et al.*, 2006 for more details on the LCM). The latent class parameter functions were estimated using maximum likelihood estimation in Latent Gold Choice 4.0 (Vermunt and Magidson 2005; Statistical Innovations, Inc.). The maximum likelihood analysis produces regression estimates (PWUs), standard errors and z-scores for each attribute level, and statistical differences are assessed using the Wald Statistic.

In the design of a discrete choice experiment, two or more hypothetical profiles are combined in choice sets, and respondents choose the most preferred alternative (profile) from each set they are asked to evaluate (Louvière et al., 2000). The hypothetical management scenarios crafted for SCS were described in terms of several attributes related to trip quality, tourist-stingray regulations, and ecological consequences (Table 1). These attributes were defined a priori as being (1) important features for management, (2) relevant to tourist satisfaction and stingray fitness, and (3) within the influence of managers. The levels for each attribute provided sufficient variation to matter for tourists and to allow for the simulation of current and potential conditions. Each attribute consisted of four levels, with one level representing the current level of management (i.e. no management). All other levels represented less congestion, stricter regulations, or lower negative ecological impacts. Although we could have chosen more ecologically intrusive attributes (e.g. higher congestion, or more lenient interaction rules, which would be rather unlikely), we were primarily interested in gauging respondents' management preferences as drafted by the Caymanian stakeholders as opposed to attributes contributing to a positive or negative tourism experience. To make the scenarios realistic, an attribute was included to describe a potential conservation access fee that would be charged to help cover the cost of implementing management initiatives at the attraction (Figure 1). The inclusion of such a 'payment vehicle' is common practice in DCEs (Louvière et al., 2000). All attributes were effects coded except the cost attribute, which was

linear and quadratic coded (Louvière et al., 2000). In the final model the quadratic term was dropped as it was not significant at the 90% confidence level.

The hypothetical scenarios in the choice experiment were generated by using a 7x4 orthogonal fractional factorial design, which permitted estimation of all main effects. In such a design, all of the levels of attributes in the choice alternatives are varied systematically (Raktoe et al., 1981). Sixteen versions of four choice sets were generated by this design for a total of 64 choice sets. Each respondent evaluated one of these versions. In each choice set, respondents were asked to choose the most preferred outcome among three identified alternatives: current scenario, management scenario '1', and management scenario '2'. The 'current' scenario served as base and was present in all choice sets, and its levels were also included in the management scenario description.

Extensions of the DCE: hypothetical management scenarios

It is important for planners and managers to be able to predict user support for management alternatives composed of all possible combinations of attribute levels (Aas et al., 2000). A decision support tool (DST) was consequently created as a forecasting tool to estimate which management scenario (and its subsequent potential ecological outcome) would garner the most and least support among respondents of each latent class. A feasible

management scenario was also included to examine how the classes would differ in their support for a plan that could readily be implemented by Caymanian officials. This overall evaluation of the hypothetical management scenarios is based on the calculation of the probability of choice for one alternative over any other alternative(s) (Haider and Rasid, 2002). The predicted probabilities were calculated by substituting the PWUs into Equation (3). Part-worth utilities were estimated without including the intercepts in the model so that the base scenario and the latent class were given equal market share in the DST (i.e. that choosing any alternative is equally likely). Deviations from this market share are calculated as the percentage of relative changes in demand over 'no management'. This type of DST modelling is possible because the current base levels were included in the descriptions of each choice set, and was done to remove any bias related to current experience.

Survey design

The survey was divided into four main sections: (1) attitudinal questions regarding the trip experience; (2) motivational questions to ascertain the importance of wildlife tourism attributes and concern for certain wildlife tourism impacts; (3) questions to establish socio-demographic and trip characteristics of the respondent; and (4) a discrete choice experiment to determine tourist

preferences for wildlife-tourism management. The purpose of questions in (1) – (3) was to explain the latent groups from the DCE in a decision-tree analysis, CHAID. In the ‘trip experience’ section of the survey, respondents were presented with 13 items (to be rated on a Likert scale) comprising visual amenity, learning, cost, crowding issues, and stingray interactions, and asked how well their expectations were met for each component. They were also given a traditional rating question of overall satisfaction with their trip to SCS. In the next section the ‘conservation values’ were measured; for instance, respondents’ level of importance conferred to wildlife and environmental conservation, their self-perceived level of knowledge about current conservation issues concerning wildlife and the natural environment, and their membership of conservation or environmental organizations. A further question asked about the contribution of eight specific activities (rated on a Likert scale) towards a satisfying wildlife-tourism experience, from interacting with animals with varying degrees of proximity, to learning, contributing and minimizing wildlife impacts. Concern about the potential effects of tourism at SCS (rated on a Likert scale) referred to specific health effects on the stingray, the surrounding environment, and to tourist safety. Questions were based, in part, on work by Birtles et al. (2002b), who conducted surveys with day-use visitors on minke whale-watching excursions, and Lewis and Newsome’s (2003) work on stingray-feeding in Hamelin Bay, Western Australia, as well as concerns identified by local Caymanian stakeholders. The third section of the survey consisted of the standard socio-demographic questions and trip characteristics, such as the

number of previous visits to SCS, the time of day the excursion took place, and the number of docked cruise ships the day of the trip.

Data collection

The survey was conducted in July and August 2004 in Grand Cayman. A pretest was administered to Department of Environment research officers and to a subset of cruise line passengers who visited SCS, to test for applicability, survey duration, and level of understanding. The final questionnaire version was targeted at cruise ship passengers only, as these make up over 85% of visitors to SCS (the others being tourists to the Cayman Islands). SCS visitors were intercepted at the tour-boat dock, immediately after their return from their boat trip to SCS. The self-administered surveys were handed out on the buses that would return the tourists to the ferry tender in Georgetown, an approximately 20 min trip. No more than 15 surveys were distributed on a given bus, and respondents were strategically selected (i.e. no one below the age of 18 was chosen, and surveys were given to only one person that appeared to be part of a family to minimize pseudo-replication). All other selection criteria were applied randomly. A small minority of tourists (approximately 5%) refused to take part in the survey when asked.

RESULTS

General respondent characteristics

Of the 744 questionnaires completed and returned, 612 contained completed choice sets (i.e. a total of 2448 choice sets), and were subject to the subsequent analyses. Generally, respondents were divided somewhat equally between sexes (61% female), were predominantly from the USA (> 95%), had a median age range of between 30 and 39, a median education level of completed university, were mostly employed as opposed to self-employed, and had a median income range between \$70 000 and \$89 000. Most respondents sailed on Carnival Cruises' boats (80%), with Royal Caribbean CruiseLine (15%), Celebrity Cruises (3.5%) and Holland America (1.5%) supplying the remaining respondents. Ship volume ranged from one to four cruise ships in port, during surveying times. The majority of respondents were intercepted when three ships were docked (50%). Respondents were sampled equally between 8:30 a.m. and 2:00 p.m., and only 11% of respondents were repeat visitors to SCS.

In terms of respondent trip experiences, the mean overall satisfaction among the tourists surveyed was a very high 6.14 out of 7 (0.92 S.D.). With regards to their conservation values, 87% of respondents strongly agreed with the statement that conservation of wildlife and the natural environment is very

important. However, less than 10% strongly regarded themselves as very informed about current conservation issues concerning wildlife and the natural environment; only 50% somewhat agreed with this statement, 24% were neutral, and the remainder either somewhat or strongly disagreed. Only 11.6% of the respondents belonged to organizations primarily concerned with the conservation of wildlife or the natural environment.

The decision tree analysis, CHAID, which will be used later to explore the characteristics of the latent classes, relies on categorical variables; therefore it was decided to reduce the survey questions with multiple items into single categorical indicator variables which are amenable to CHAID analysis and interpretation. For instance, the questions related to the concerns of potential impacts occurring at SCS (eight items rated on a Likert scale) were added to an overall concern score, and then grouped into three categories. About one quarter of respondents (26%) had 'very high concern', while about half (52%) voiced a 'mild concern' and 22% had a 'very low concern'. Principle component and subsequent cluster analyses (after Légeré and Haider, 2008) were used for the questions elucidating visitors' expectations regarding their trip to SCS, and the importance of various wildlife-tourism attributes for a satisfying wildlife experience. For the 'trip expectations' question, the analysis of the 13 items (rated on a Likert scale) produced three meaningful segments: 'crowd-sensitive' (46% of respondents) to people and boats, 'ray interaction was not a highlight' (18%), and 'everything novel, and learned much' (36%). The second analysis of

the eight items evaluating the importance of wildlife-viewing activities produced two segments: those who desire wildlife-tourism features to bring them 'up close and personal' to the wildlife (85%), and others who feel 'learning and contributing' (15%) are features of a more satisfying wildlife experience.

Latent class choice model

In estimating the latent class models, 1, 2, 3, and 4-segment solutions were assessed. All statistical indicators (i.e. log likelihood at convergence, Akaike Information Criterion (AIC), and Bayesian Information Criterion (BIC)), suggested that latent classes improved the model compared with the single segment model, thus supporting the existence of heterogeneity in the data. The optimal number of segments was chosen at two, as it represented the lowest BIC and the lowest marginal change in AIC ($BIC_{2\text{-segment}}=4347.42$; $AIC_{2\text{-segment}}=4157.86$), which are the standard statistical criteria for comparing the various model solutions (Swait, 1994; Bhat, 1999).

The results of the DCE are presented in Table 2 and Figure 2. For simplicity the overall model is not shown, but only the part-worth utility estimates for the two-class latent class model. The interpretation of the classes is in part a function of the statistically significant intercept, revealing that Class 1 (68% of respondents) very much favours any kind of management intervention over the

status quo, while Class 2 (32%) is indifferent between the average managed scenarios and the base alternative. Further interpretation of the classes can be made by looking more closely at the attributes themselves and at the individual levels. All variables, except the number of boats, are statistically significant in both classes, indicating that they significantly affect a respondent's choice of alternatives (Table 2: Wald Statistic I); and all estimates point in the intuitively correct direction. A quick overview of the estimates (Figure 2) also shows some significant differences between segments on several variables (Table 2: Wald Statistic II), as well as statistical differences in levels between classes (Table 2: t-statistic), but in no case do they contradict themselves in their fundamental directions. While fewer people are preferred overall (Wald I), a high density of people affect Class 1 respondents more negatively when compared with the average. Both classes also feel that too few encountered rays would detract from the experience, but the highest number of rays is more strongly preferred by Class 2 when compared with Class 1. Similarly, a reduction in the risk of injury to stingrays is preferred, but a high risk is strongly disfavoured and no-risk is strongly favoured by Class 1 respondents. The main class differences, all of which are statistically significant (Wald II), however, occur between variable levels relating to animal welfare and the conservation access fee. Class 1 is amenable to having its feeding and handling regulations with the rays regulated, whereas Class 2 is not; furthermore, Class 1 is more willing to pay a conservation access fee despite the price; Class 2 strongly prefers an inexpensive fee. In sum, Class 1 shows concern about animal welfare and

ecological consequences, is in favour of implementing regulatory frameworks, and is willing to pay a conservation fee; therefore, it has been labelled 'pro-management'. Class 2 clearly favours the status quo with regards to feeding and handling regulations, and consequently has been labelled 'pro-current'.

The next question worth exploring is whether these two segments differ significantly on some of the other survey variables. Given the fact that these exogenous variables are categorical variables, and are potentially correlated with each other, CHAID (chi-squared automatic interaction detection analysis) was applied to explore potential relationships between latent class membership as the dependent variable, and psychographic, socio-demographic, and trip characteristics variables as independent variables. A chi-square goodness-of-fit test screens out and subsequently selects a set of predictors and their interactions that optimally predict the dependent variable, i.e. class membership (Magidson and Vermunt, 2005). For this analysis, all external variables were added and a maximum tree depth of 10 levels was specified, with the minimum number of cases in the initial and terminal nodes set at 25 and 5, respectively (SPSS v.14, SPSS Inc., Chicago, Ill.). Of the 14 external variables entered into CHAID, six related to the two latent groups in a significant way (Figure 3): extent of concern for potential impacts occurring at SCS, their attribute preferences for a satisfying wildlife tourism attraction, membership in wildlife conservation organizations, previous site visits, trip experience at SCS, and gender. The first split, based on 'concern for potential impacts' occurring at SCS, does not come

as any surprise. Respondents with low concern for impact belonged predominantly to the status quo class (57% out of 105 respondents), while at the other end of the spectrum, the vast majority of high-concern respondents belonged to the pro-management class (82% of 126). These two relationships are so strong that no further splits emerged as significant, and therefore they represent terminal nodes. However, the vast majority of respondents (N=381) belonged to the 'mild concern' category, which contained a similar relative proportion of the two latent classes. Here, CHAID produced interesting further insights during subsequent rounds of splitting. A small terminal group of respondents was interested in learning of and contributing to the wildlife tourism experience, with very few individuals representing the pro-current segment, and is contrasted by a large group interested in getting up close and personal with the stingrays. In a further split among this latter assemblage, a small terminal group represents members of conservation organizations who were mostly pro-management, while the majority had no such membership. Next, a small terminal group represents repeat visitors, of whom more than half belonged to the pro-current class. Most of the first-time visitors to SCS belonged to the pro-management class, with the exception of males whose trip experience was characterized by a novel learning environment: this small, terminal node belongs to the pro-current segment (6.2%).

Extensions of the LCM: management scenario analyses

Three possible future scenarios are described and evaluated in Table 3. The first two scenarios (i.e. attribute combinations of the DCE) describe profiles that would produce the highest and lowest support from the respondents' perspective, and the third column represents an attribute combination of a feasible management plan from a manager's perspective. The last row of the table indicates the support these scenarios would garner when compared with the status quo of 'no management' (the comparison is based on the contrast between the status quo situation and the respective profile, and reports the percentage of relative change from the original 50% situation of initial equal market share). This comparative assessment shows that 'pro-management' and 'pro-current' respondents behave rather similarly when confronted with the least popular management scenario (declines of -68.5% and -99.7%, respectively vis-à-vis the current situation). The management scenario that both groups would prefer most results in a similar magnitude of relative change, but in the positive direction (+96.7% for 'pro-management' tourists and +68.3% for 'pro-current'). While these two latent segments apparently more or less agree with their evaluations of the best and worst scenarios, they differ fundamentally in their preferences for scenarios in between. The scenario representing a feasible management plan consists of a reduction in the congestion variables, an 'operator only' wildlife-interaction rule, a resultant drop in the number of rays and

their injury risk, as well as a \$5 fee (in US currency). Whereas support for this management option drops by only about 2% to 94.5% for the 'pro-management' respondents, it changes from +68% to -62% for 'pro-current' tourists; i.e. this segment would rather stay with the current, no-management situation.

DISCUSSION

Tourists visiting Cayman Islands' 'Stingray City Sandbar' are not homogeneous. Instead, when they are divided into two latent groups based on their responses to the stated choice task, they seem to divide around management preferences: one group, representing approximately two-thirds of the respondents, was labelled as 'pro-management' as they prefer actions that reduce congestion, impacts on stingrays, and the number of stingrays present. This group is also amenable to the payment of a conservation fee, and is concerned about a dramatic reduction in the risk of injury to rays. The second group of about one-third of respondents was labelled as 'procurrent' as they would support a small access fee but strongly desire to continue directly interacting with the stingrays and engaging in potentially injurious activities. Congestion reduction is of no importance, and the excitement of being surrounded by a multitude of rays would be diminished with fewer animals.

Although it might be expected that all tourists would be sensitive to crowds, as they indicated in a separate question on 'trip expectations' (46% were

crowding sensitive), the sensitivity of the PWUs for the number of people (250 to 1000) and boats (10 to 40) allowed was comparatively low compared with other attributes. This somewhat surprising result might be influenced by the high density situation on cruise ships, as well as the short amount of time visitors are allocated for sightseeing trips. Overcrowding behaviour on day-tours and its resultant effect on cruise ship passenger satisfaction is a rather neglected area of research with potentially important implications for nature-based tourism product development for cruise lines (Thurau et al., 2007).

Two attributes in the DCE were purposefully chosen to reflect activities that both can have fitness impacts on wildlife and contribute to tourist satisfaction: feeding and handling of animals. Results show that management plans designed to strictly limit these activities - and therefore lessen potential impacts on stingrays - produced the largest negative part-worth utilities and hence the lowest support among the tourist groups (for pro-current more so than pro-management respondents). Again, the result may reflect the nature of the attraction, as getting close to the stingray is a major part of tourists' expectations, and affects the quality of their experience accordingly. The attraction of getting close to a focal animal is not unique and has been documented by others: swimming with whales and whale sharks (Davis et al., 1997; Valentine et al., 2004); and stingray feeding in Western Australia (Lewis and Newsome, 2003). Moscardo (2006) recommends that for the long-term success of wildlife tourism, more research be directed into this type of consumer satisfaction, as wildlife-

based tourism is rarely considered a tourism service. An interesting upshot of this study is that although a low risk of injury to the animal is acceptable by the majority of participants, tourists are largely unaware of the potentially negative risks involved in feeding and handling wildlife in general (Orams, 2002), and specifically at SCS (Semeniuk and Rothley, 2008), as they still wish to have direct interactions with the rays. Furthermore, half of the respondents were characterized as having mild concern for potentially undesirable impacts occurring at SCS (52%), and in the CHAID analysis, 71% of these respondents were labelled 'pro-management', which seems to be in contradiction to their strong desire to minimize the risk of injury to stingrays in the DCE. This discrepancy might be a consequence of a lack of information concerning the actual impacts of these interactions on the stingrays and are discussed further below.

The attribute 'number of surrounding rays' was chosen as an ecological outcome to reflect either stingray emigration or death, without being explicit about the cause (and hence biasing respondents' choice). Fewest number of rays (10) was least preferred by both classes, although a slight reduction from the current estimate (40) was preferred by 'pro-management' respondents. In other studies, wildlife tourists confer importance on the number and variety of wildlife seen for a satisfying wildlife experience (e.g. birders (Scott and Thigpen, 2003) scuba divers (Rudd and Tupper, 2002), and wildlife viewers in National Parks (Hammit et al., 1993)). The somewhat contrary results of this study may in part have been

influenced by the large number of stingrays already encountered; the lowest level in this attribute (10 rays) represents an 80% reduction from what is currently experienced, which may be perceived as undesirable by some. In contrast, in a similar stingray-feeding site in Western Australia, the average number of rays seen was 6.7, and garnered a satisfaction rating of 4.65 (out of 5) (Lewis and Newsome, 2003). First-time visitors to the site are likely to have no prior expectations, and because only 11% of visitors are return visitors, a reduction in rays may not be too influential to the overall quality of the tourist experience.

Lastly, the payment-cost attribute demonstrates that an imposed conservation access fee of \$5 (US) or less would not be regarded as unfavourable by the vast majority of cruiseship passengers. Typical tourism and outdoor recreational valuation studies focus on use values to determine consumer surplus either for investment purposes or non-market value assessments (Nunes and van den Bergh, 2001). Very few valuation studies assess tourists' willingness-to-pay for the management of nature tourism, especially those that are wildlife-based (although see Davis and Tisdell, 1998; Walpole et al., 2001; and Sorice et al., 2007 for WTP studies on the management of komodo-dragon, whale-shark, and scuba tourism, respectively). The willingness to pay any additional amount (in the form of an access fee) comes as some surprise for this mass tourism product (Tremblay, 2001). The mass tourism character of this stingray-feeding attraction is indeed confirmed by the small percentage of respondents who are interested in learning of and contributing to

the wildlife tourism experience in contrast to the majority who wish to partake in direct interactions with the animals (Weaver, 2001). Garrod (2002) attributes the lack of valuation studies in ecotourism to a wariness of planners and managers to accept valuation studies as these have been inefficient in supporting the fundamental goals of ecotourism. In this present study, the WTP attribute was embedded in a multi-attribute scenario, forcing respondents to simultaneously assess tradeoffs between several variables. This grounding in realistic options should lead to less biased WTP estimates and hence be of interest to managers.

In 2003, the Cayman Island stakeholders convened a committee to agree upon a set of detailed rules for crowding alleviation and stingray protection for Stingray City Sandbar. Regulations included limits of a maximum of 100 people per boat, a 20-boat maximum at any one time, and 1500 people in the water at any one time; restrictions on feeding the stingrays (details are undetermined at this point); prohibitions on taking marine life of any kind, including the removal of stingrays from the water; and the nature and collection mechanisms for a proposed access fee. Issues that needed to be addressed, however, were the acceptability of the proposed management plan to tourists, the pricing structure for trips to SCS (although a \$0.25 to \$1 fee per visitor has been discussed), and the effect, if any, these plans would have on both stingray fitness and visitor response.

Within the scenarios presented, tourists seemed relatively unconcerned about crowding conditions. In addition, alleviating crowding will not be sufficient to offset the decrease in visitor satisfaction if managers at SCS are intent on implementing tourist-stingray regulations. Despite the relevancy of these results from a tourist perspective, alleviating crowding conditions for stingrays is essential, as research has shown a high rate of physical trauma to the rays as a consequence of boat collisions (Semeniuk and Rothley, 2008). According to Newsome et al. (2005), policy priority for wildlife tourism must be given to ecological sustainability. Feeding and handling stingrays can have negative impacts on their fitness (Newsome et al., 2004; Semeniuk et al., 2007; Semeniuk and Rothley, 2008); and although tourists are unwilling to have their interactions with stingrays severely limited, explaining to and informing tourists of the conservation purpose of these regulations and the ecological outcomes to be expected (i.e. fewer, but healthier stingrays), may increase support for the plan, since any reduction in the risk of stingray injury is strongly favoured by both latent classes (i.e. a teleological approach; Garrod and Fennell (2004)). Nevertheless, the marketing and promotion of the Cayman Island stingray attraction cultivates an expectation of being able to feed and touch the stingrays and of being surrounded by a multitude of animals. Wildlife tourism marketing is essential in order to inform prospective tourists what the experience has to offer, as well as persuade them to visit it (Kibicho, 2006). A crucial management initiative, therefore, may be to alter the marketing and operation of Stingray City Sandbar, including more realistic imagery of what one can expect (including a decrease in

the number of surrounding rays). Finally, the unanimous acceptance of tourists to pay a conservation access fee has promising implications. The cruiseline industry has a large stake in Caribbean tourism, and may be reluctant to allow any form of tax imposed on its clientele (Lester and Weeden, 2004), or permit changes in the price structuring of the SCS trip as most packages are sold on-board (Tapper, 2006). With the findings that strongly support the feasibility of a fee of up to \$5 (regardless of tourist typology) which could either improve the incomes for tour operators, or be declared a conservation fee to support management and conservation actions, the Cayman government can demonstrate to the cruise industry the acceptability of the access fee as well as its conservation-related purpose.

PWUs, however, send an even more powerful message to management if they are used in a decision support tool (DST), which calculates the change in visitor support for a scenario compared with the status quo (Table 3). It becomes clear that the two segments would react fundamentally differently to the most feasible management plan as proposed by CI. The 'pro-management' respondents would prefer this plan over status quo, while 'pro-current' respondents would strongly oppose it and their support would decrease relatively by 62%. What appears to be driving the divergent support is the restriction of handling and feeding rays by 'the tour operator only'. Opposition to this regulation is so strong by the 'pro-currents' group that no other feasible attribute levels can compensate for it, while in the case of the 'pro-management' segment, the loss of

one desirable attribute level is offset by other variables, especially the reduction in risk of stingray injury. Of course, this hypothetical behaviour suggests that implementation of this feasible management plan in SCS will lead to a shift in user characteristics over time, with 'pro-current' typologies being usurped almost completely by 'pro-management' visitors; the assumption behind this argument is a displacement process of pro-current visitors by additional pro-management tourists. The findings from our DST demonstrate the need for information on the sample of the population using the natural resources, especially when sensitive decisions concerning trip experience are being considered (Jurowski et al., 1995).

In identifying the latent segments to target, a range of psychographic, trip characteristic and socio-demographic variables was used. Models using respondent characteristics to describe latent heterogeneity in individuals' preferences among alternatives have recently been introduced in recreation research (Boxall and Adamowicz, 2002; Hunt et al., 2005; Morey et al., 2006). The decision-tree CHAID analysis revealed that psychographic typologies were more important overall than demographic variables in explaining the latent class membership. These results are consistent with previous research that showed psychographic information to be more powerful in understanding nature-tourists' behaviour (Mehmetoglu, 2007). Concern for potential impacts at SCS was the most important distinguishing factor of the latent classes (Figure 3). Although an attitudinal segment, it is nonetheless an actionable one, since education of tourist

consequences can be used to increase support for the proposed management plan (as discussed above). In the attempt to split the 'mild concern' sub-group into further definable segments, it was found that 'pro-current' respondents were more likely to be male (by a small percentage) and also more likely to return to SCS. This latter finding suggests that these visitors' previous trip behaviours and motivations significantly affected their preferences for certain management characteristics, a result consistent with previous research (Woodside and Dubelaar, 2002). Considering that the 11% repeat visitors belong mostly to the pro-current segment (from CHAID), the likelihood that any management plan imposed at SCS may cause a decline in 'pro-current' tourists increases further. Consequently, this visitor reaction is most likely a desirable outcome for managers.

Summarizing, the existence of divergent preferences from the study suggests several implications for the Caymanian resource managers charged with the responsibilities of protecting the environment and providing recreational opportunities: (1) different groups may require different management practices; (2) communication and education through various forms of media may play a key role in resolving conflicting preferences; and (3) the wildlife tourism attraction may need to undergo marketing and promotional restructuring in order to implement the desirable changes. The results of this study strongly suggest that not all visitors will be affected equally, and therefore an understanding of the various segments of tourist preferences for management actions and their

ecological outcome at SCS is essential. This consideration will consequently enable resource managers to formulate practical management guidelines that would garner support over the status quo, initiate regimes that would be acceptable to all segments, or design wildlife experiences that are preferred by the targeted segments (Kibicho, 2006).

The purpose of the study was to evaluate visitor preferences for wildlife-tourism management options. It is acknowledged, however, that this study is not without its limitations. The sample is composed of predominantly American tourists in the summer. While it is considered that low season results are conservative, further research is needed to determine whether tourists during the high season (i.e. mainly UK residents in winter) differ significantly in their preferences for management. Furthermore, the respondents were cruise ship passengers only. However, tourists who actually stay on the islands make up less than 15% of the visitors to SCS (CI MoT, 2002), but it would be equally informative if their preferences were explored, especially if Cayman Island managers decide to launch a marketing campaign to increase the representation of these visitors to SCS. Another limitation of the study is the omission of other exogenous variables that could explain variability in the data. Management preference may be influenced by contextual and situational variables such as type of weather, water conditions, and tourist state of mind (e.g. sea-sickness). A more detailed data collection and analysis would be required. Lastly, it is stressed that this case study represents a rather unique tourist attraction with an associated set of

tourist types not necessarily found in other tourism wildlife destinations, and therefore generalizations should be made with caution.

CONCLUSION

Marine tourism is one of the fastest growing market segments in the tourism industry (Orams, 1999), and marine wildlife tourism, a component of the wider ecotourism sector, is considered to be growing rapidly in both volume and value (Cater, 2003). As demand for wildlife interaction experiences increases in most countries with coastlines, so does the need to develop wildlife tourism attractions that meet tourist demand and shape the tourism experience while maintaining environmental quality and wildlife health.

Nonetheless, it has been demonstrated that a detailed understanding of tourist preferences and tradeoffs is an essential component of wildlife tourism management. Studies such as this can assist in describing the composition of the tourist population of interest, in explaining who will be affected by management planning and how, and in suggesting conceivable strategies that can satisfy the sometimes conflicting goals of wildlife health and visitor satisfaction. By allowing respondents to evaluate and trade-off several attributes simultaneously, the discrete choice survey provided a more comprehensive assessment of visitor preferences than traditional opinion surveys that ask respondents about attributes one at a time. Furthermore, a latent class approach to the DCE

estimated segments that were behaviour-based, providing a richer interpretation of results that allow for the effective targeting of the consumer population, as discussed above. This study is the first to date to demonstrate preference heterogeneity for wildlife-tourism management, using a latent class approach to a discrete choice experiment, and employing exogenous tourist typologies to identify these preference classes. Due to the quantitative nature of the study that incorporates both social and ecological attributes, further research can include the integration of these findings with biological studies on wildlife fitness, for example, in a simulation model that predicts the outcome of various management plans on tourist population numbers, stingray population size, and stingray life expectancy; this is the focus of ongoing research.

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Table 2.1 Attributes and levels used in the stated preference discrete choice experiment. Bolded levels represent the current situation of no management.

Attribute	Description	Level
Number of boats	Average number of boats tourist experiences at any one time	1. 40 2. 30 3. 20 4. 10
Number of people	Average number of people tourists encounter at any one time	1. 1000 2. 750 3. 500 4. 250
Feeding rules	Who is allowed to feed	1. Operator and tourist 2. Operator only 3. No feeding on this trip 4. No feeding at all
Handling rules	Who is allowed to hold rays	1. Operator and tourist hold ray out of water 2. Operator and Tourist hold in water 3. Operator only hold in water 4. No holding of ray
Number of surrounding stingrays	Number of stingrays tourist will be able to see definitively and up close	1. 55 2. 40 3. 25 4. 10
Risk of injury to stingrays	Injuries caused by boat collisions, other aggressive rays, and people.	1. High 2. Medium 3. Low 4. None
Conservation access fee	Fee for accessing SCS in addition to the cost of the trip itself. Proceeds are earmarked for the improvement of the tourism experience and stingray health	1. 20\$ USD 2. 10\$ USD 3. 5\$ USD 4. None

Table 2.2 Part-worth utility parameter estimates (z-statistics) for the two-class latent class model. Attribute levels were effects coded (except conservation fee), and underlined levels represent situations which correspond to the current state of no management. Bolded t-statistics denote significant difference between classes.

Variable	Levels	Segment 1 'Pro- Management'	Segment 2 'Pro-Current'	t-statistic
Number of boats	<u>40 boats</u>	-0.115 (-1.643)	-0.029 (-0.163)	-0.443
	30 boats	0.022 (0.303)	-0.131 (-0.680)	0.784
	20 boats	0.142* (-2.045)	-0.004 (-0.018)	0.810
	10 boats	-0.049 (-0.703)	0.163 (0.954)	-1.314
Number of people ¹	<u>1000 people</u>	-0.394* (-5.567)	-0.166 (-0.790)	-1.106
	750 people	0.015 (0.16)	-0.004 (-0.019)	0.145
	500 people	0.268* (3.657)	0.243 (1.329)	0.006
	250 people	0.114 (1.521)	-0.074 (-0.362)	0.976
Feeding rules ^{1,2}	<u>Operator and Tourist feed</u>	0.470* (6.544)	1.532* (9.288)	-5.824
	Operator feeds only	0.126 (1.771)	-0.265 (-1.187)	1.777
	No feeding on this trip	-0.273* (-3.743)	-0.589* (-2.468)	1.097
	No feeding at all	-0.322* (-4.551)	-0.679* (-2.794)	1.456
Handling rules ^{1,2}	<u>Operator and Tourist hold ray out of water</u>	-0.046 (-0.653)	0.753* (4.289)	-4.421
	Operator and Tourist hold ray in water	0.568* (7.898)	0.416* (2.416)	0.735
	Operator only holds	0.102	0.012	0.485

	ray in water	(1.386)	(0.062)	
	No holding of ray	-0.6239*	-1.181*	2.238
		(-8.6805)	(-4.658)	
Number of surrounding rays ¹	<u>55 surrounding rays</u>	-0.0211	0.353*	-2.121
		(-0.291)	(2.013)	
	40 surrounding rays	0.2452*	0.285	-0.295
		(3.268)	(1.646)	
	25 surrounding rays	0.158*	-0.062	1.185
		(2.19)	(-0.335)	
	10 surrounding rays	-0.382*	-0.576*	0.959
		(-5.086)	(-2.646)	
Risk of injury to rays ¹	<u>High injury risk to ray</u>	-0.972*	-0.486*	-2.497
		(-12.273)	(-2.549)	
	Medium injury risk to ray	0.125	0.143	-0.105
		(1.837)	(0.834)	
	Low injury risk to ray	0.474*	0.399*	0.417
		(6.622)	(2.487)	
	No injury risk to ray	0.373*	-0.056	2.456
		(5.316)	(-0.319)	
Conservation access fee ^{1,2} Intercept ¹	<u>0\$ - 20\$ (numerical)</u>	-0.021*	-0.059*	
		(-3.850)	(-3.794)	
	Management	0.306	0.033	
	Scenarios 1 and 2	(4.09)	(0.203)	
	Current, No Management	-0.306	-0.033	
	Scenario	(0.138)	(-0.241)	
<i>Observations</i>		2448		
<i>Log Likelihood</i>		-2056.0		
<i>Rho-Squared_{Overall}</i>		0.403		

¹Indicates the attribute has a significant impact on respondent choice of alternatives at the 5% level (Wald Statistic I).

²Indicates the attribute parameter estimates are significantly different between segments at the 5% level (Wald Statistic II).

* denotes levels with significantly different z-scores; i.e., the level is significant with respect to the reference point, which in effects coding, is defined as the average of the estimated coefficients.

Table 2.3 Decision support tool. Relative change in support of various hypothetical management scenarios per latent segment when compared to the base scenario (No Management) given equal market share (i.e., that choosing any alternative is equally likely). ‘Best’ and ‘worse-case scenarios’ are derived from the respondents’ perspective, and ‘feasible management plan’ from the managers’.

Attribute	Best-Case Scenario		Worse-Case Scenario		Feasible Management Plan	
	PM	PC	PM	PC	PM	PC
Number of boats	20	10	40	40	20	20
Number of people	500	500	1000	1000	500	500
Feeding rules	Operator and Tourist	Operator and Tourist	No feeding at all	No feeding at all	Operator only	Operator only
Handling rules	Operator and Tourist hold <u>in</u> water	Operator and Tourist hold <u>out</u> of water	No handling at all	No handling at all	Operator only holds in water	Operator only holds in water
Number of surrounding stingrays	40	55	10	10	40	40
Risk of injury to stingrays	Low	Low	High	High	Low	Low
Conservation access fee	None	None	20\$	20\$	5\$	5\$
<i>Relative change in support (%) over ‘no management’</i>	+96.7	+68.3	-68.5%	-99.7	+94.5	-61.6

Figure 2.1 One of the 128 choice sets used in the discrete choice experiment.

A. If you had the opportunity to return to Stingray City Sandbar, please choose the one management scenario that would maximize your experience if there were only these 3 options:

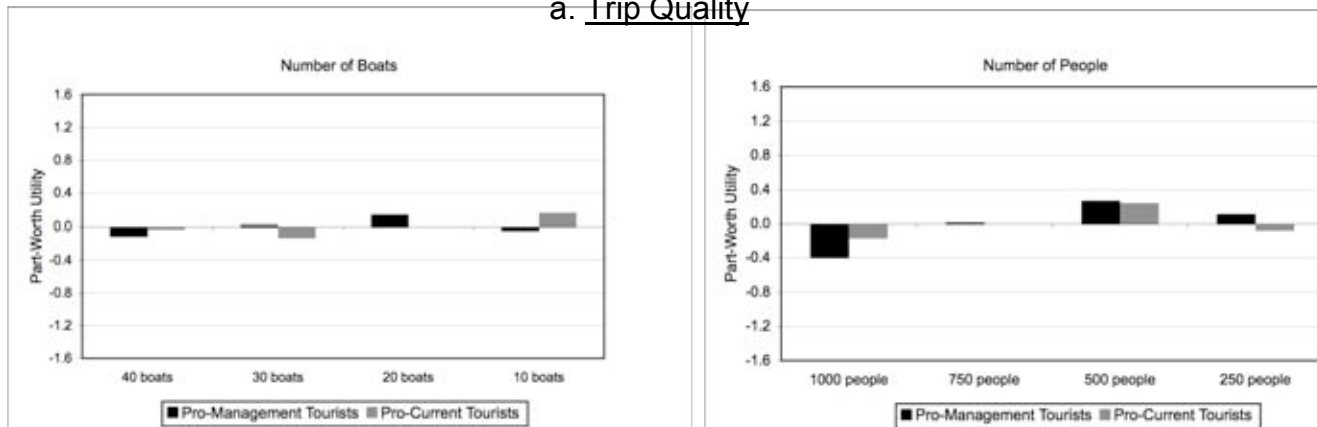
Please check one box only:

☐
☐
☐

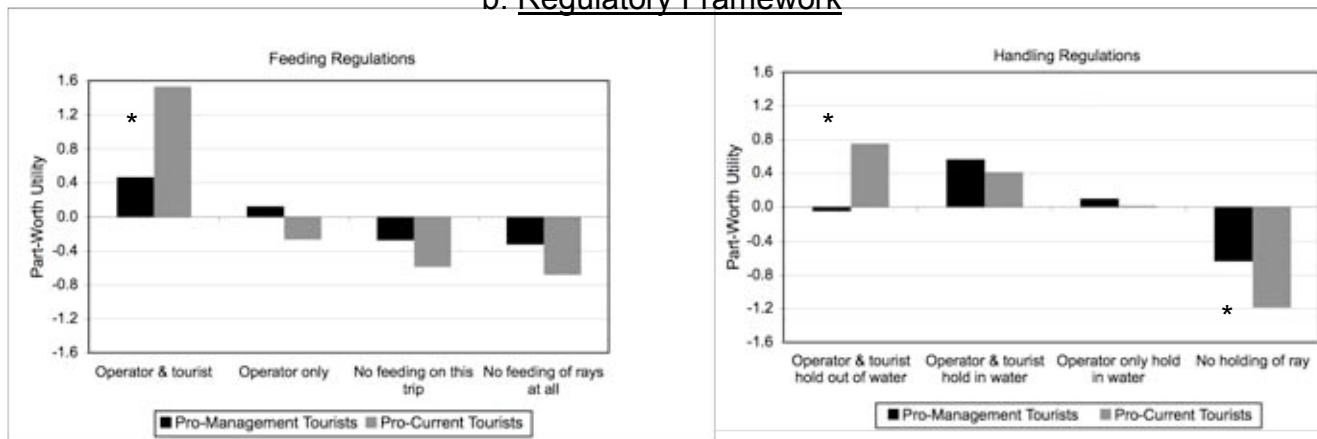
Site Characteristics	Current	Scenario #1	Scenario #2
# Boats allowed	40	20	30
# People allowed	1000	250	500
Stingray Feeding By:	Operator and Tourist	No feeding on this trip	Operator only
Stingray Handling By:	Operator and Tourist hold <u>out</u> of water	Operator and Tourist hold <u>in</u> water	Operator only hold <u>in</u> water
Number of surrounding stingrays	55	55	10
Risk of Injury to Stingrays	High	None	Medium
Conservation Access Fee	No fee	10\$ US	20\$US

Figure 2.2 Part-worth utilities (PWU's) estimated from the latent class discrete choice experiment of management options for Stingray City Sandbar, in particular, a. Trip Quality; b. Regulatory Framework; c. Ecological Consequence; and d. Willing-to-Pay. 'Pro-management' refers to the latent segmentation of tourists who prefer some form of management to be implemented at Stingray City Sandbar, while 'pro-current' tourists are in support of no management measures. * denotes levels that are significantly different between classes.

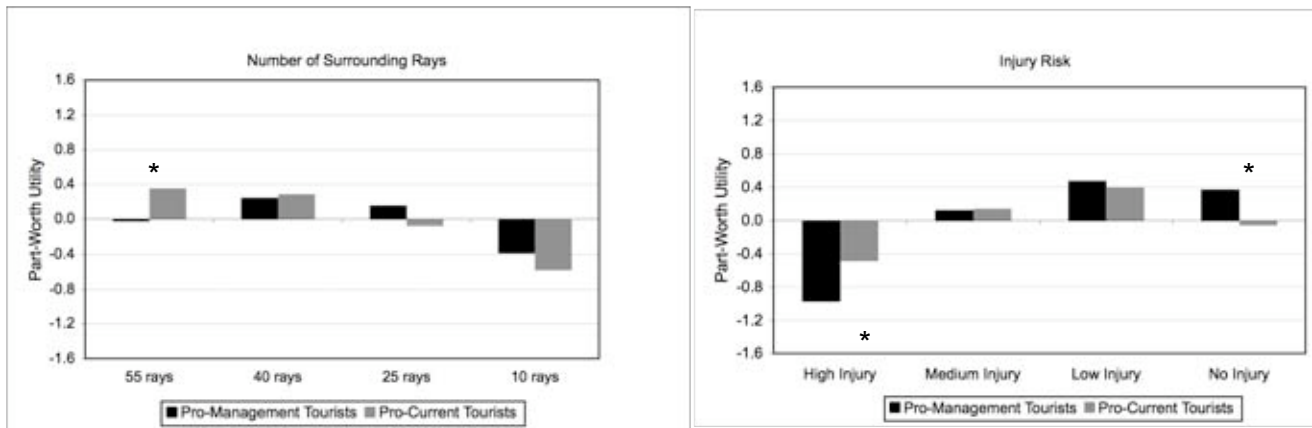
a. Trip Quality



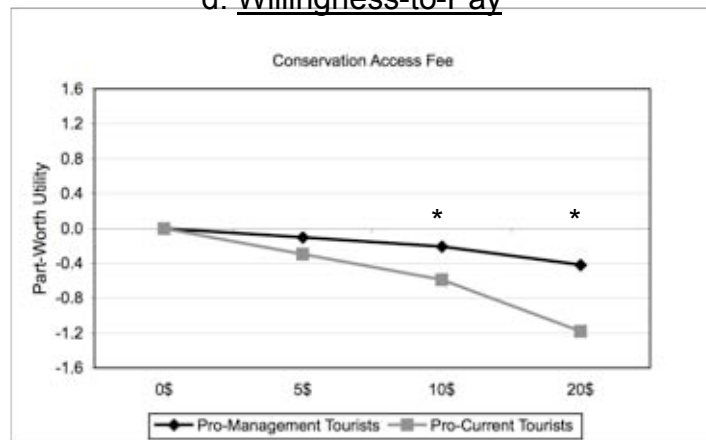
b. Regulatory Framework

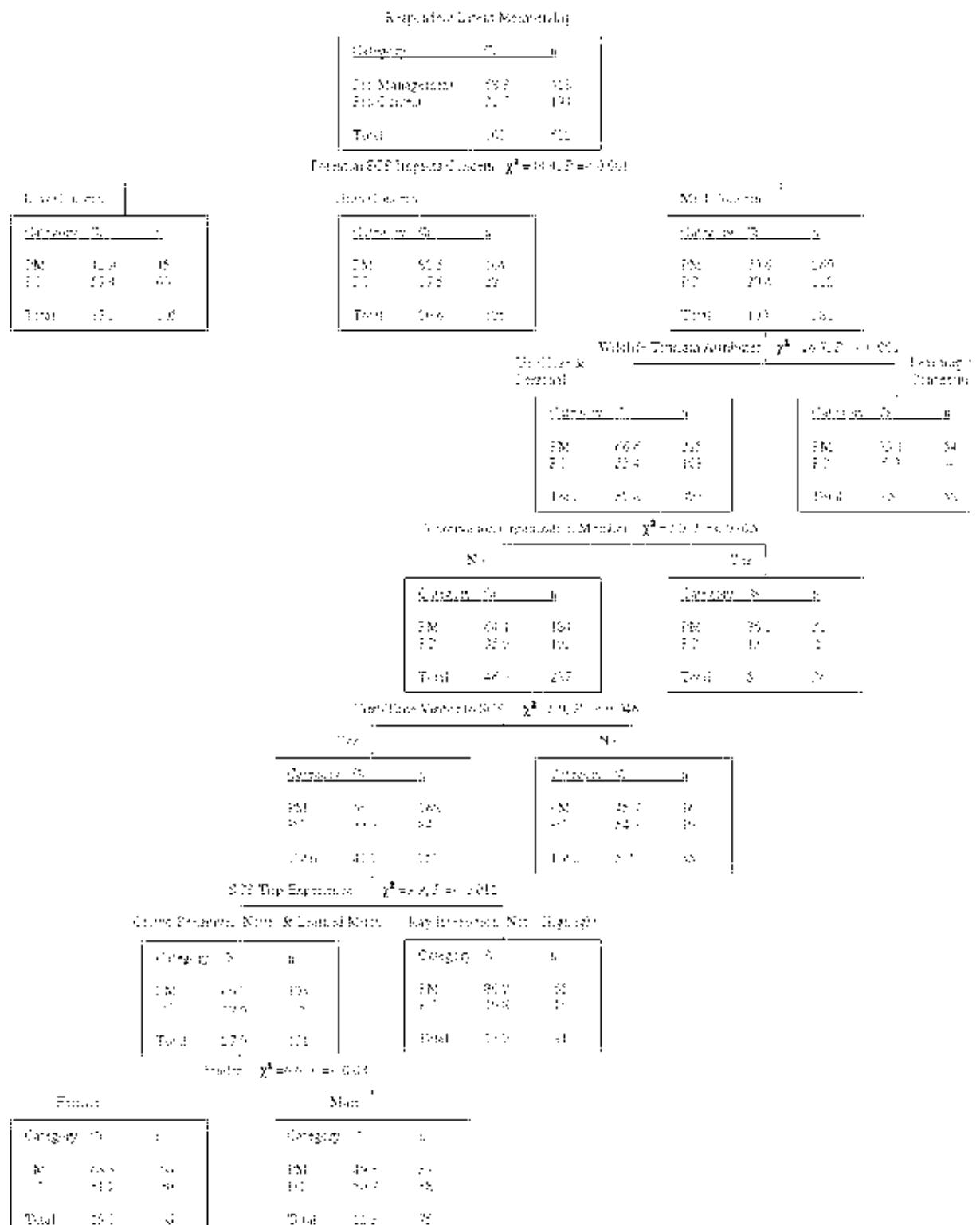


c. Ecological Consequence



d. Willingness-to-Pay





CHAPTER 3: USING FATTY-ACID PROFILE ANALYSIS AS AN ECOLOGIC INDICATOR IN THE MANAGEMENT OF TOURIST IMPACTS ON MARINE WILDLIFE: A CASE OF STINGRAY-FEEDING IN THE CARIBBEAN

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Abstract

Feeding marine wildlife as a tourism experience has become a popular means by which to attract both people and wildlife, although management efforts are still in their infancy. “Stingray City Sandbar” in the Cayman Islands, where visitors can hand feed free-ranging Southern Stingrays (*Dasyatis americana*), is a world-famous attraction currently undergoing visitor and wildlife management. One plan is to decrease the amount of nonnatural food provided by tourists with the intention of decreasing stingray habituation to the artificial food source and promoting stingray health. However, the effectiveness of this action is uncertain given that neither the extent of squid composition in the stingray diet nor the degree of nutrient similarity between the fed and natural diets is unknown. We used fatty acid (FA) profile analysis to address these questions by assessing the serum nonesterified FA composition of fed and unfed stingrays around the island and compared them with FA profiles of (1) the provisioned food source (squid) and (2) other warm-and cold-water elasmobranchs (sharks and rays). Our results indicated that fed stingrays were distinct. The FA profiles of the fed stingray population were expressly different from those of the unfed populations and showed a remarkable similarity to the FA composition of squid, suggesting that squid is the main food source. The tropical fed stingrays also exhibited essential FA ratios, specific to both species and habitat, comparable with those of elasmobranchs and squid from cold-water environs, implying that the provisioned food does not provide a similar nutritional lipid composition to that eaten in the wild. Our results suggest that FA profiles are a valuable indicator for the

management and monitoring of fed Southern Stingrays because they can be used to assess differences in diet composition and provide an index of nutritional similarity. Our findings are currently being used by Caymanian stakeholders in designing practical management actions for their wildlife attraction.

Introduction

In recent years, a growing worldwide demand to interact with wildlife has given increase to a wide range of wildlife tourism products (Reynolds and Braithwaite 2001). Marine wildlife tourism (MWT), in particular, has become one of the leading foreign exchange earners for countries with coastlines (Green and Higginbottom 2000, Garrod and Wilson 2004). The ultimate benefit of MWT is its potential to create a positive feedback between resource persistence and tourism demand that results in a common incentive to protect the natural environment. Despite benefits, MWT is not a panacea for conservation that can unfailingly both protect the environment and support economic activity. Instead, MWT can be prone to unmitigated development that is progressed at the cost of ecologic integrity (Miller 1993, Orams 1999). The ironic negative outcome of people's increased value of and desire for wildlife interaction opportunities stems from the conflict amongst conservation values, visitor satisfaction, and profitability of the stakeholders involved (Reynolds and Braithwaite 2001).

Deliberate feeding of marine wildlife as a tourism attraction is one such opportunity that has potential for conflict. Marine tourists are now sanctioned to hand-feed wild dolphins, coral reef fish, sharks, and stingrays (and manatees and sea turtles without permission; Mark Orams, Massey University, pers. comm..). Although this activity permits close observation of the focal species, allows the tourist to experience unusual or exciting animals, and returns a large economic benefit, feeding can also affect the wildlife. Food provisioning has been

demonstrated to alter an animal's natural behavior patterns and population levels beyond carrying capacity and to increase aggression levels and habituation to human contact (see Orams 2002 for a review). Other suspected disturbances include dependence, overfeeding, malnourishment, and disease. The pathologies of these latter outcomes are often subtle and delayed (especially in long-lived species) and are therefore difficult to assess without explicit physiologic examinations. Conversely, feeding can also produce positive impacts in the form of increased reproduction and enhanced survival during nutritionally stressed periods (Orams 2002, Dunkley and Cattet 2003). The issue of wildlife feeding as a tourism attraction is consequently complex because the social and economic benefits are vast and the negative ecologic outcomes uncertain at best, particularly in a marine setting. Addressing the issue of feeding wildlife therefore involves a considerable amount of empirical research, management, and understanding (Newsome and others 2005).

The Cayman Islands in the Caribbean are internationally known for their stingray-feeding tourism attraction. Stingray City Sandbar (SCS) is a warm, shallow water (1.6 m maximum depth) sandbar in the North Sound of Grand Cayman, approximately 7740 m² in area and located roughly 300 meters inland from the fringing reef. Here, a congregation of Southern Stingrays (*Dasyatis americana*) gather to be fed frozen squid (*Illex* and *Loligo* spp.) by tourists and tour-boat operators. SCS is an enormous attraction draw to the Cayman Islands, with its off season during the spring and summer months and its on season in fall and

winter. Today, the site supports at least 56 local dive and snorkel tourism operations (increased from 36 in 1998; Shackley 1998) and hosts > 1 million tourists a year (almost half of the entire tourism visitor market). Visitor numbers have more than doubled from 3 years ago (Cayman Islands Ministry of Tourism 2002), and \leq 2500 tourists (from approximately 40 boats) can be simultaneously present at the sandbar, feeding, touching, and holding stingrays as part of their marine tourism experience.

With no concerted management effort of the site since its inception in 1984, Caymanian stakeholders (The Cayman Islands Department of Environment, Cayman Islands Marine Conservation Board, local residents, Cayman Islands Tourism Association, and tour operator representatives) are concerned that this wildlife-based recreational activity has negative impacts on the fed stingray population. The Department of Environment has distributed a press release regarding its misgivings with stingray feeding, fearing ray fitness consequences ([http:// www.divecayman.ky/divemaster/press 01.asp](http://www.divecayman.ky/divemaster/press01.asp)). In 2003, the Caymanian stakeholders formed the North Sound Committee—Status Overview panel to discuss possible management options for SCS. The resultant ecologic plan (in addition to social and economic ones) suggested the control of the quantity of food (squid) provided to the stingrays with the intent to decrease their habituation to the constant supply of squid. This action would also serve to encourage stingrays to increase foraging in their own natural habitat, thus ensuring a more balanced diet in terms of nutritional composition. However, the panel was

hesitant regarding the appropriateness or adequacy of the feeding restrictions, owing to the uncertainty of the extent to which the provisioned squid makes up the fed stingrays' diet and whether it has a nutritional composition dissimilar to one obtained naturally in the wild. The panel could not, therefore, predict whether management, including food restrictions, would prove effective in terms of their concern about stingray well being.

The composition and nutritional requisiteness of an animal's diet can be partly determined through an analysis of its fatty-acid (FA) profile (Cartland-Shaw and others 1998, Ishigame and others 2006). Because prey lipids and the constituent FAs are integrated during a significantly longer period than the "snap-shot" provided by direct observation of dietary intake, stomach content, and scat analysis (Schaufler and others 2005), FA compositions can provide a more complete picture of animals' diets with time. The use of FAs as indicators of diet composition is particularly applicable to the marine environment because marine profiles have been quantitatively established, are qualitatively diverse, and possess unique FAs. FA structures can also be transferred largely unaltered across trophic levels and thus can have distinctive groupings traceable to a specific origin (Smith and others 1997). FA profiles have been used to characterize the foraging ecology and diet of a wide variety of marine species (Ackman and Eaton 1966, Iverson and Oftedal 1992, Virtue and others 2000), to assess among-and within-species population differences (Guitart and others 1999, Seaborn and others 2005) and to determine the nutritional adequacy of

artificial diets fed to captive aquaculture fish (Seaborn and others 2000, Rodriguez and others 2004).

In addition to diet characterization, FA levels can be used as physiological biomarkers because they directly reflect the physiologic status of an animal and are therefore useful indices of marine animal population health (Ballantyne and others 1996, McKinley and others 1993). Essential FAs (EFAs) are preformed long-chain FAs important for normal growth, development, and reproduction. Because EFAs cannot be biosynthesized in sufficient quantities to ensure optimal physiologic performance (Sargent and others 1999, Arts and others 2001), marine fishes (including elasmobranchs, i.e., sharks and rays) require dietary sources of EFAs (Ballantyne 1997, Sargent and others 1995). The EFA requirements of marine fish can be met by supplying, by way of the diet, three long-chain polyunsaturated FAs (PUFAs) of the n-6 and n-3 varieties: 20:4n-6 (arachidonic acid [AA]), 20:5n-3 (eicosapentaenoic acid [EPA]), and 22:6n-3 (docosahexaenoic acid [DHA]). The relative and absolute amounts of these EFAs can be linked to the metabolic demands of disease resistance and immune response (Lall 2000) and are species- and habitat specific (Sargent and others 1999). A comparison of EFA compositions of tissues of artificially fed marine fish with those of naturally foraging fish can provide an estimation of the suitability of the provisioned diet, assuming that the natural diet presumably contains the desirable composition for the lipid nutrition of the fish species in question (Rodriguez and others 2004).

We examined the capacity of FA profile analysis to serve as an ecologic indicator for the management of Southern Stingrays fed by Cayman Island tourists. This is the first study using FAs to investigate human-induced physiologic changes in a wildlife-tourism context. Our objectives were to (1) compare FA composition in the serum, measured as nonesterified FAs (NEFAs), between unfed Cayman Island rays from nontourist sites and rays fed by tourists; (2) compare the stingray FA profiles with the FA signature of squid, the provisioned food source, to establish any similarities in FA composition; and (3) explore the degree of correspondence in FA composition between the provisioned and natural diets through a comparison of EFA profiles of fed and unfed Cayman Island rays with those of warm-water elasmobranchs (sharks and rays), cold-water elasmobranchs, and squid. Our results provided information for Caymanian stakeholders to determine regulations to minimize any potential impacts of food provisioning as well as the means by which to monitor their effectiveness.

Materials and Methods

Study Species and Study Site

The Southern Stingray is a long-lived, common inshore ray frequenting tropical and subtropical shallow bays of the Southern Atlantic Ocean, the Caribbean, and the Gulf of Mexico. The Southern Stingray is a continuous forager, feeding opportunistically on a varied diet of crustaceans and teleosts, and to a lesser

extent, on molluscs and annelids (Gilliam and Sullivan 1993). Stingrays are typically solitary animals, forming groups only for mating purposes annually or for antipredator protection when protective cover is lacking (Semeniuk and Dill 2005). Although Southern Stingrays inhabit all shallow bays around the Cayman Islands, it is only in the vicinity of SCS that these rays can be found year-round in a dense aggregation of individuals of both sexes. This amassment results from the unregulated quantity of provisioned squid (*Illex* and *Loligo* spp.), a nonnatural diet item shipped in from the North Atlantic and North Pacific (C. A. D. S., personal observation; Gina Ebanks-Petrie, Director, Cayman Islands Department of Environment, personal communication). The feeding routine (daily, except for the off season when weekends are excluded) lasts from early morning until mid-afternoon as tour boats continuously deliver tourists (mainly cruise line passengers) for an average 45-minute visit to SCS. As a result of this regime, the fed rays have become diurnal (compared with their nonfed counterparts around the island) and have confined their activity space to the shallow waters immediately surrounding the feeding area (Corcoran 2006). Nearly 170 individuals from the fed group have been tagged since 2002. The rays have a mean yearly recapture rate of 92.5% (0.03% SD; CADS unpublished data, Corcoran 2006), indicating a very strong temporal and spatial fidelity to the feeding site.

Sample Collection

During a 3-month period from May until July 2004, blood samples were collected from a total of 168 stingrays (90 from SCS) as part of a larger study on the physiological effects of stingray feeding. For this study, a subsample of serum aliquots was selected from 25 immature and adult stingrays at SCS and from two control nontourist sites on the southern (opposite) side of Grand Cayman (under a Cayman Islands research permit and Simon Fraser University animal care protocol 708R-04). Stingrays with similar disc widths were selected from the fed and unfed sites so that diets would be comparable. Because stingrays from the two southern nontourist sites do not interact with the tourists in SCS (acoustic telemetry tracking data; Corcoran 2006), all of their food is presumed to come from natural sources. Sampled rays included both male and female animals in a range of disc sizes:

1. Fed Site_{Females}: n = 7, size (disc width) = 87-95 cm, weight = 21-31 kgs;
2. Fed Site_{Males}: n = 3, size = 56 cm, weight = 5-5.4 kgs;
3. UnFed Site 1_{Females}: n = 5, size = 87-95 cm, weight = 19.5-26 kgs;
4. UnFed Site 1_{Males}: n = 3, size = 48-54 cm, weight = 4-5.4 kgs;
5. UnFed Site 2_{Females}: n = 4, size = 88-93 cm, weight = 22-26 kgs;
6. UnFed Site 2_{Males}: n = 3, size = 38-46 cm, weight = 1.4-2.7 kgs.).

The fed rays at SCS are habituated to human presence and easily captured by simply holding them against one's chest when they approach for food. Once caught, a ray was placed in a landing net (1-m diameter) and transferred into a

seawater-filled canvas pool (4 m²) aboard a 24-foot long, 225-hp dusky boat. Control rays from nontourist sites were located visually from a 14-foot long, 45-hp double-hull boat and then encircled in a hand-drawn seine net (30 feet long), guided into a landing net, and transferred aboard into the holding pool. Once transferred, binder clips were placed over the barb on the ray's tail for protection, and in an average of 15 minutes, the ray was identified or tagged, weighed, and its disc width measured, injuries recorded, dermal parasites counted, and venous blood collected from the underside of the tail. All but one ray from the tourist site had been previously captured and tagged within the last year. On completion, stingrays were placed back into the landing net, had the tail clip removed, and were gently returned to the water. When released, fed stingrays resumed feeding at once, and nonfed rays swam away from the immediate area. For all rays, blood was drawn from the caudal vein using 21G x 1.5-inch needles into 3-mL serum vacutainers, and samples were kept chilled until their return to the wet laboratory at Georgetown, Cayman Islands, where they were immediately centrifuged. The separated serum was then stored at -70°C. Samples chosen for analysis came from rays that were caught on 22 separate occasions, with no more than 2 samples originating from the same day. Five capture events occurred in May, 8 in June and 9 in July, all between 9:00 AM and 4:30 PM.

FA Analysis

Serum non-esterified FAs were methylated as described in Singer and others (1990), and then extracted from the sera via the addition of and subsequent

centrifugation of hexane. The methyl esters were next redissolved in 25 µl of carbon disulfide. Next, 1 µl of solution was injected into a gas chromatograph (6890N, Agilent Technologies, Palo Alto, CA, USA) fitted with a flame ionization detector and an automatic injector. Methyl esters were separated on a DB-23 column (J&W Scientific, Folsom, CA, USA). The column temperature was initially 50°C, increased to 180°C over 10 minutes, held at 180°C for 5 minutes, and then increased over 5 minutes to 240°C where it was held for 5 minutes. Fatty acids were identified by comparing their retention times to those of known standards (GLC 463 augmented with 22:5(*n*-6) and 23:0, Nu-Check Prep, Elysian, MN, USA). Absolute FA amounts were calculated by adding a known amount (15 µg) of the internal standard heptadecanoic acid (17:0), to the serum samples prior to methylation. Preliminary analyses showed only trace amounts of endogenous 17:0 in the samples.

Data Analysis

Comparisons of total FA concentrations per site were made using analysis of variance (ANOVA) in JMP 6.0 (version 6; SAS, Cary, NC) to determine differences in the sum total concentration of 23 FAs between tourist and nontourist sites. Four FAs were not included in the analysis because their detection was negligible (see Appendix 1). Data were tested first for univariate normality and homogeneity of variance before proceeding. To compare FA

composition (i.e., different types of FAs) between sites, we minimized the number of FA variables, and using nonparametric multivariate ANOVA (MANOVA) with an unbalanced design and with location as a fixed factor (DISTLIM; Anderson 2004a), carried out a compositional analysis of FA concentrations with FAs grouped as either saturates, monoenes (monounsaturates), or PUFAs n–3 and n–6. Because of the small sample size and our inability to confirm multivariate normality and homogeneity of covariances, we selected a nonparametric technique. The nonparametric MANOVA analysis uses a test statistic analogous to Fisher's F ratio calculated from a distance matrix generated from the original data. P values were obtained using permutations. Because nonparametric MANOVA analysis is sensitive to differences in multivariate dispersion between groups (which can inflate Type-1 error even when centroids have identical locations), the same model was tested for differences in dispersion using the program PERMDISP (Anderson 2004b). In this test, an F statistic is generated to compare the average distance of observation units to their group centroid (or spatial median), which is defined in the space identified by the chosen dissimilarity measure. A P value is then obtained by permuting appropriate residuals. Significant results would indicate that the significant effect observed in DISTLIM was an artefact of variable dispersions. The effects of location on the individual FA groups (in nmol/mL) were further explored within each population using posthoc nonparametric Kruskal-Wallis tests in SPSS (v.14, SPSS, Chicago, IL), with $\alpha = 0.0125$ ($\alpha = 0.05/4$; Bonferroni method to decrease the risk of a Type-1 error). Mann-Whitney U tests were then used to examine the nature

of the differences for each FA group as indicated by the significant nonparametric ANOVAs. Effect sizes were also calculated with confidence intervals (CIs) based on the Mann-Whitney U statistic after Newcombe (2006). θ , the test statistic, can be regarded as a measure of separation, or equally, a measure of discriminatory ability. Its value ranges from 0 to 1, with values of 0 and 1 indicating no overlap, and a value of 0.5 indicating that the two variables are identically distributed.

Fatty acid concentrations (nmol/mL) were analyzed using classification and regression trees (CART) with SEE 5.0 (Rulequest Research 1997) to provide a quantitative estimate of diet similarity and to determine which set of FAs were most important in discriminating diets between tourist and non-tourist sites. CART is a nonparametric multivariate classification technique that allows the statistical interpretation of fatty acid patterns containing a high number of variables (fatty acids) per observation (Smith and others 1997). This analysis sequentially selects the 'best' variable and the best splitting point of that variable to separate the data into two groups (or nodes) that are as divergent as possible (Kirsch and others 1998). The splitting continues until one of two stopping criteria (based on deviance and number of observations) is met. Classification is made as well as a misclassification rate. CART is particularly appropriate for data in which the number of variables exceeds the number of samples. A second CART was used on selected FAs that contributed to 80% or more of the total NEFA concentration to ascertain whether diets differed with respect to the most abundant FA. A final CART was performed using mean percent of the most

dominant FA to compare the FA signature of both fed and unfed stingray groups to the FA signature of squid (*Illex* spp., obtained from Kirsch and others 1998, and re-normalized using the same subset of 23 FAs) .

Finally, we conducted a discriminant analysis in JMP 6.0 (SAS, 2006) comparing the nutritional balance of percent dietary EFA between fed and unfed Cayman Island rays, squid, and cold- and warm-water elasmobranchs to determine the extent to which fed stingrays could be distinguished from the other elasmobranch and squid groups using their EFA profiles as discriminating variables. Group classification was computed, and differences in mean canonical scores between groups were examined using ANOVAs with $\alpha = 0.01$ ($\alpha = 0.05/5$). Post hoc comparisons were made using Scheffé's test ($\alpha = 0.05$) when results were significant. We were less concerned about violating the key assumption of equality of variance-covariance matrices in this case as our purpose was to use discriminant analysis as an exploratory means to describe the gradients of variation in the data set; moreover, in wildlife research, there is little evidence that moderate violations significantly change classification success (McGarial and others 2000). A scatterplot of mean canonical scores for the significant discriminant functions was constructed to show the positions and orientations of the integrated profiles of individuals in their species-groups relative to each other. The relative percentage values of arachidonic acid (AA; 20:4n6), EFA eicosapentaenoic acid (EPA; 20:5n3), and docosahexaenoic acid (DHA; 22:6n3) of squid and other elasmobranchs were obtained from various

published and unpublished sources. Data for cold-water elasmobranchs *Amblyraja radiata* and *Raja rhina* (homogenized tissue total FA) were used from Budge and others (2002), and *Squalus acanthias*, *Leucoraja erinacea*, *Raja rhina*, and *Bathyraja* spp. (plasma NEFA) data were from B.S-R. & J.S. Ballantyne (unpublished data). Warm-water elasmobranch *Chiloscyllium punctatum* and *Taeniura lymma* (plasma NEFA) data were obtained from B.S-R. & J.S. Ballantyne (unpublished data), *Dasyatis zugei* (muscle total FA) data came from Gibson and others (1984), and *Dasyatis kuhlii* (muscle total FA) data came from Hansel and others, (1993). Squid: *Illex illecebrosus* (homogenized tissue total FA) data were used from Jangaard & Ackman (1965) and Kirsch and others (1998), and *Moroteuthis ingens* (mantle total FA) data were from Phillips and others (2001).

Results

The sum total serum NEFA concentrations of the ten fed and fifteen unfed stingrays were similar (mean \pm SEM total NEFA concentration (nmol/mL)): Fed = 455.4 ± 18.9 , Unfed 1 = 465.9 ± 21.2 , Unfed 2 = 463.2 ± 22.6 ; ANOVA: $F_{2,22} = 0.075$; $P = 0.93$). However, the NEFA profiles – total saturates, monoenes, n-3 FAs and n-6 FAs - of the fed rays exhibited marked group compositional differences (non-parametric MANOVA: $F = 11.9$; $P < 0.01$; Table 1). The overall test for differences in dispersion among groups was non-significant ($F = 2.02$, $P = 0.16$), indicating that the effect of location was to cause a shift in the FA composition, not to make the compositions either more or less variable. All but

total saturated FAs were found to differ significantly between the fed and unfed sites (Kruskal-Wallis: $H = 13.7$, $P < 0.001$). The two non-tourist sites did not differ significantly for any FA subgroup (see Appendix). Fed rays had significantly higher concentrations n-3 polyunsaturated FAs, but significantly lower amounts of monoenes and n-6 PUFA (Table 1). Effect sizes between fed and unfed stingrays for each significant FA group were large (θ : 0.01-0.11; 95%CI: 0.0-0.39).

We initially investigated variation in FA profiles using concentrations (nmol/mL) of all 23 FAs. The classification and regression tree (CART) analysis resulted in the algorithm selecting a minor component (20:3n6) that maximized the change in deviance between groups at the root node (90.9%). Classification required only 4 FAs (Table 2a) and resulted in a simple tree of 5 terminal nodes. Fed stingrays were immediately resolved into a terminal node, with the two non-tourist sites needing further classification to enable differentiation. Only 2 of the 25 stingrays were misclassified; one error occurred between rays from the non-tourist sites, and one fed ray was classified nearer to the root node as an unfed ray from the second non-tourist site.

In a second CART analysis, we used six of the 23 FAs that contributed to at least 80% of total FAs in all three sub-populations (16:0, 18:0, 18:1, 20:4n-6, 20:5n-3, 22:6n-3). The same trend as when using the full set of FAs was observed with similar classification accuracy. A tree using 20:5n3 at the root

node generated 5 terminal nodes using only three FAs with an overall classification success rate of 92% (Table 2b). All fed rays were correctly classified and terminated in a single node according to one FA (20:5n3). Again, only two individuals were incorrectly classified, this time as a result of difficulty differentiating rays between the two non-tourist sites.

In the CART analysis to compare the FA signature of Cayman Island rays to the FA signature of squid (the tourist-provided diet) we again used the six dominant FAs as in the previous test, but added the additional sample of the percent FA composition of squid (*Illex illecebrosus*, using the same six FAs). A similar classification accuracy resulted, with two FAs needed to fully resolve all Cayman Island ray groups, and one FA to distinguish fed rays from non-fed rays. One misclassification error occurred, with CART classifying squid as a fed ray (Figure 1).

Discriminant analysis resulted in the five species groups being classified correctly 82% of the time (Table 3). As expected, unfed rays were misclassified more frequently than the other groups, owing to their similarity in essential FAs to other warm-water elasmobranch species. Two significant discriminant functions were produced (Wilk's Lamda = 0.04; $F_{12,82} = 15.1$; $P < 0.01$; Figure 2), with fed Southern Stingrays having a statistically similar first mean canonical score to cold-water elasmobranchs and a statistically similar second mean canonical score to squid (ANOVA, both $P < 0.001$; Scheffé's test with $\alpha < 0.05$; Table 3).

The scatter plot of mean canonical scores showed that the two discriminant functions could be used to differentiate between the five species groups (although there was a great deal of overlap between warm-water and unfed elasmobranchs). The first canonical axis was also more effective than the second at separating the five groups. While the assumption of homogeneity of group dispersions was not met (Box's *M*-test: $P < 0.05$), the canonical functions that resulted from the discriminant analysis are of ecological significance as they (1) have an ecologically meaningful and consistent interpretation; (2) contribute more to group separation than any other canonical functions which fail to satisfy (1); and (3) result in significant separation of at least two groups consistent with the ecological interpretation of the functions (McGarial and others 2000).

Discussion

This study examined the value of using FA profiles as an indicator in describing the diet composition of provisioned stingrays and as an indicator of diet similarity between naturally feeding elasmobranchs and provisioned stingrays in terms of lipid nutrition, specifically EFAs. Our results support the utility of FA analysis in the assessment of human-induced physiological change in a wildlife tourism context. Although we acknowledge that no “control” group is truly representative of the natural state of the environment because of global anthropologic impacts, we nonetheless believe the rays used as baseline correspond to the closest natural condition of the environment and are foraging on species still common to the area. Our analysis detected significant differences

in serum FA composition between the unfed and fed Southern Stingrays in Grand Cayman as a result of their contrasting diets. With there being no difference in the sum concentration of FAs between rays from the tourist and nontourist sites, we nonetheless found substantial differences between the NEFA profiles. These results therefore indicate that fed rays had significantly higher relative and absolute concentrations of PUFA n–3 and lower PUFA n–6 and monoene concentrations than unfed rays. Although the differences between the fed and unfed Cayman Island rays were significant, the FA profiles within these groups were internally consistent. These findings suggest that the tree classifier model assigned rays according to their FA profile into fed or nonfed groups with high accuracy. Indeed, using CART analysis models, discrimination between the two unfed ray populations was possible with some error, but both groups were distinctly different from fed rays, which in turn had a minimal misclassification rate. The differences in NEFA profiles between fed and unfed Cayman Island rays were so pronounced that the two groups could be differentiated solely by the comparison of the proportion of one FA. Although these results are typical of evaluations made between farm-reared and wild sea turtles and teleosts (Joseph and others 1985, Seaborn and others 2000, Rodriguez and others 2004), or between geographically and seasonally separated individuals (Bradshaw and others 2003), its usefulness in detecting human-induced changes from wildlife tourism is as yet underappreciated.

Our FA analysis also indicates that squid provided by tourists are the SCS stingrays' major food source. Although the technique we used cannot quantify the diet *per se* (as discussed later), we can describe the FA composition with confidence. To begin with, CART analysis discriminated between fed and unfed rays but was unable to differentiate squid into its own terminal node, instead mistakenly classifying squid as a fed ray. Although this result is based on one sample for squid and may be an oversimplification, it nevertheless reveals that the contribution of squid to the diet is extremely high because the FA profile of fed stingrays more closely resembled that of squid rather than their unfed counterparts (whose profiles reflected the assimilation of natural-prey FAs into their lipid metabolism). Next, canonical discrimination analysis further demonstrated that fed Cayman Island rays' essential FA profiles were significantly different from those of warm-water species groups, but again they most closely resembled EFA profiles of squid and other cold-water elasmobranchs. Finally, FAs can have distinctive groupings traceable to a specific origin (Smith and others 1997); therefore, it is not unreasonable to suggest that the rays' food source was predominantly the provisioned one.

Although FAs from a storage tissue (e.g., liver) would clearly demonstrate the long-term dependency of Southern Stingrays on squid, we suggest that serum NEFAs are equally valuable. First, plasma NEFAs in fish show percentages of FAs that match very closely the levels seen in muscle and liver (Henderson and Tocher 1987, Greene and Selivonchick 1987). Second, plasma

NEFAs partially represent mobilized FAs from the liver and not just recently acquired dietary lipids (Greene and Selivonchick 1987). Third, the stingray groups in our study (from tourist and nontourist sites) were sampled at various times during the day during a 3-month period, and the fed rays (all but one) had been previously caught and tagged within the previous year. This suggests that our sample of stingrays came from a resident population, and that our results reflect a long-term integration of dietary FAs. In sum, because we have tested what the rays were eating during an extended period of time, and in every instance the profile returned had resembled that of squid, it is reasonable once again to assume that the rays were feeding predominantly on squid. Our serum NEFA data, therefore, reflect the body composition of FAs in the Southern Stingray and provide conclusive evidence of a strong, enduring incorporation of tourist-fed squid in their diet.

Our results further reveal that fed, tropical Cayman Island rays do not exhibit the typical essential FA profile of their unfed counterparts but instead possess a profile that more closely resembles those of elasmobranchs and squid from cooler waters. Patterns resulting from the canonical discrimination analysis of EFAs revealed that marine elasmobranchs living at latitudes characterized by cold waters have a higher proportion of DHA and EPA than AA, whereas elasmobranchs in warm waters have relatively higher concentrations of AA and lower concentrations of DHA and EPA (Fig. 2 and Table 4). Not surprisingly, squid from temperate-zone and sub-Antarctic waters had EFA profiles similar to

those of other cold-water species in this analysis. These trends are widespread in the marine environment: $n-6$ FAs (especially AA and its essential precursor 18:2 $n-6$) are more common in inshore tropical versus cold-water marine food webs, whereas high concentrations of PUFA $n-3$, such as EPA and DHA, are generally found in marine organisms inhabiting cooler environs (including flagellates and diatoms that are a major trophic source of these FAs and their precursors; Sinclair and others 1984; Castell and others 1994). An outcome of the Southern Stingray's diet of squid is a shifted essential FA profile that does not correspond to what occurs naturally in unfed Southern stingrays' serum.

Management Implications

The goal of our study was to determine the efficacy of FA profile analysis as an indicator tool for the ecologic management of SCS in the Cayman Islands. Specifically, we set out to address concerns raised by Caymanian stakeholders as to the degree to which fed Southern Stingrays were habituated to the nonnatural provisioned food source and whether this source provided a diet comparable with that of the wild. Our results revealed that squid represents a major prey item in the fed-stingray diet and that this food source does not provide a diet comparable with one of the nonfed wild rays with respect to monoene, $n-3$ FA, and $n-6$ FA concentrations (in particular, EFAs). Health implications and management options that stem from these findings are discussed here.

The longevity of stingrays (many decades), in combination with their protracted gestational time and small litter sizes, suggests that diet-related impacts on growth, reproduction, and survival rates would take many years to detect. For these reasons, our discussion here of the possible consequences of differences in FA composition, while compelling, are speculative and based on what is known for piscivorous fishes. Potential areas for further research on fed Southern Stingrays are identified.

Recent developments in research exploring fish nutrition suggest that differences in EFA requirements for different fish species reflect dietary and metabolic adaptations to distinctive habitats and ecosystems (Sargent and others 1999, Harel and others 2002, Bell and Sargent 2003). Moreover, the optimal tissue requirement for any individual long-chain PUFA cannot be considered meaningfully in isolation (Sargent and others 1999). Instead, the relative levels (i.e., ratios of all three EFA) must be considered because conjointly they are crucial requirements of lipid nutrition that influence immune health, disease resistance, and membrane fluidity in an optimal manner (Sargent and others 1999, Tocher 2003, Rodriguez and others 2004). As such, care should be exercised in deviating too far from “natural” ratios of n–3 to n–6 PUFA (for example, in commercial fish diets; Sargent and others 1995). With regard to the fed Cayman Island Southern Stingrays, they are acquiring a diet that is disproportionate in FA and EFA composition compared with the diet of naturally

feeding Cayman Island Southern Stingrays (which presumably reflects a dietary and metabolic adaptation to the environment). Fed stingrays are not only receiving less absolute amounts of AA and higher amounts of EPA and DHA from their diet (note the similar sum total NEFA concentrations between the stingray groups; see also Appendix 1), but their essential FA ratios (AA:EPA and AA:DHA) are also relatively skewed in the opposite direction from related warm-water species (Table 4). Furthermore, these FA profiles are present as plasma-free FAs, a metabolically dynamic fraction of serum lipids, and thus represent mobilized FAs that are actively important in metabolic processes (Henderson and Tocher 1987, Ballantyne and others 1996). Based on the premise that a diet should match the environment and its requirements, there may be long-term effects on the fed stingrays' growth, immune function, resistance to parasites and disease, and eventual survival. The implications of these findings, and the possibility of other physiological differences between the fed and unfed Southern Stingrays, should be further studied (e.g., an assessment of macrophage and lysozyme activities to determine circulating levels of leukocytes, and quantifying serum cytokines; Rice and Arkoosh 2002), and considered in future management plans.

Potential management options stemming from these findings include decreasing the amount of artificial food so that stingrays become less habituated and forage in their natural habitat (as originally suggested by the North Sound Committee – Status Overview panel) and/or changing the composition of the

provisioned food to a higher quality, varied diet more characteristic of a tropical environment as a precautionary approach. Because serum FA profiles provide evidence of tourist effects and are labile enough to reflect changes in diet (Kirsch and others 1998), they also can be used as a monitoring tool to gauge whether there is continued evidence of stingrays feeding disproportionately on squid and whether any management actions concerning food quality are having an effect. If properly managed, tourist-provisioned food could be used in a positive manner (i.e., the appropriate ratio of EFAs), and FA markers would serve as a bioindicator of such use.

Conclusion

In this article, we chose to focus on FA analysis as an ecologic indicator of (physiologic) change in tourism settings where feeding wildlife is the main attraction. However, we must stress that this is only one indicator and that the behavioural effects of fed animals and resulting ecologic effects (e.g., effects on habitat, incidental effects on nontarget species, effects of surpassing carrying capacity, and predator–prey dynamics, etc.) are equally important. We nonetheless wished to demonstrate the physiologic changes that can be brought about by artificial feeding (and diet), to caution about the possible negative impacts of skewed (essential) FA ratios of an unbalanced diet, and to discuss the use of FA analysis as an indicator and monitoring tool. FA analysis can be used in a qualitative manner (such as in this study) in a wide range of animals to describe temporal and spatial patterns in the diet and is therefore especially

relevant to other studies in which artificial feeding of wildlife is an issue. This technique is particularly appropriate for when direct observation of feeding is rarely possible and when indirect methods of scat or regurgitation analysis are prone to differential rates of digestion among prey species that can seriously bias estimates in favor of species with large and robust hard parts (Iverson and others 2004). Although tissue analysis of FAs is preferred, when biopsy samples are not an option, plasma or serum FAs can be used provided that samples are collected during a range of days and at various times during the day to minimize reflecting a point-source feeding bout. Because the techniques required are instrument intensive, we recommend collaborating with other laboratories that are adequately equipped. Another type of FA analysis involves quantifying the composition of prey species in the diet. However, this task is more challenging and necessitates multiple sources of information, such as an understanding and correction for the effects of predator lipid metabolism on FA deposition, consideration of variability in FA composition within and among prey species, appropriate sampling and chemical analysis of predator and prey lipid tissue, and a statistical estimation model (quantitative FA signature analysis; Thiemann and others 2004). Nevertheless, we believe that FA analysis is an important first step in determining whether changes are present in lipid nutrition and in pinpointing possible downstream effects that require further investigation.

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Table 3.1 Mean (\pm S.E.) NEFA concentrations (nmol/mL) of total saturated fatty acids (FA), monoenes, n-3 polyenes and n-6 polyenes of Southern Stingrays (*Dasyatis americana*) fed at tourist sites or unfed from non-tourist sites around Grand Cayman†.

Fatty Acid Group	Fed	Unfed 1	Unfed 2
	<i>D. americana</i>	<i>D. americana</i>	<i>D. americana</i>
Total saturated FA	172.9 (7.9) ^a	180.1 (8.9) ^a	178.2 (9.5) ^a
Monoenes	68.0 (3.4) ^b	90.3 (3.8) ^a	94.6 (4.0) ^a
n-3 polyenes	173.5 (11.3) ^b	96.4 (12.6) ^a	98.2 (13.5) ^a
n-6 polyenes	41.0 (5.4) ^b	99.1 (6.0) ^a	92.1 (6.4) ^a

†non-parametric MANOVA significant at the 0.01 level. Different superscript letters between stingray groups denote significant differences (Kruskal-Wallis and Mann-Whitney tests $P < 0.0125$, with Bonferroni correction).

Table 3.2 Results from the CART analysis from using mean percentage of: (a) all 23 fatty acids, and (b) the six most common fatty acids in all three sub-populations of Cayman Island Southern Stingrays that contributed to greater than 80% of all fatty acids (see text for information).

	No. of terminal nodes	Residual mean deviance	Misclassification error rate	Variables used in tree construction [†]	Tree structure ^{††}
(a)	5	0.747	2/25	20:3n-6, 18:4n-3, 23:0, 18:1	[Fed Rays (UF2 (UF1 (UF2, UF1)))]
(b)	5	0.736	2/25	20:5n-3, 20:4n-6, 16:0	[Fed Rays (UF1 (UF1 (UF2, UF1)))]

[†] The shorthand notation used for FA specifies the number of carbon atoms, the number of double bonds, and family membership (position of the ultimate double bond relative to the methyl end). For instance, 22:6n3 denotes an FA that contains 22 carbon atoms with six double bonds and is a member of the omega-3 family of FA.

^{††}UF1 and UF2 are unfed (UF) *D. americana* from two Cayman Island non-tourist sites.

Table 3.3 Classification and mean canonical scores (SEM) for two significant discriminant functions generated from mean percent of three essential fatty acids (AA, EPA and DHA) for different species groups from cold and warm water environs.

Membership	Predicted membership						Mean canonical scores (SEM)†	
	CWE	WWE	SQ	F	UF	% correct	Score 1	Score 2
Cold-water elasmobranchs (CWE)	5	0	0	1	0	83	-4.3 ^a (0.4)	4.8 ^a (0.4)
Warm-water elasmobranchs (WWE)	0	3	0	0	1	75	0.22 ^b (0.5)	8.1 ^{b,c} (0.4)
Squid species (SQ)	0	0	3	0	0	100	-6.5 ^c (0.6)	9.5 ^b (0.6)
Fed <i>D. americana</i> (F)	0	1	0	8	1	80	-3.7 ^a (0.3)	8.3 ^{b,c} (0.3)
Unfed <i>D. americana</i> (UF)	0	4	0	0	11	73	-0.1 ^b (0.25)	7.4 ^c (0.3)
Total	5	8	3	9	13	82		

†Different superscript letters within each canonical score denote significant differences (ANOVA $P < 0.01$, Scheffé's post hoc test $\alpha = 0.05$).

Table 3.4 Percent mean (\pm SEM) essential fatty acid profile† of elasmobranch species from temperate and tropical zones, squid species from temperate and sub-Antarctic regions, and fed and unfed Southern Stingrays (*D. americana*) from the Cayman Islands.

Species	<i>n</i>	AA	EPA	DHA
Cold-water elasmobranchs	6	3.9 (0.5)	14.7 (1.8)	16.1 (1.7)
Warm-water elasmobranchs	4	11.6 (0.8)	2.5 (0.5)	14.6 (2.0)
Squid	3	1.4 (0.3)	14.6 (0.6)	36.0 (0.7)
Fed <i>D. americana</i>	10	5.2 (0.9)	10.1 (0.9)	25.5 (1.7)
Unfed <i>D. americana</i>	15	11.5 (0.4)	4.7 (0.2)	12.7 (0.9)

†AA: arachidonic acid (20:4n-6), EPA: eicosapentaenoic acid (20:5n-3), DHA: docosahexaenoic acid (22:6n-3).

Figure 3.1 Regression tree showing generalized relationships between fed and unfed stingrays of the Cayman Islands. Tree shows mean percent common fatty acids of Southern Stingrays from sub-populations that are either fed squid by tourists ('Fed rays'; n=10) or not (non-tourist site 1: 'Un Fed 1', n = 8; and non-tourist site 2: 'Un Fed 2', n = 7), and of squid (*Illlex* spp.; Kirsch and others 1998); n = 1), the non-natural food source. The fatty acid and the cutpoint are given for each node in the tree, with the '>' sign referring to the right-hand decision. The fractions under each terminal node refer to the total number of observations for that node (numerator) over the number and source of misclassifications (denominator).

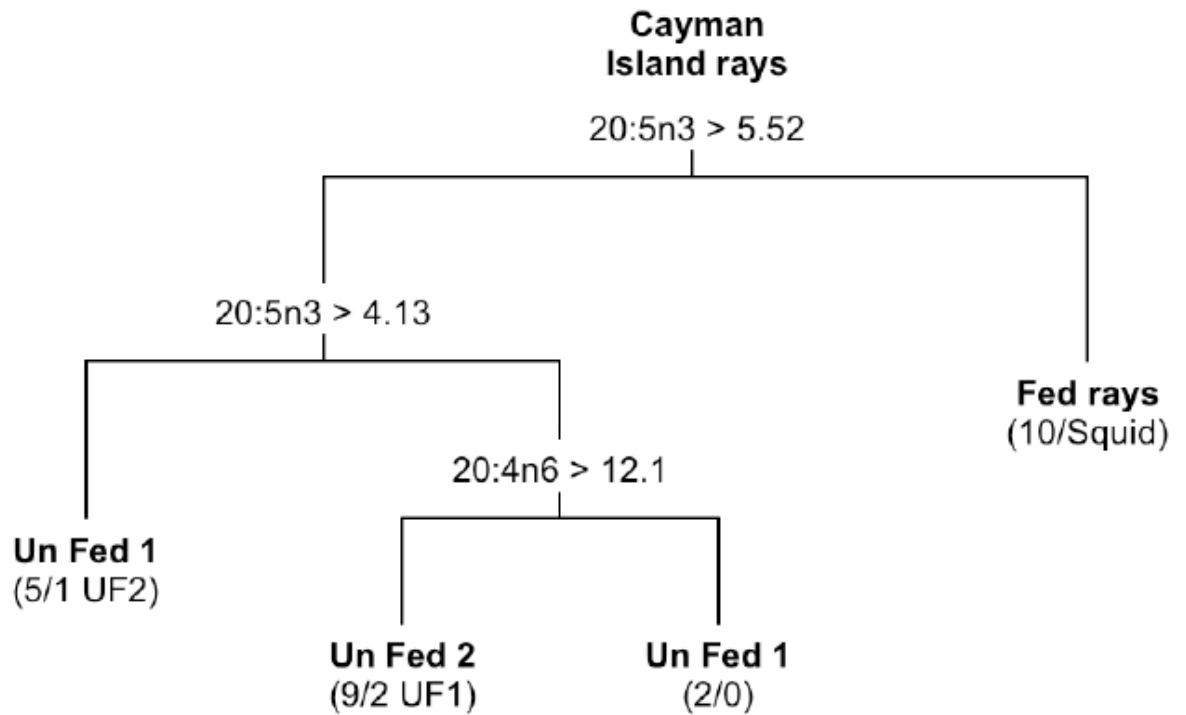
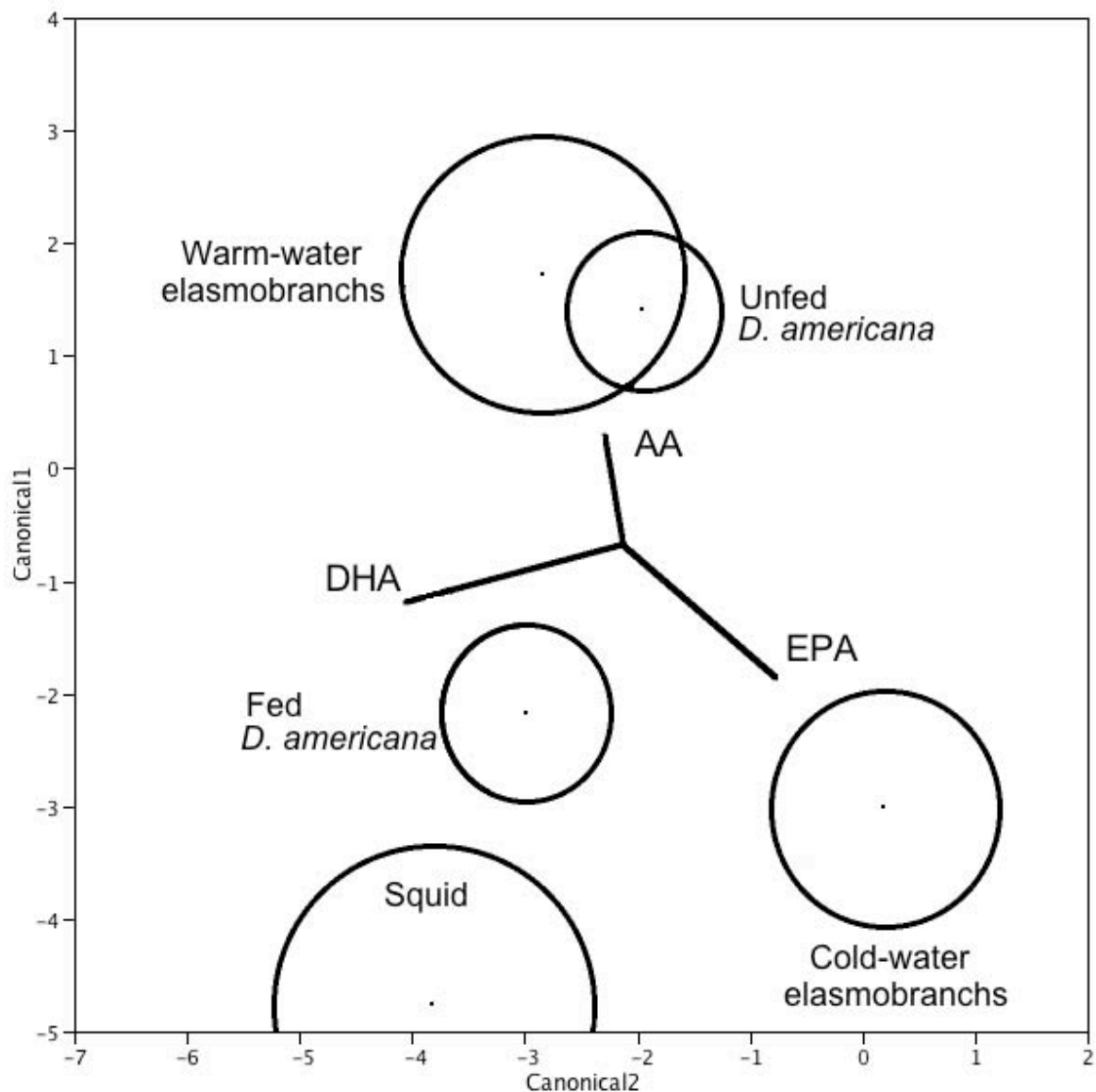


Figure 3.2 Segregation of integrated essential fatty acid (EFA) profiles for warm (n = 4)- and cold-water (n=6) elasmobranchs, fed (n=10) and unfed (n=15) *D. americana*, and squid (n=3). Circles represent the profile means and their 95% confidence radii. Contributions of individual EFA to the separation of locality centroids are indicated by the magnitude and direction of EFA vectors, which are scaled relative to the pooled within-group standard deviations. AA: arachidonic acid; EPA: eicosapentaenoic acid; DHA: docosahexaenoic acid.



APPENDIX. Fatty acid composition of Southern Stingrays in the Cayman Islands.

	Fed rays (Tourist site) n = 10	Unfed rays 1 (Control site) n = 8	Unfed rays 2 (Control site) n = 7
Fatty acid			
Saturated fatty acids			
14:0	9.17 ± 0.42	6.72 ± 0.73	7.28 ± 0.41
16:0	135.11 ± 5.78	127.97 ± 10.95	124.76 ± 5.29
18:0	27.86 ± 1.90	44.20 ± 2.02	44.12 ± 2.33
20:0	0.14 ± 0.14	0.49 ± 0.24	0.90 ± 0.24
22:0	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
23:0	0.60 ± 0.25	0.75 ± 0.31	1.16 ± 0.21
24:0	0.00 ± 0.00	0.00 ± 0.00	0.02 ± 0.02
Monounsaturated fatty acids			
14:1	1.34 ± 0.07	1.33 ± 0.10	1.11 ± 0.15
16:1	9.58 ± 0.89	16.70 ± 1.35	19.65 ± 1.31
18:1	46.67 ± 2.55	65.17 ± 3.25	65.41 ± 2.76
20:1	8.13 ± 1.01	3.48 ± 0.59	6.00 ± 1.32
22:1	1.98 ± 0.17	2.29 ± 0.19	2.17 ± 0.47
24:1	0.25 ± 0.25	1.28 ± 0.55	0.24 ± 0.16
Polyunsaturated fatty acids			
18:2n6	3.55 ± 0.41	7.41 ± 0.62	7.63 ± 0.83
18:3n3	0.35 ± 0.18	1.30 ± 0.51	1.47 ± 0.38
18:4n3	0.29 ± 0.19	0.19 ± 0.19	1.24 ± 0.82
20:2n6	1.56 ± 0.12	2.69 ± 0.24	3.05 ± 0.27
20:3n6	0.13 ± 0.13	1.39 ± 0.12	2.17 ± 0.33
20:4n6	22.85 ± 3.57	56.18 ± 3.88	50.20 ± 2.68
20:3n3	1.93 ± 0.47	0.00 ± 0.00	0.16 ± 0.16
20:4n3	0.39 ± 0.24	3.79 ± 1.95	2.57 ± 1.37
20:5n3	46.39 ± 5.04	20.34 ± 1.41	23.65 ± 1.25
22:2n6	0.00 ± 0.00	0.00 ± 0.00	0.09 ± 0.09
22:4n6	8.30 ± 1.36	19.75 ± 1.39	19.07 ± 1.97
22:5n6	4.64 ± 1.20	11.66 ± 1.42	9.93 ± 1.32
22:5n3	6.57 ± 0.51	10.33 ± 0.39	10.22 ± 0.79
22:6n3	117.59 ± 10.11	60.46 ± 7.32	58.90 ± 8.07
TOTAL	455.39 ± 17.59	465.88 ± 27.48	463.15 ± 14.34
Total Saturates	172.89 ± 6.58	180.13 ± 12.45	178.24 ± 5.56
Total Monoenes	67.96 ± 3.14	90.26 ± 4.35	94.58 ± 3.53
Total Polyenes	214.55 ± 10.29	195.49 ± 12.74	190.33 ± 9.93
n-3 Polyenes	173.51 ± 14.89	96.41 ± 8.99	98.19 ± 9.30
n-6 Polyenes	41.04 ± 6.31	99.08 ± 5.58	92.14 ± 4.86
n3/n6 ratio	5.37 ± 0.88	0.98 ± 0.08	1.09 ± 0.14
monoenes/polyenes ratio	0.32 ± 0.02	0.47 ± 0.03	0.51 ± 0.04
unsaturation index	263.89 ± 7.26	216.80 ± 4.37	213.60 ± 7.57
chain length	18.86 ± 0.05	18.61 ± 0.05	18.57 ± 0.05

Note: Values are mean ± S.E.M. of 23 fatty acids (nmol/L) and of grouped fatty acid composites.

CHAPTER 4: COSTS OF GROUP-LIVING FOR A NORMALLY SOLITARY FORAGER: EFFECTS OF PROVISIONING TOURISM ON SOUTHERN STINGRAYS *DASYATIS AMERICANA*

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ABSTRACT

Animals can perceive tourists as predators, and will incur fitness costs should their predator-avoidance behaviours result in forgone resource acquisition. Not all wildlife, however, treat tourists as predators; animals can respond positively to tourists, especially when food is used as an attractant. We investigate the costs posed by novel grouping over a tourism-provisioned food resource in a normally solitary forager, the southern stingray *Dasyatis americana*, in Grand Cayman. Specifically, we test the hypotheses that group-living stingrays in a new environment — which includes both the presence of tourists and quickly renewing food patches — will be exposed to increased injuries, ecto-dermal parasites and aggressive interference competition that result from the unusual grouping behaviour. We found that, in comparison to stingrays from non-tourist sites, tourist-fed stingrays are more likely to have lower body condition, be injured by boats and predators, be susceptible to ecto-dermal parasites, and be engaged in intense interference competition (in the form of conspecific bite marks). Stingrays from tourist sites also have significantly higher mean numbers of injuries, parasites, and median bite marks. By exploring alternative hypotheses to explain the pattern of our findings (e.g. natural causes/behaviour), we unequivocally show that the impacts incurred by the stingrays stem from the effects of tourism. These findings suggest that novel grouping poses costs to the stingrays; the tourist site represents a riskier habitat with regards to injury and predation; and there may be long-term fitness consequences. From a

management perspective, measures should be taken to alleviate the crowded conditions at tourist sites, in terms of both boat and stingray density.

INTRODUCTION

Understanding how animals perceive humans is an important aspect of conservation and wildlife biology, as it allows managers to predict animal responses to human disturbances, determine whether these actions are adaptive, and to effectively mitigate human-wildlife conflicts. A burgeoning concern in wildlife management is the direct interaction between humans and wildlife in the form of wildlife tourism (Duffus & Dearden 1990, Reynolds & Braithwaite 2001). Wildlife tourism is an example of a rapidly growing industry seen as a catalyst for economic and social development, and a way for wildlife to 'pay for itself' (Rubenstein 1998, Milazzo et al. 2006). However, wildlife tourism can be prone to unmitigated development to promote visitor satisfaction that is progressed at the cost of ecological integrity (Newsome et al., 2005). Attempting to control the impacts of wildlife tourism on the focal species requires research into how different species respond to different types and levels of human disturbance so that management can be implemented accordingly.

One form of response evoked by human-caused disturbance stimuli is predator-avoidance strategies in animals. These behaviours create tradeoffs between avoiding perceived predation risks and other fitness-enhancing activities (Lima & Dill 1990, Gill & Sutherland 2000). For instance, many animals respond to human disturbance as they do to their natural predators by increasing vigilance, increasing group size, abandoning the site, selecting alternate habitats, altering mate choice, and/or adjusting life history decisions (Frid & Dill 2002,

Beale & Monaghan 2004, Blumstein 2006). These behavioural outcomes thus pose a cost to the animal in terms of fitness-maximization in reproductive success and/or survival. Wildlife tourists represent an example of a disturbance stimulus, and indeed, a multitude of studies have demonstrated that in the presence of tourists, animals exhibit increased predator-avoidance energy expenditure, augmented circulating stress hormones, compromised immune function, reduced body condition, and decreased reproduction and survival of animals (Knight & Cole 1995; Ikuta & Blumstein 2003, Lusseau 2003, Müllner et al. 2004, Amo et al. 2006). While overwhelming, evidence of reacting to tourists as predators is not the sole response elicited from wildlife. Tourists can also be perceived as refugia, either through reducing the risk of predation from conspecifics (i.e, vulnerable age/sex class; Nevin & Gilbert 2005), or through providing resources such as food (Milazzo et al. 2006, Laroche et al. 2007), thereby increasing energy allocation to other fitness activities such as rest and reproduction (Orams 2002). Wildlife in these instances are attracted, not repelled, to tourists since the immediate outcomes of this association can provide benefits. However, even when tourists are considered a positive stimulus, indirect costs can still result, especially if the life history characteristics of the animal are altered by the wildlife-tourism activity. In particular, grouping in a normally solitary animal due to the attraction to tourists is predicted to give rise to costs.

Animals typically form groups to enhance foraging efficiency, improve locomotory ability, increase mating encounters, benefit from alloparental care, maintain physiological parameters, or to lower individual risk of predation. Animals may also form groups incidentally, in response to limited, patchy resources such as mates, refuge habitat, and food. Although grouping can be an effective fitness strategy, not all individuals are found in groups, some groups are maintained at sizes well below their predicted optimum (Steenbeek & van Schaik 2001), and some animals group only under certain conditions. Such evidence suggests there are costs associated with the formation of groups, including increased conspicuousness, increased competition for resources, increased levels of aggression, and increased exposure to parasites or disease agents (Krause & Ruxton 2002). While these explanations can describe why animal populations can presently be found to live in groups or alone, i.e. already at their evolutionary equilibrium, they can equally explain what costs, if any, exist for animals newly transitioning from solitary to grouping behaviours.

In the present study, we investigate some potential costs of grouping in a typically solitary forager, the southern stingray *Dasyatis americana*, which congregates over a quickly renewing, patchy resource, namely, provisioned food (squid) supplied by marine-wildlife tourists in the Caribbean. At Grand Cayman, 'Stingray City Sandbar' (SCS) is a tourist attraction approximately 7740 m² in area and located in a shallow sound in the north of the island. Up to 2500 tourists from 40 tour boats can be simultaneously present at SC5 feeding, touching, and

holding stingrays as part of their marine tourism experience, which occurs year-round (Shackley 1998). Since the site's inception in 1984, an aggregation of over 100 tagged and identified stingrays of both sexes can now be found at SCS at a given time, feeding on squid provided by tourists. Previous research in the Grand Cayman system has established that the tourist stingrays have altered their behaviours in response to the provisioned food in terms of reduced activity space, strong and persistent site fidelity, and a shift to diurnal behaviours in comparison to stingrays from non-tourist sites at Grand Cayman (Corcoran 2006). Stingrays are also accustomed to the supply of artificial food; a comparison in serum fatty acid profiles between stingrays from tourist and non-tourist sites show marked differences, suggesting squid to be the major food item in the diet (Semeniuk et al. 2007). Additionally, SCS now represents not only a foraging patch but also a mating site, as stingrays can be observed mating (Chapman et al. 2003), and are presumed to copulate year-round, since females in obvious states of gravidity (stingrays are live-bearers) can be readily observed throughout the year (M. Corcoran pers. comm.). As a result, SCS has now become a permanent habitat for a large population of rays. Despite the purported benefits of stingray group-living at SCS, such as reduced energy expenditure in searching, capturing and handling prey, and possibly increased reproductive effort, potential costs of grouping have not been examined in this normally solitary forager.

The grouping costs examined in the present study focus on the possible negative impacts incurred by grouping: (1) in a novel environment, i.e. in the presence of tourists, and (2) around a newly occurring food source. Specifically, we set out to test the hypotheses that, in comparison to solitary stingrays from non-tourist sites, group-living stingrays at the tourist site would have increased incidence of injuries (from boats and predators), higher parasite loads (due to increased transmission rates), and a greater number of conspecific bite marks (CBMs, due to increased interference competition between individuals over the centralized food sources). While speculated, no study has systematically measured the suggested costs of altered behaviours of the targeted species from marine-provisioning tourism. We conclude with speculations as to whether the costs imposed by the tourism attraction can be of any consequence to the long-term physiological fitness of the stingray population, and discuss our findings in the light of wildlife management.

MATERIALS AND METHODS

Study species and study site

The southern stingray *Dasyatis americana* is a long-living (ca. 26 yr; Henningsen 2002), common inshore ray frequenting tropical and subtropical shallow bays of the southern Atlantic Ocean, Caribbean and the Gulf of Mexico. It is a continuous forager, feeding opportunistically on a varied diet of crustaceans and teleosts, and, to a lesser extent, on molluscs and annelids

(Gilliam & Sullivan 1993). Although southern stingrays inhabit all shallow bays around the Cayman Islands, it is only in the vicinity of SCS that these rays can be found year-round in a dense aggregation of individuals of both sexes. This amassment results from the unregulated quantity of provisioned squid (*Illex* and *Loligo* spp.), a non-natural diet item shipped in from the North Atlantic and North Pacific (C.A.D. Semeniuk pers. obs., Gina Ebanks-Petrie, Director, Cayman Islands Department of Environment pers. comm.). The feeding routine (daily, except during the summer months when weekends are excluded) lasts from early morning until mid-afternoon as tour boats continuously deliver tourists (mainly cruise line passengers) for an average 45 min visit to SCS. The food provided is abundant, but delivered at discrete focal points (multiple floating buckets supplied by each tour boat). In general, benthic stingrays forage solitarily; they congregate during the breeding season, and occasionally aggregate when resting or when space is limited (Tricas et al. 1997). As a result of the tourist-feeding regime, the stingrays from tourist sites have become diurnal (in contrast to their non-tourist counterparts around the island), and have reduced their activity space to the shallow waters immediately surrounding the feeding area (Corcoran 2006). A total of 172 individuals from the tourist site have been tagged since 2002. The rays have a mean yearly recapture rate of 92.5% (0.03 SD; C.A.D. Semeniuk unpubl. data), and tracking studies over 2 yr show restricted movements to the tourist site (Corcoran 2006), indicating a very strong temporal and spatial fidelity to the feeding site.

Data collection

Immature and adult stingrays were captured at SCS and from 3 control, non-tourist sites on the southern (opposite) side of Grand Cayman. Stingrays from the non-tourist sites do not interact with the tourists at SCS (from acoustic-telemetry tracking data; Corcoran 2006). Stingrays from tourist sites are accustomed to human presence and easily captured by simply holding them against one's chest when they approach for food. Once caught, a ray was placed in a landing net (1 m diameter) and transferred into a seawater-filled canvas pool (4 m²) aboard a 24 ft long, 225 hp dusky boat. Control rays from non-tourist sites were located visually from a 14 ft long, 45 hp double hull boat, and then encircled in a hand-drawn seine net (30 ft long), guided into a landing net, and transferred aboard into the holding pool. Once transferred, binder clips were placed over the barb on the ray's tail for protection, and, in an average of 15 min, the ray was identified or tagged (with a passive integrated transponder, PIT), weighed, its disc width measured, injuries recorded, and dermal parasites counted in the spiracles (ventilatory organs located behind the eyes that pump oxygenated water over the gills). Upon completion of the examination, stingrays were placed back into the landing net, had the tail clip removed, and were gently returned to the water. When released, fed stingrays usually resumed feeding at once, while non-fed rays swam away from the immediate area.

Data used in the present study are from 2 sampling periods: May to July 2004, and October to November 2005. Because this study is part of larger research program investigating the general, physiological and immunological impacts of stingray provisioning tourism, different indicators were analysed from different sampling occasions. Analyses of injuries and dermal parasites originate from the 2005 dataset as this represents the most complete dataset; CBMs are from the 2004 dataset, and body condition indices are presented for both years. Due to strong site fidelity, stingray longevity and consistent environmental conditions, we do not expect significant yearly differences within tourist and non-tourist groups. With the exception of CBM data, all other data are presented for females only, as just 18% of the 172 tagged rays at the tourist site are males. Moreover, as the tourist attraction is currently undergoing ecological (and social) management directives, we focused our research on females, as animals of this sex will be the major recipients of any management actions. Hence, for monitoring purposes, targeting females is the most efficient choice. Males are incorporated into the analysis of CBMs solely to test the alternative hypothesis that increased bite mark incidence and number are attributable to increased mating attempts, not interference competition.

Analysis

A size-distribution comparison between rays from tourist and non-tourist sites was made by fitting an analysis of covariance to log-transformed weight versus length data with location (tourist site and non-tourist sites, pooled) as a factor variable for 2004 and 2005. The size data were then pooled between the sites within each year, and residuals were calculated to estimate body condition. A non-parametric *t*-test (as our assumption of homogeneity of variances was violated) was next conducted to determine whether stingray body condition differed significantly between tourist and non-tourist sites for the two different years.

The effect of location on the probability of captured stingrays having a boat-, predator-, or conspecific-inflicted injury, ectodermal parasites in their spiracles, or a conspecific bite mark was analyzed separately with General Linear Model (GLM) nominal logistic fit regression. Analyses were executed in JMP IN 6.0 (SAS Institute Inc. 2005), treating presence and absence of wounds and parasites as a binary dependent variable, and location as a dummy independent variable. Also included in the model as continuous independent variables were: disc width (cm, log transformed) to control for the effect of stingray size, and body-size metrics (taken as residuals of stingray length-weight regression for all sites combined) to control for stingray body condition.

To test for differences in the mean number of injuries and parasites when present (i.e., stingrays exhibiting no injuries or parasites were excluded) between tourist and non-tourist sites, these dependent variables were first transformed to satisfy the assumptions of normality and equality of variance, and then analyzed in a least-squares multiple regression using location as a dummy independent variable, and disc width (cm, log transformed) and body-size metrics as continuous independent variables.

As stingrays at the tourist site are larger, on average, than those sampled from non-tourist sites (Table 1), we tested the alternative hypothesis using Chi-squared contingency tests that injury frequency is a function of age (using size as a surrogate), and not a result of the impacts of tourism. Therefore, larger (i.e., older) animals should have proportionally more injuries than smaller animals, at both tourist and non-tourist sites. Injury type was also explored and compared between tourist and non-tourist sites, with injuries separated into three categories: injuries that affect predator-detection/ defense (e.g., missing, damaged or broken sections of the tail and barb), injuries that can cause infection (e.g., abrasions, fresh wounds, severe CBMs, boat-propeller cuts, abnormal growths), and injuries that can affect motility (e.g. excisions out of the pectoral fins, missing fins, old, calcified scars, reset skeletal-cartilage breaks). The proportions of these injury types were compared with Chi-square tests between tourist and non-tourist locations.

Conspecific-bite-mark counts were compared between tourist and non-tourist groups controlled for size (cm, log disc width) and sex using a GLM with a log-link Poisson distribution. Effects of sex were then explored independently, to determine whether bite marks were indicative of increased mating effort or of interference competition. Specifically, CBM counts were compared between immature (<47 cm disc width; Guy Harvey Research Institute unpublished data) and mature males at both the tourist and non-tourist groups separately; and differences in the number of CBMs were compared among females of three size categories, ≤ 65 cm dw, 66–90 cm dw, and ≥ 91 cm dw, and between tourist and on-tourist sites, by using the contrast option of the GLM procedure of JMP software.

RESULTS

Size distribution, body condition

Female stingrays were larger, both in terms of disc width and weight, at the tourist site than females sampled from the non-tourist sites for both the 2004 and 2005 years ($\text{median}_{\text{tourist}} = 99\text{--}100$ cm, 32–33 kg; $\text{median}_{\text{non-tourist}} = 76.5\text{--}78$ cm, 14.5–15 kg; Table 1). However, despite the larger size, growth trajectories (i.e., log-transformed disc width and weight relationship) were not significantly different between the two locations (ANCOVA, 2004: $F_{2, 127} = 2.74$, $p_{\text{location}} = 0.28$; 2005: $F_{2, 96} = 1.92$, $p_{\text{location}} = 0.12$), signifying tourist-fed rays are not significantly

heavier for a given size. Body condition, measured as residuals of the logarithmic relationship between disc width and weight for the tourist and non-tourist sites combined, did not differ significantly between sites in the 2004 season ($\bar{x}_{\text{non-tourist}} = -0.026 \pm 0.64 \text{ SE}$, $\bar{x}_{\text{tourist}} = -0.840 \pm 0.54 \text{ SE}$; Mann-Whitney $U = 0.72$, $p = 0.47$, Effect Size = 0.17; Power = 0.16). The effect was, however, in the opposite expected direction. In 2005, body condition, in this instance, was significantly lower at the tourist site ($\bar{x}_{\text{non-tourist}} = 0.92 \pm 0.76 \text{ SE}$, $\bar{x}_{\text{tourist}} = -1.11 \pm 0.79 \text{ SE}$; Mann-Whitney $U = -2.15$, $p = 0.03$), again in the opposite direction of what was expected.

The logistic models showed no significant effect of body condition on the incidence of wounding or CBMs, but did have an effect on the likelihood of being host to ectoparasites (non-tourist site only).

Injury Frequency, Type

The probability of a stingray being injured increased with increasing disc width, and was much higher for tourist-stingrays than for non-tourist-stingrays ($\chi^2_{\text{Model}} = 36.32$, $p < 0.001$; $\chi^2_{\text{disc width}} = 4.78$, $p = 0.026$, $\beta = -2.23$; $\chi^2_{\text{location}} = 19.42$, $p < 0.001$, $\beta = 1.11$). Thirty percent ($n = 50$) of stingrays from the non-tourist sites were injured versus 85% ($n=46$) of tourist stingrays (Fig. 1). This pattern was not the result of stingrays at the tourist site being larger on average, since, when

categorized by size (i.e., ≤ 65 cm disc width (dw), 66–100 cm dw, and ≥ 101 cm dw), the proportion of stingrays injured at the tourist site was equally distributed across the three size categories (60%, 85%, 86%, respectively; $\chi^2 = 3.00$, $p = 0.22$). In the non-tourist sites, proportion injured increased (as expected) with size (17%, 30%, 60%, respectively; $\chi^2 = 13.35$, $p = 0.001$).

The average number of injuries per stingray (square-root transformed) was positively influenced by stingray size and by location, with tourist rays having significantly more injuries ($R^2_{\text{adj}} = 0.28$, $t_{\text{disc width}} = 2.21$, $p = 0.032$, $t_{\text{location}} = -3.26$, $p = 0.002$, Effect Size = 0.9; Least squares back-transformed means: 3.6 ± 0.1 (S.E.) injuries/tourist stingray and 1.9 ± 0.17 injuries/non-tourist stingray; Table 1). With regards to injury type, predator detection-defense injuries were common to both tourist- and non-tourist rays (Table 2), whereas one half of the infection-susceptibility and motility impairment injuries were unique to tourist rays (Fig. 2). Only the fish-hook injury was unique to non-tourist rays. With respect to the proportion of injury types, 33% of the injuries at the tourist site were predator-detection/defense injuries; 47% were susceptible-to-infection wounds, and 20% were motility-impairment injuries. These percentages are in significant contrast to the injuries recorded at the non-tourist sites, whose distribution of injuries was as follows: 41% of were predator-detection injuries, 18% were susceptible-to-infection wounds, and 41% were motility impairment injuries ($\chi^2 = 36.67$, $p = 0.001$).

In specific, the predominant injury to non-tourist stingrays was a shortened tail, which we assume to be the result of a predator attack (Dahlberg, 1970). As for predator scars or injuries at SCS, missing and damaged tails could not necessarily be attributed to predation attempts since propellers can also be the cause of these injuries. However, with regards to obvious predator bite wounds and scars (i.e., teeth marks and/or notches out of the tail-fold; Fig. 2e-f), tourist rays had more than twice the number of predator wounds (13 rays out of 46) than non-tourist rays (6 /50 rays).

Parasite Loads

The likelihood of a stingray being host to a dermal/gill isopod parasite was significantly affected by stingray size, body condition, and location ($\chi^2_{\text{Model}} = 36.60$, $p < 0.001$). Larger stingrays, stingrays with larger body size residuals, and stingrays at the tourist site were more likely to have parasites located in their spiracles ($\chi^2_{\text{disc width}} = 27.33$, $p = 0.001$, $\beta = -10.85$; $\chi^2_{\text{body condition}} = 6.94$, $p = 0.008$, $\beta = -0.43$; $\chi^2_{\text{location}} = 4.47$, $p = 0.035$, $\beta = 1.63$, respectively). When exploring the effect of body condition in more detail, it was found that this variable was significant for non-tourist stingrays only ($\chi^2_{\text{Model}} = 3.95$, $p = 0.04$, $\beta_{\text{non-tourist}} = -0.19$). All but one stingray from the tourist site had spiracle parasites (a 37 cm dw female; $n = 45$), and 8 of the 50 rays sampled from the non-tourist sites were spiracle-parasite free (Fig. 1).

Excluding rays with no spiracle parasites, the average number of parasites per ray (square-root transformed) was significantly higher at the tourist site, with the significant effect of disc width included in the model ($R^2_{adj} = 0.37$, $t_{disc\ width} = 5.31$, $p = 0.001$, $t_{location} = -2.20$ $p = 0.031$, Effect Size = 0.5; Least squares back-transformed means: 9.1 ± 1.7 (S.E.) parasites/tourist stingray and 6.7 ± 1.7 parasites/non-tourist stingray; Table 1). There was no effect of body condition.

Conspecific Bite Marks

With both sexes included in the model, large stingrays and stingrays from the tourist site had a higher likelihood of being bitten by conspecifics ($\chi^2_{Model} = 145.83$, $p < 0.001$; $\chi^2_{disc\ width} = 39.16$, $p = 0.001$, $\beta = -6.18$; $\chi^2_{location} = 22.77$, $p < 0.001$, $\beta = 6.62$). Although sex was not a significant predictor, this was most likely due to the fact that the majority of small rays were also males. With respect to the number of bite marks per individual, all of the rays sampled at the tourist site had at least one CBM ($n = 90$). At the non-tourist sites, only 48% of the rays exhibited CBMs ($n_{total} = 79$; and 68% of females, $n_{females} = 53$). Count data of CBMs were analyzed separately for the sexes. No statistical analysis was performed on males from the non-tourist site due to the low incidence of bite marks in general. Of the nineteen immature males sampled at the non-tourist sites (34 cm - 44 cm dw), one had a single CBM (39 cm dw). Four mature males were caught (48 cm – 54 cm dw), and one individual only (48 cm dw) had a

single CBM (Table 1). Of the males at the tourist site ($n = 14$), 3 were immature and ranged from 39 cm to 47 cm dw. Mature males ranged from 49 cm – 68 cm dw. All males had bite marks. There was no significant effect of disc width or maturity stage on the number of CBMs per individual males (Poisson GLM: $\chi^2_{\text{Model}} = 10.4$, $p = 0.005$; $\beta_{\text{disc width}} = 1.09$, $\chi^2 = 2.35$, $p = 0.12$; $\beta_{\text{immature/mature}} = -0.16$, $\chi^2 = 0.10$, $p = 0.75$). The median number of bite marks for immature males was 7; for mature males, 14 (Table 1).

Females stingrays were divided into size categories: ≤ 65 cm dw, 66–90 cm dw, and ≥ 91 cm dw. and CBM count data were compared between tourist and non-tourist sites (with females with no CBMs excluded from analysis). In addition to the significant location and size–category effects (Poisson GLM: $\chi^2_{\text{Model}} = 111.6$, $p = 0.005$; $\chi^2_{\text{location}} = 23.38$, $p < 0.001$; $\chi^2_{\text{size category}} = 28.39$, $p < 0.001$), there was also a significant interaction effect between these two variables ($\chi^2_{\text{location} \times \text{size category}} = 13.67$, $p = 0.001$). The size-category effect was consequently explored separately for each location using contrast analysis. Specifically, amongst non-tourist females, the number of CBMs in the 66–90 cm dw category ($n = 24$) was significantly higher than in the ≤ 65 cm dw ($n = 6$; $\beta = 1.21$, $\chi^2 = 5.13$, $p = 0.02$; Median CBMs: 5 vs. 0, Table 1). Females ≥ 91 cm dw ($n = 8$) had significantly more CBMs than females in the midsize category ($\beta = 1.08$, $\chi^2 = 27.86$, $p < 0.001$; Median CBMs: 15 vs. 5). This pattern was dissimilar amongst the tourist rays in that, while midsize category females ($n = 15$) had more CBMs than the smallest size category ($n = 6$; $\beta = 1.01$, $\chi^2 = 10.27$, $p =$

0.001; Median CBMs: 22 vs. 6), the largest sized females ($n = 54$) did not have significantly more CBMs than females ranging between 66-90 cm dw ($\beta = -0.02$, $\chi^2 = 0.04$, $p = 0.84$;). They had, in fact, slightly fewer median bite marks (21 vs. 22, respectively, Table 1).

DISCUSSION

This paper set out to explore whether the change in stingray *Dasyatis americana* behaviour, namely the permanently aggregative attraction to tourist-induced stimuli (i.e. provisioning of food), imposed detectable costs. We found that in comparison to stingrays from non-tourist sites about Grand Cayman, tourist stingrays are more likely to be in lower body condition, injured, susceptible to ectodermal parasites, and engaged in intense interference competition. Tourist-rays also have significantly higher mean numbers of injuries and parasites and median CBMs. Studying fitness repercussions of altered behaviours attributable to the effects of marine provisioning-tourism is complicated owing to the inaccessibility of the marine environment, the longevity of the species in which effects may be manifested only long-term (e.g. dolphin provisioning at Moreton Island, Australia; Neil & Brieze 1998), the indirect interaction effects on non-target species (e.g. increased predation frequency on damselfish nests by target-fed labrid species; Milazzo et al. 2006), and the seasonality of the tourism attraction, in which changes in behaviours are

consequently temporary (e.g. white shark provisioning in South Africa; Laroche et al. 2007). With the provisioning of stingrays at SCS, the effects of novel grouping behaviours can be readily investigated because the shallow-water habitat is readily accessible; the attraction has been in operation for approximately 20 yr; and these long-lived stingrays exhibit strong site fidelity owing to the year-round activities at the site.

Injury frequency, type

The positive response of stingrays to the presence of tourists engenders a large injury cost. The majority of rays at the tourist site were injured, and those injured had almost twice as many injuries as those from non-tourist sites, even after controlling for size. These results are not due to the animals being older at SCS and hence accumulating wounds with age. The proportion of injured rays is not significantly different between the 3 size categories at SCS; however, the proportion injured at the non-tourist sites does increase with size. These results suggest that SCS represents a riskier environment for the rays in terms of injury hazards compared with wild habitats.

Boat collisions are generally the dominant form of injuries to animals that are the focus of marine-based tourism attractions (e.g. manatees, dolphins, whales; Aipanjiguly et al. 2003, Bejder & Samuels 2003, Lusseau 2005). The

majority of injuries incurred at SCS, regardless of injury type, are indeed caused by boat propellers, anchor chains, or anchors that have resulted in a myriad of boat-related injuries (Table 2, Fig. 2b–d). As for obvious predator scars or injuries at SCS (Fig. 2e,f), if we assume that predator-injury frequencies reflect capture rates rather than rates of survival following capture, the tourist site also represents a higher predation risk to stingrays than do the non-tourist environments sampled (as stingrays from tourist sites had more than twice the number of predator wounds). This is discussed in more detail below.

Parasite loads

Another cost of grouping is increased parasite transmission due to the facilitation of transfer between animals that are in closer contact, such as in groups, compared to single individuals. The type of parasites in stingrays' spiracles are mobile flabelliferan isopods of the family *Aegidae*. These parasites seek their hosts actively by swimming in the water column until they can settle on the animal to feed. Aegid isopods feed on whole blood, and can be found in sharks and rays on the skin, buccal and branchial chambers, and gills.

At SCS, all but 1 ray was host to a spiracle parasite, and had, on average, one-third more parasites than rays from non-tourist sites after controlling for body size. Isopods are considered to be an emerging problematic taxon, especially in

aquarium-confined elasmobranchs, due to their health impacts on the host. For instance, isopods are known to cause gill and skin lesions and blood loss. Heavy infections may cause osmotic imbalance, deleterious metabolic demands, and may open lesions facilitating invasion by opportunistic pathogens (Benz & Bullard 2004). Parasite counts at the tourist site were as high as 32 parasites per ray, and were confined to the spiracles. It is therefore possible that because of the high density of rays and the strong temporal and spatial fidelity to the tourist site, stingrays may have altered distribution and density loads of aegid or other parasite families located directly on their gills or in other body locations (e.g. trematodes) that were inaccessible to our non-invasive sampling methods. It would be worthwhile, therefore, to determine if any physiological changes have occurred in the ability to respond to the intense prevalence of ecto-parasites in stingrays at SCS.

Conspecific bite marks

When animals incidentally group in the course of acquiring resources such as food or mates, interference competition over the resource can result, especially if it is concentrated either temporally or spatially (Case & Gilpin 1974). Every ray sampled at the tourist site showed evidence of CBMs. The most likely explanation for this high incidence can be attributed to aggressive interference competition over the centrally provisioned food sources. Exploitative competition

cannot explain the occurrence of CBMs, as this would occur if the resource was limited (which it is not). However, 2 alternative hypotheses can be used to explain the high incidence of bites: increased mating effort and indiscriminate biting over the food resource. With regards to the first hypothesis, male stingrays bite the edges of the female's fins to secure a hold when attempting internal fertilization, thereby producing scrapes, abrasions, or wounds in the process (Kajirura et al. 2000). Large males can also exhibit bite marks from mistaken identity or competition over females. Females become reproductively mature at approximately 75 cm disc width (Henningson 2000), a larger size than males at maturity (47 cm). We would not expect immature males or small females to possess any bite marks (akin to the stingrays from the non-tourist sites), even through accidental or competitive mating attempts, since they are too small to be reproductively fertile. Nevertheless, our results indicate that these smaller rays still show a high frequency of bite marks. Moreover, we would not expect the largest females to have the same number of bite marks than mid-sized females (unlike the stingrays from non-tourist sites, in which the largest rays have 3 times as many CBMs). Since fecundity increases with size (Henningson 2000), larger females should be preferred. Also, as mature females are not a limiting resource to mature males (they outnumber males 7:1; (from unpublished tagging data from 2002 to 2005), smaller females should not be experiencing the same intensity of male courtship. Again, our results do not support these expected outcomes.

The second hypothesis concerns stingrays mistakenly biting conspecifics in the scramble competition over the food resource. The mouth of a stingray is ventrally positioned, and, since a ray locates its food through electroreception, it can indiscriminately bite any ray passing underneath. This occurrence may also explain the multitude of bite marks on the rays. However, we would therefore expect to see the largest animals having the highest number of bites, as, due to their sheer size and number (they outnumber mid-sized females 2.5:1), they would be most likely to 'get in the way'; we did not find this. An alternative explanation is that of increased aggression and dominance. Because the food provisioning is done from a concentrated source, namely from around one of the many floating buckets in the water, an individual positioning itself as close to the source as possible would ensure a high probability of food capture. Large females have been observed to display pushy behaviour, ramming themselves into tourists holding food, and actively biting and pursuing other stingrays nearby. This size-dependent, dominant-aggressive behaviour of large females has also been noted at the other stingray-feeding tourist attraction in Western Australia (Newsome et al. 2004): females at Hamelin Bay were observed shoving other rays (as well as tourists) with their snouts, and aggressively chasing smaller males away from the feeding site. Being more dominant than smaller females and males, larger females at SCS should therefore be most active in biting subordinates in the water, and therefore not necessarily exhibit the most number of bite marks themselves.

As the majority of fresh wounds recorded on rays from the 2005 season stemmed from CBMs, the aggression and competition between stingrays at the tourist site may have health implications. Open wounds can be sources of pathogen entry, or tax the ray's allostatic abilities (the cumulative result of physiological allocation in relation to environmental stimuli) with resultant effects on long-term health (McNamara & Buchanan 2005). In addition, high levels of activity associated with aggressive interference competition for food can lead to greater energy expenditure, elevated metabolic rates, decreased food utilization efficiency and impaired immune function, as have been shown in aquaculture fish (reviewed in Ashley 2007). These potential physiological outcomes require further investigation.

Benefits of grouping

As mentioned previously, the decision of animals to join or remain in a group depends on a balance of the associated costs and benefits. The resource dispersion hypothesis (RDH) (Macdonald 1983) proposes a mechanism for the passive formation of social groups where resources are dispersed, even in the absence of any benefits of group-living per se (Johnson et al. 2001). An alternative explanation to group-living is that, should costs be substantial, animals may still choose to live in groups since the benefits accrued are still relatively greater. Lastly, and particularly relevant to anthropogenically altered

habitats, animals may aggregate due to perceived and immediate benefits, but may unknowingly incur relatively greater costs in the, longer term. This last phenomenon is known as an ecological trap (Schlaepfer et al. 2002). According to the RDH, rays at SCS may be forming groups because, whilst there may be no intrinsic benefits, the costs of doing so are trivial. We believe, however, that the general costs in this tourist system are not insignificant, in particular, the risk level of the habitat with regard to injury hazards. However, associating a risk with an area can lead to its avoidance (Whittaker & Knight 1998). Despite this risk, SCS stingrays are continuing to form dense aggregations. As such, these rays may be accruing possible advantages. The 2 most beneficial outcomes of group-living are typically increased vigilance and numeric dilution. Both factors can reduce the chances that individual group members will suffer fitness losses due to predation (Krause & Ruxton 2002).

With regards to vigilance, stingrays primarily rely on vision to detect approaching predators, namely sharks (Semeniuk & Dill 2005). While feeding at SCS, stingrays are engaged in intense interference competition, an unnatural behaviour, and may consequently be less vigilant of predators and more vigilant of conspecifics (Cresswell 1997). Stingrays can also detect predators via the mechanoreceptors along the length of their body and tail (which senses differential changes in water pressure; Maruska & Tricas 1998). At SCS, however, 65% of rays sampled at the tourist site had predator-detection/defence injuries (i.e. shortened, damaged tails, Fig. 2a), suggesting that their secondary

means of vigilance is also impaired. As tails can be considered expendable body parts to predators, shortened tails can furthermore increase a ray's vulnerability (Semeniuk & Dill 2006); 10% of the injured tails were shortened above the positioning of the barb, which additionally impedes defence. Furthermore, 40% of sampled rays had motility-impairment injuries, which could affect the speed at which a ray can flee from a predator. Finally, increased group size has been demonstrated to hinder the escape ability and speed of an individual ray (Semeniuk & Dill 2005). We also believe that stingrays may not be benefiting from the dilution effect. Large groups can be more conspicuous and may therefore attract more predators (Krause & Godwin 1995). Because the stingray relies on crypsis (by burying itself in the sand) as its main predator-avoidance strategy from visually searching predators during the day, the forming of large milling groups around the food source may attract predators at a higher frequency rate, thus reducing the net benefits incurred through dilution. The higher incidence of predator bite marks would therefore lend credence to this supposition. Tourists themselves do not act as deterrents to predators, as sharks are visibly apparent at SCS, and efforts to cull them from the immediate vicinity take place whenever they are detected (Tim Austin, Assistant Director, Cayman Islands Department of Environment, pers. comm.).

Another possible benefit to rays at the tourist site, indirectly related to group-living, could be the increased time allocated to activities other than foraging efficiency. Because tourist food can be obtained at little or no energy

cost, alternative allocated activities can be either rest, growth, or reproduction. Extra resting time may be beneficial for stingrays from tourist sites so that they can invest energy into allostatic maintenance, and resistance to and repair of parasitic impacts and injuries. However, a recent acoustic-telemetry tracking study of Cayman Island stingrays demonstrated that, although they had a much smaller activity space, stingrays from tourist sites did not have significantly lower rates of movement (km h^{-1}) than those from non-tourist sites (Corcoran 2006). These findings suggest that, despite having a readily available, centralized food source, stingrays are still as active as they would be under natural conditions and are therefore not accruing the advantages of additional resting time. Alternatively, stingrays can be capitalizing on the surplus resource and allocating it to faster growth rates and/or reproduction. This may certainly explain why stingrays are larger at the tourist site, but would not explain why the rays would then have lower body condition. In addition, since larger females have larger litter sizes (Henningsen 2000), females may also be trading off the costs of grouping with higher fecundity (although we would have then expected residuals of the length–weight relationship for tourist rays to be positive, not negative, if this were the case; Table 1). We believe the poorer body condition of stingrays from tourist sites is indicative of the cumulative, long-term effects of provisioning tourism. At this time, the potential positive impacts of provisioning tourism cannot be supported without further examination.

CONCLUSION

Many studies that have investigated the impacts of humans on the behaviour of wildlife have established that species respond to people as if they were predators. In the present study, we show that, while some tourism activities can instead be considered a positive stimulus and thus attract animals, costs still do occur. Suggested costs of grouping, used to explain present-day occurrence of solitary living in animal systems, are equally applicable to and empirically evidenced in this study of a population that has traditionally been solitary and has transitioned only recently to group-living. Because these costs are being experienced continuously, fitness consequences can result. Animals under chronic stress should allocate resources so as to minimize the risk from the current threats, while not compromising long-term survival by incurring too much damage (i.e. reduced physiological reserves of essential nutrients, increased levels of oxidative stress, or reduced body condition) to individual physiological state (McNamara & Buchanan 2005). If stingrays at the tourist site are not allocating the surplus of food resources to increased rest (and hence addressing the costs of increased injuries, parasites and aggression) and because of the unnatural balance of essential fatty acid ratios from their diet (Semeniuk et al. 2007) that is important for disease resistance, stress-management and gamete quality, it is possible that the tourist rays may be experiencing negative physiological and immunological impacts that can affect long-term fitness. Consequently, we are currently examining these physiological impacts (authors' unpubl. data). Indeed, should there be no investment of energy into somatic

and/or reproductive growth, or, equally, should the following generations of stingrays born from SCS rays seek out the tourist site themselves, then the distinct possibility exists that SCS will represent an ecological trap for southern stingrays, more so than simply a risky habitat. From a management perspective, long-term monitoring and management of the tourist site is therefore required.

Education and awareness of the risks posed to stingrays are other key tactics in mitigating the negative impacts of tourism. Furthermore, measures should be taken to alleviate crowding conditions at SCS by limiting the number of people and boats, or by expanding the site into nearby areas to accommodate the current level. Less food provisioned to the rays would also alleviate interference competition, and ensure that the rays resume foraging naturally and solitarily, further away from the tourist site. Additionally, safety devices on boat propellers, such as cages and guards, can also aid in reducing injuries.

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Table 4.1 Variable medians and means.

Variables	Tourist Site	Non-Tourist Sites (pooled)
2004 median disc width (cm) and weight (kg)*	99, 32 (n = 74)	78, 14.5 (n = 53)
2005 median disc width (cm) and weight (kg)*	100, 33 (n = 46)	76.5, 15 (n=50)
2004 mean \pm S.E. body condition (length-weight residuals)	-0.84 \pm 0.55 (n = 74)	-0.02 \pm 0.65 (n = 53)
2005 mean \pm S.E. body condition (length-weight residuals)*	-1.11 \pm 0.79 (n = 46)	0.92 \pm 0.76 (n = 50)
Least-squared mean number of injuries (back-transformed) \pm S.E.*	3.6 \pm 0.10 (n = 39)	1.9 \pm 0.17 (n = 15)
Least-squared mean number of spiracle parasites (back-transformed) \pm S.E.*	9.1 \pm 1.7 (n = 44)	6.7 \pm 1.7 (n = 42)
Median number of conspecific bite marks*		
• immature male	• 7 (n = 3)	• 0 (n = 19)
• mature male	• 14 (n = 11)	• 0 (n = 4)
• \leq 65 cm dw female	• 6 (n = 6)	• 0 (n = 6)
• 66 – 90 cm dw female	• 22 (n = 15)	• 5 (n = 24)
• \geq 91 cm dw female	• 21 (n = 54)	• 15 (n = 8)

* significant difference between tourist and non-tourist sites

Table 4.2 List of injuries recorded and their category type.

Injury Type		
Predator Detection/Defense	Susceptible-to- Infection	Motility-Impairment
Missing tail	Propeller cut*	Excisions in fin
Missing barb	Fresh wound/abrasion	Large clefts in fin*
Damage to tail (broken)	Abnormal body growths*	Missing fin*
Notches out of tail fold	Knife wound*	Old, calcified scar
	Fish hook in gut**	Breaks in fin rays/cartilage*

*denotes injuries recorded from tourist-stingrays only

** denotes injuries recorded from non-tourist-stingrays only

Figure 4.1 Proportion of female stingrays injured, parasitized and bitten by conspecifics in relation to tourist and non-tourist sites. Numbers above bars indicate percentages. Numbers in parentheses refer to sample sizes.

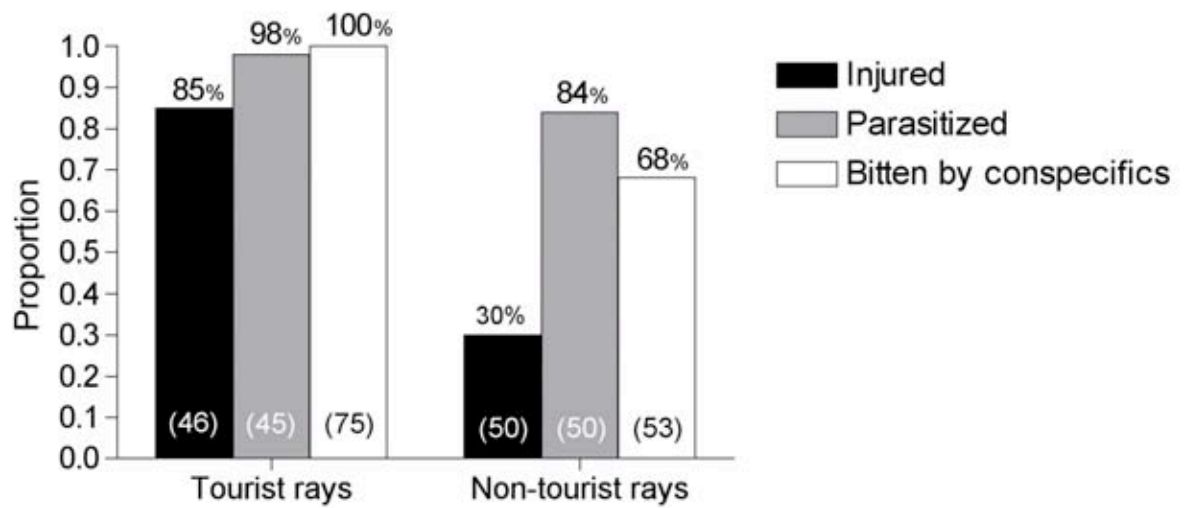
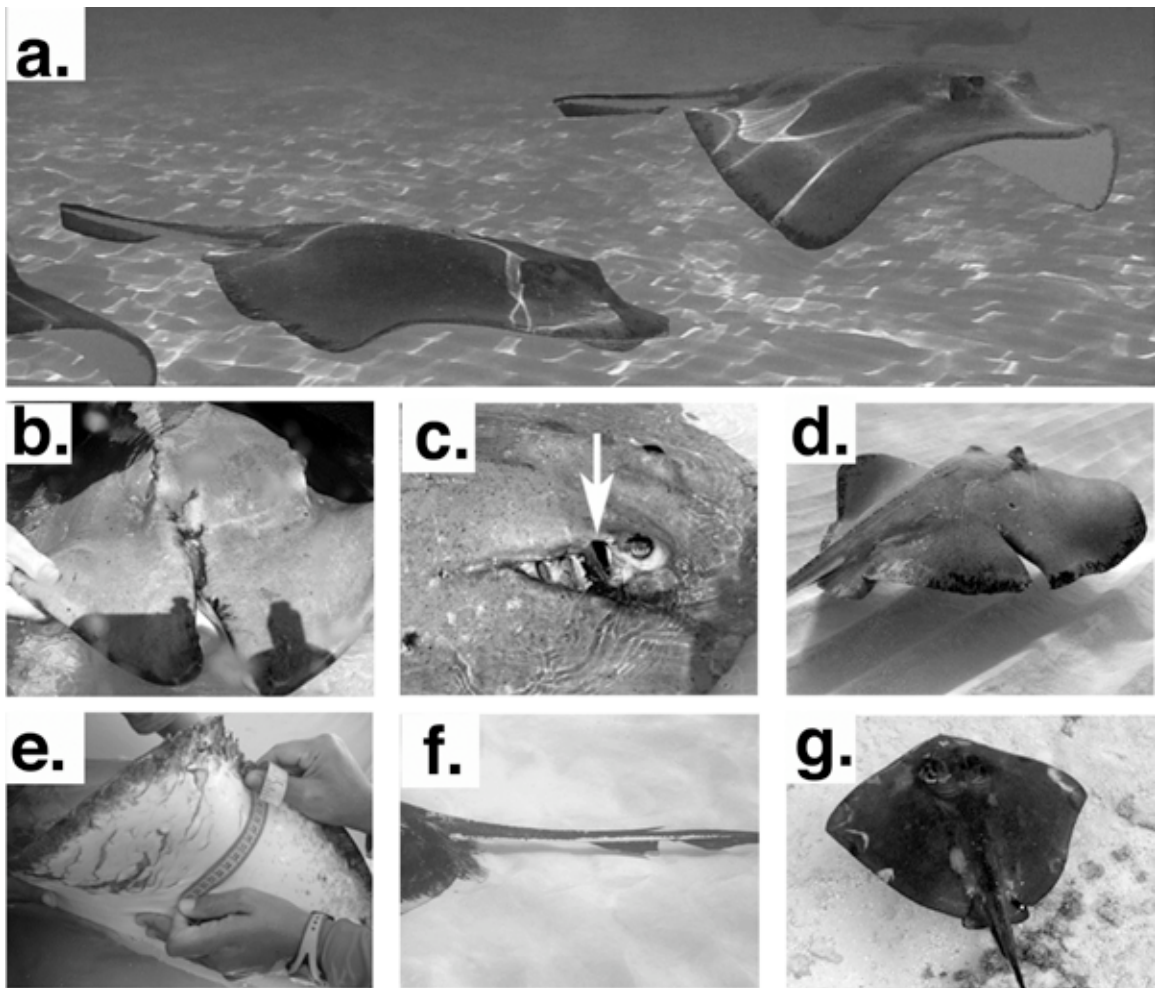


Figure 4.2 Types of injuries recorded at the tourist site: (a) predator-detection injury (missing tail); (b) susceptible-to-infection wound (propeller caused, now sustained by swimming into anchor ropes); (c) susceptible-to-infection wound (propeller caused, note exposed gills; arrow indicates spiracle opening); (d) motility-impairment injury (propeller caused); (e) predator bite mark, fresh; (f) predator bite mark (notch out of tail fold); and (g) conspecific bite marks (arrow indicates fresh bite wound). Photographs (a) to (d), (f) and (g) courtesy of Matthew Potenski; photograph (e) courtesy of Ben Bondzio.



CHAPTER 5: HEMATOLOGICAL DIFFERENCES BETWEEN STINGRAYS AT TOURIST AND NON-VISITED SITES SUGGEST PHYSIOLOGICAL COSTS OF WILDLIFE TOURISM

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Abstract

Wildlife tourism alters the environmental conditions in which the focal animal lives, and it is therefore necessary to assess the ability of the animal to adjust to and persist in these novel conditions if the industry is to be sustainable. Here, we report on the physiological responses of southern stingrays (*Dasyatis americana*) which are the focus of intense marine provisioning-tourism in the Cayman Islands. Using stingrays from non-tourist sites about Grand Cayman as a basis for comparison, we show in this natural experiment that tourist-exposed stingrays exhibit hematological changes indicative of physiological costs of wildlife tourism. The novel conditions with which the stingrays must interact include non-natural food, higher injury rates (from boats, conspecifics and predators), and higher parasite loads (from crowding conditions). As a result of this year-round environment, stingrays display sub-optimal health: lower hematocrit, total serum protein concentrations, and oxidative stress (i.e., lower total antioxidant capacity combined with higher total oxidative status). Moreover, they show evidence of attenuation of the defense system: for tourist rays only, animals possessing both injuries and high parasite loads also exhibit lowest leukocrit, serum proteins and antioxidant potential, as well as differing proportions of differential leukocytes indicative of suppression (lymphocytes and heterophils) and down-regulation (eosinophils), thus suggesting that the physiological changes of tourist rays are in partial response to these stressors. Together, and situated within ecological context, the physiological measures indicate that the long-term health and survival of tourist stingrays, a long-lived marine species, have a significant

probability of being affected. Consequently, management of the tourism attraction is essential. The indicators chosen in this study reflect general health indices and defense capabilities used across taxa, and represent a tradeoff between ease of collection/analysis and interpretation so that managers can continue the research for monitoring purposes.

1. Introduction

Animals which are the focus of nature-based tourism are exposed to changes in their environment that may influence their survival and reproduction. Their response to these changes depends on whether they perceive humans and their associated activities as a disturbance, predatory threat (Frid and Dill, 2002), refuge, or new food source. Responses within the range of the animal's normal behavioural and physiological repertoire may pose minimal costs (e.g., brown bear, *Ursus arctos*, wildlife viewing; Rode et al., 2006), and in some cases animals can alter their life-history traits to take advantage of the novel conditions created by tourists (Alaskan grizzly bear, *Ursus arctos*, wildlife viewing; Nevin & Gilbert, 2005). If, however, the new environment causes animals to shift their energetic balance at the cost of maintaining homeostasis, there may be negative impacts on the animal's reproductive effort, survival, and health (e.g., yellow-eyed penguin, *Megadyptes antipodes*, viewing; Ellenberg et al., 2007), particularly for animals exposed to persistent conditions of tourism activities.

Several significant challenges arise when determining the impacts of tourism on marine animals, particularly those that spend their entire life cycle confined to marine waters (unlike seals or penguins). First, marine organisms that do not depend on some above-water-surface resource are often difficult to access and/or observe. The measurement of reproductive success is not always feasible due to the existence of communal nursing grounds or the complete absence of

parental care. Similar to terrestrial organisms that are the focus of wildlife tourism, many marine species are long-lived so that tourism effects may be manifested only in the long-term, and have large home ranges and migrate over long distances making monitoring and population estimates difficult. Finally, the lack of control populations or baseline estimates for comparison hampers the effectiveness of long-established conservation indicators.

As a result, most studies on the impacts of marine wildlife tourism focus on behavioural changes of the focal species, rather than assessing traditional indicators in conservation biology and wildlife management (animal abundance, food habits, home range size, reproductive success and survival rates; although see Bejder et al., 2006a for an exception). There are difficulties, however, in using deviations in animals' behavioural repertoires to establish cause and effect and/or to demonstrate net cost (Orams, 2004). For instance, many tourism-impact studies rely on wildlife avoidance movements to ascertain energetic costs (Williams et al. 2006), or to establish effective buffer zone distances around viewed animals (Davis et al. 1997). However, sites where avoidance responsiveness is high are not necessarily sensitive areas in need of greater protection; animals in good energetic condition may adopt risk-averse behaviours and initiate avoidance early, whereas animals in poorer condition remain if the cost of escaping is too high (Gill et al., 2001). Alternatively, short-term behavioural responses are insufficient indicators of impacts of anthropogenic disturbance, as moderated responses may not be attributable to habituation but

rather due to the absence of sensitive individuals which have already left (Bejder et al., 2006b, Ellenberg et al., 2006).

To fully determine the impacts of tourism, it is imperative to quantify the organism's ability to persist in face of novel selection processes in altered environments (Reznick & Ghalambor, 2001; Stockwell et al., 2003). However, in the absence of the ability to actually determine persistence (i.e., survival and reproduction), a promising alternative or complement to behavioural methods is the use of physiological indicators, the changes in which may be indicative of altered survival and reproductive capabilities. For instance, physiological trade-offs arise when animals have limited resources to allocate between competing life-history traits (Stearns, 1992). Therefore, changes in animals' physiological state may indicate that some important change in their environment has occurred, as well as signify resultant or potential costs. When used in conjunction with other fitness measures, physiological tools can enable the development of effective countermeasures (Hofer and East, 1998, Wikelski and Cooke, 2006) to the effects of wildlife tourism. Indeed, in the absence of population, reproductive and survival estimates, physiological methods are also often the only tools available to assay the perception by an animal of its environment (Wingfield et al., 1997). Moreover, recent advances towards an integrated ecosystem approach to conservation and management have included organismal physiological adaptation as an important link in understanding the relationship between individual- and population-level plasticity (Stevenson et al., 2005); and

marine resource management and conservation initiatives are calling upon 'conservation physiology' (Wikelski and Cooke, 2006) to improve fisheries and top pelagic predator conservation (Block 2005, Young et al., 2006).

Wildlife-tourism impacts on animal physiological defenses have been receiving attention, with recent advances being made. Studies have demonstrated that Galapagos marine iguanas, *Amblyrhynchus cristatus* (Romero and Wikelski, 2002), and adult Magellanic penguins, *Spheniscus magellanicus* (Fowler, 1999), seemed to habituate to tourist disturbances as measured by the stress hormone corticosterone. The chicks of the hoatzin, *Opisthocomus hoatzin*, however, had lower body mass and higher mortality (Müllner et al., 2004), and Yellow-eyed penguins (*Megadyptes antipodes*; Ellenberg, 2007) had higher chick mortality and lower fledgling weight as a result of tourist visitation, using the same hormone as a titer for disturbance. Incubating Royal penguins, *Eudyptes schlegeli*, displayed higher heart rates in the presence of tourists, more so than in the presence of predators (Holmes et al., 2005), and common wall lizards, *Podarcis muralis*, in tourist areas exhibited lower body condition, a higher infection to ticks, lower cell-mediated immune response, and consequently reduced reproductive output (Amo et al., 2006). The ability of physiological measures to reflect health state and predict survival and reproduction of animals exposed to wildlife tourism is therefore a reasonable possibility. Although conservation physiological approaches have been applied in terrestrial wildlife-

tourism settings, we know of no studies to date which have examined animal physiological responses to wildlife tourism confined to the marine environment.

Here, we investigate the physiological responses of the southern stingray (*Dasyatis americana*), the focus of intense tourism activity in Grand Cayman.

'Stingray City Sandbar' (SCS) is an internationally-known tourist attraction approximately 7740 m² in area and located in a shallow sound along the island's north coast that began operating in 1984. Year-round, up to 2500 tourists from 40 tour boats can be simultaneously present at any one time at the sandbar feeding, touching, and holding stingrays as part of their marine tourism experience (Shackley, 1998). An estimate of 150 stingrays of both sexes simultaneously aggregate (southern stingrays are normally solitary foragers) at SCS to feed on squid, a non-natural food item, provided by tourists. Corcoran (2006) found that the Grand Cayman tourist stingrays have altered their behaviours in response to the provisioned food including a reduced activity space, strong and persistent site fidelity, and a shift to diurnal behaviors in comparison to stingrays from non-tourist sites. A comparison in serum fatty acid profiles between tourist and non-tourist stingrays suggested that squid is the major food item in the diet of the SCS animals (Semeniuk et al., 2007). Semeniuk and Rothley (2008) have found that as a result of this feeding regime, SCS has now become a permanent habitat for a large population of rays which are more likely to have lower body condition (measured as residuals of length-weight relationship), be injured by

boats and predators, be susceptible to ecto-dermal parasites, and be engaged in intense interference competition (in the form of conspecific bite marks).

Although behavioural changes have been noted in the SCS stingrays, it is inconclusive whether they represent long term costs to the animal. Our decision to use physiological indicators was motivated by several factors: comparisons of population size with control populations could not be performed due to the very low recapture probabilities of solitary, control stingrays; reproductive effort (fecundity, pup survival) was not measurable as stingrays give live birth in communal pupping areas around the island; and the southern stingray has an estimated longevity of 26 years (Henningesen, 2002), and therefore mortality was not readily observable. Accordingly, physiological indicators were chosen to reflect the ability of stingrays to persist in response to their altered behaviours, non-natural diet, and grouping costs that result from interactions with tourists. Our hypothesis is that group-living stingrays at the tourist site will exhibit differences in their hematological parameters that are indicative of increased physiological costs, in comparison to solitary stingrays from non-tourist sites. The indicators measured include general-health and defense-system parameters: hematocrit, leukocrit, total serum protein concentration, differential white blood cell counts, and anti-oxidant capacity and oxidative status. We therefore predict that tourist-exposed stingrays will show evidence of reduced general health (Hct, Tsp), immunosuppression (Lct, white blood cell counts) and oxidative stress due to the long-term ecological conditions to which they are exposed. We discuss

whether the physiological changes represent costs to the stingray, what consequences, if any, they may have on the long-term fitness and survival of the stingray population, and conclude with implications for wildlife management.

2. Materials and Methods

2.1. Study species and study site

The southern stingray is a long-lived, common inshore ray frequenting tropical and subtropical shallow bays of the Southern Atlantic Ocean, Caribbean and the Gulf of Mexico. It is an opportunistic forager, feeding on a varied diet of crustaceans and teleosts, and to a lesser extent, on molluscs and annelids (Gilliam & Sullivan, 1993). Although southern stingrays inhabit all shallow bays around the Cayman Islands, it is only in the vicinity of SCS that these rays can be found year-round in a dense aggregation of individuals of both sexes. This amassment results from the unregulated quantity of tourist-provisioned squid (*Illex* and *Loligo* spp.), a non-natural diet item shipped in from the North Atlantic and North Pacific (Semeniuk pers. obs., Gina Ebanks-Petrie Director, Cayman Islands Department of Environment pers. comm.). The feeding opportunities (daily, except during the summer months when weekends are excluded) last from early morning until mid afternoon as tour boats continuously deliver tourists (mainly cruise line passengers) for an average forty-five minute visit to SCS. As a result of this regime, and with no visitor management in place since the site's

inception, nearly 170 individuals have been tagged between 2002 and 2005 with a mean yearly recapture rate of 92.5% (0.03 S.D.; C.A.D.S. unpublished data, Corcoran, 2006), reflecting their long life span, as well as indicating very strong temporal and spatial fidelity to the feeding site.

We captured immature and adult stingrays at SCS and from three control, non-tourist sites on the southern (opposite) and eastern side of Grand Cayman during May-July 2004 and October-November 2005. Stingrays from the non-tourist sites do not interact with the tourists in SCS (based on acoustic-telemetry tracking data; Corcoran, 2006). Tourist stingrays are accustomed to human presence and were easily captured by hand when they approached for food. Once caught, a ray was placed in a landing net (1 m diameter) and transferred into a seawater-filled canvas pool (4 m²) aboard a 24 ft. long, 225 hp dusky boat. Control rays from non-tourist sites were located visually from atop a 14 ft long 45 hp double hull boat, encircled in a hand-drawn seine net (30 ft. long), guided into a landing net, and transferred aboard into the holding pool (average time from first site to capture: 15 minutes). Once transferred, binder clips were placed over the barb on the ray's tail for protection. We then, in an average of 15 minutes from when the ray was captured, collected blood, and recorded the ray's identity (rays that did not already possess an identification tag were tagged with a passive integrated transponder – PIT), weight, disc width, injuries, dermal parasites count (in the spiracles), and conspecific bite marks (counted in 2004 and noted in 2005). Because this study is part of an overall larger research program

investigating the general, physiological and immunological impacts of stingray-provisioning tourism, different indicators were analyzed from different yearly sampling occasions. Due to the rays' strong site fidelity and longevity, and the consistent environmental conditions, we did not expect significant yearly differences within tourist and non-tourist groups. For all rays (2004 and 2005), blood was drawn from the caudal vein using 21G x 1.5 inch needles into 3 mL serum vacutainers, and samples were kept chilled until their return to the wet lab at Georgetown, C.I. where they were immediately centrifuged. The separated serum was then stored at -70°C . In 2004, blood samples (ca. 100-150 microlitres) were collected into two heparinized micro-capillary tubes from the vacutainers upon immediate blood withdrawal and kept cool until centrifugation a few hours later for hematocrit and leukocrit measurement. In 2005, blood smears were made in duplicate on microscope slides from freshly drawn blood, and slides were allowed to air dry. Upon completion of the stingray examination, animals were placed back into the landing net, their tail clip was removed, and they were gently returned to the water. Released, tourist-fed stingrays usually resumed feeding at once, while rays from the non-tourist sites swam away from the immediate area. We present data only for the female rays, as just 31 (18%) of the 172 tagged rays at the tourist site were males. Moreover, as the tourist attraction is currently undergoing ecological (and social) management directives, we focused our research on females as this sex will be the major recipients of any management actions. In addition to their higher relative abundance, females are live-bearers, nourish their embryos via uterine nourishment (i.e.,

matrotrophy), and have associated low fecundity, thus making females the more efficient target for monitoring purposes.

2.2. Hematological Parameters Studied

2.2.1. Hematocrit, Leukocrit and Total Serum Protein from 2004 Sampling

Hematocrit measures the relative amount of red blood cells in total blood volume, and reflects the intensity of oxygen transport into tissues (Birchard, 1997). Low values are indicative of bacterial or parasite infections, starvation (Ots et al., 1998), or a scarcity of some micronutrients such as iron, copper, and vitamin B12 (Cho, 1983, Sturkie and Griminger, 1986). Leukocrit, an indicator of the fraction of white blood cells in total blood volume, can suggest a possible pathogen infection if values are high, or stress-induced immunosuppression if values are low (Barton et al., 2002). Circulating proteins in peripheral blood, measured as total serum proteins, are thought to be an index of total protein reserves in an animal (blood proteins are in a dynamic equilibrium with tissue proteins) and therefore can be used to assess dietary inadequacies. Other vital biological functions of Tsp include: (1) maintenance of osmotic pressure; (2) transport of minerals, hormones, lipids, catabolites and drugs; (3) defense against infection (accumulation of antibodies responding to antigen of bacterial or viral origin); (4) blood clotting and lyses of fibrin; and (5) enzymes and inhibitors of enzymes (Silverman et al., 1986; Řehulka et al., 2005). The time-course response of these

parameters in indicating condition/nutritional effects is relatively more rapid in comparison to the other parameters measured in this study (Barton et al., 2002).

2.2.2. Leukocytes from 2005 Sampling

Differential white blood cell counts determine the percentage of each type of white blood cell in an animal's peripheral blood. The three types of leukocytes (lymphocytes, granulocytes (heterophils and eosinophils), and monocytes) in elasmobranchs (sharks and rays) each have different functions. Lymphocytes (of both the B- and T- types) are found in elasmobranch peripheral blood, and function the same way as in mammalian systems, namely, in being responsible for the production of antibodies (immunoglobulins) and cell-mediated immunity. Heterophils, the most actively phagocytic and pinocytic cells in elasmobranchs, can increase in number resulting from infection, disease, and stressful conditions. Eosinophils, mildly phagocytic, play a role in the control of parasite infection and are involved in immune responses to a variety of antigens. Monocytes are involved in non-specific immune responses and are highly phagocytic; they also play a role in inflammation and accumulate at the site of injury or infection (Stoskopf, 2000, Luer et al., 2004). Thrombocytes have also been included in our count as 'white-blood cells', as they are speculated to play a role in immune function (phagocytosis), in addition to their blood-clotting function (Walsh and Luer, 1998). The differential cell count reveals if these white-blood cells are present in a normal distribution, or if one cell type is increased or decreased. This information can help identify sources of altered health, as

differential cell counts have limited sensitivity and are relatively insensitive to observer-induced biases (Ochs and Dawson, 2008). Substantial alterations in immune status are therefore necessary before significant changes are observed in the relative percentages of white blood cell populations (Gelsleichter et al. 2006).

2.2.3. Oxidative Stress from 2005 Sampling

The last physiological response investigated was oxidative stress. Cellular metabolism generates reactive oxygen (and nitrogen) species (ROS) that can damage cell structures, deplete energy, and cause early apoptosis (programmed cell death). To counteract the harmful effect of ROS, organisms rely on antioxidants in the form of endogenously produced enzymes and low-molecular weight molecules, and exogenous, food derived anti-oxidants (Hörak et al., 2007). Oxidative stress results when there is an imbalance between the production of ROS and the biological system's ability to readily detoxify the reactive intermediates or easily repair the resulting damage. Oxidative stress can occur during times of environmental stress and/or high energy demand, and these processes are associated with the appearance of and increase in the severity of many diseases (Martínez-Álvarez et al., 2005). The processes that lead to the occurrence of oxidative stress vary significantly over large gradients and at different temporal scales in many environmental factors (Lesser, 2006); however, a build-up of oxidative stress in excess over the organism's lifespan is hypothesized to contribute to early ageing and shortened life span (Finkel and

Holbrook, 2000). Thus, to maintain proper cellular homeostasis, a balance must be struck between reactive oxygen production and consumption by antioxidants. Determination of a system's capability to prevent oxidative stress is accomplished by measuring total antioxidant capacity (TAC) as well as total oxidative status (TOS), and contrasting the magnitude of the ratio under differing environmental challenges.

2.3. Laboratory analyses

2.3.1. Hematological preparation

After coagulation on ice for 4–6 h, blood samples in vacutainers were centrifuged at 5,500 rpm for 10 min. Serum was separated from sedimented cells, aliquoted into eppendorf tubes, and frozen at -70°C. Serum samples were then transported on dry ice to Simon Fraser University for subsequent analysis of total serum protein (Tsp) and TAC/TOS. Microcapillary tubes (two per individual) were centrifuged for 5 min at 11,500 rpm, and hematocrit (Hct) and leukocrit (Lct) were twice measured for each tube with a sliding caliper to the nearest 0.1 mm (coefficient of variation in duplicated measurements: 2.4% and 7.1%, respectively). Blood smears prepared for determining the contribution of different leukocyte cell populations were stained with Wright's-Giemsa stain (Sigma Chemical Co. St. Louis, MO) and shipped to Florida International University for quantification.

2.3.2. Serum protein quantification

The total protein concentration in the sera was determined by the Bradford protein (BioRad, Hercules CA). Briefly, 20 μ l of the diluted sera were placed in the flat bottomed 96-well plate in triplicate and the protein concentration determined following the manufacturer's instructions. The optical density was read at 595 nm in a plate reader. Protein concentrations (mg/mL) were obtained from a standard curve made with gamma-globulin, as elasmobranchs are not thought to possess albumin (the typical standard; Metcalf and Gemmell, 2005), and we wished to use a purified preparation of the protein being assayed for comparative purposes.

2.3.3. Differential white blood cell count

Differential immune cell counts were performed using a compound microscope via oil immersion (1000X). Circulating concentrations of total white blood cells (WBCs) were performed by a single observer and estimated by enumerating the number of leukocytes (and thrombocytes) per 100 cells (red plus white) in duplicate and subsequently averaged. In a separate count (again, performed in duplicate on different sections of the microscope slide and then averaged), the contribution of each leukocyte population (lymphocytes, heterophils, monocytes, eosinophils and thrombocytes) was determined as a percentage per 100 white blood cells counted (r^2 between mean duplicate counts = 0.99).

2.3.4. Total Antioxidant Capacity/Total Oxidative Status

Total antioxidant capacity (TAC) was measured according to a modification of the commercially available Randox TEAC (Trolox equivalent antioxidant capacity) assay (Erel, 2004). The reduced ABTS molecule (a free radical standard) is oxidized to ABTSS⁺ using hydrogen peroxide in acidic medium (the acetate buffer, 30 mmol.L⁻¹, pH 3.6), where the colour is spontaneously and slowly bleached. Antioxidants present in the sample accelerate the bleaching rate to a degree proportional to their concentrations. This reaction can be monitored spectrophotometrically and the bleaching rate is inversely related with the TAC of the sample. The reaction rate is calibrated with Trolox, a water-soluble vitamin E analogue widely used as a traditional standard for TAC measurement assays. Samples were tested in triplicate and assay results are expressed in mmol Trolox equivalent/L in reference to a standard curve.

The total oxidative status (TOS; Erel, 2005) assay uses two reagents: ferrous ion-o-dianisidin complex and xylenol orange. Oxidants present in the sample oxidize the ferrous ion-o-dianisidin complex of the reagent to ferric ion. The oxidation reaction is enhanced by glycerol molecules, which are abundantly present in the reaction medium. The ferric ion then makes a colored complex with xylenol orange in the acidic medium. The colour intensity, which can be measured spectrophotometrically, is related to the total amount of oxidant molecules present in the sample, which was tested in triplicate. The assay is

calibrated with hydrogen peroxide and the results are expressed in terms of micromolar hydrogen peroxide equivalent per liter ($\mu\text{mol H}_2\text{O}_2 \text{ Equivalent.L}^{-1}$).

2.4. Statistical Analyses

The interpretations of the hematological parameters requires discretion, because a particular pattern can arise for a variety of reasons (Adamo 2004, Matson et al., 2006). Additionally, the bi-directionality of change in certain parameters necessitates the incorporation of ecological context in the form of intrinsic (i.e., 'condition') and extrinsic (i.e., tourist 'treatment') variables (Beldomenico et al., 2008). Therefore, for the aggregate health indicators (Hct, Lct, Tsp and oxidative stress) we created a 'fitness' variable to assign a general health score to individual rays. This was done by applying a principle components analysis to stingray parasite load, number of injuries (fresh wounds and other injuries, 2005) and number of conspecific bite marks (2004) to generate a single principle component (PC) of stingray fitness for each year. This action allowed us to then use the PC as a covariate in our models to ascertain whether an animal simultaneously exhibiting high amounts of injuries and parasites (i.e., poorer condition) determined to a certain extent the pattern of stingray general health. To investigate the relationship between the PC and its original variables to define the directionality of the PC scores, we used linear and quadratic curve estimation regressions.

Hematocrit, Lct, Tsp and TAC/TOS responses were each analyzed in a least-squares, multiple regression model using treatment (non-tourism versus tourism) as a factor variable, and fitness PC, disc width (cm) and body size metric (residuals of log-transformed disc-width and weight variables) as continuous, independent variables. Starting with all of the independent variables, we used backward deletion of least significant terms until only significant terms remained. A Student's t-test was used to determine if total WBC counts differed among sites: 1) when all five cell types are grouped, and 2) when thrombocytes are not included in the cell counts.

Because different leukocytes have cell-specific responses to differing stressors - for example, tissue injury causes heterophilia whereas parasite infection promotes eosinophilia (Tizzard, 2004, Feldman et al., 2000), we explored how number of injuries and parasite loads as individual covariates influenced the proportion of individual cell types between treatments, using least-squares, multiple regression. Lastly, we used linear and quadratic curve estimation regressions within treatments to investigate any (non)linear relationships between ray physiological responses and body condition and stingray fitness PC, as we wanted to more fully explore the effects of the treatment-specific differences in condition, parasite loads, and injuries. We performed all statistical analyses using JMP IN 6.0 (SAS Institute Inc., 2005) employing two-tailed tests of probability. We report the significance at both the 5% and 10 % levels following the recommendations of Field et al. (2004) and Fidler et al. (2006), who

caution against interpreting non-statistical results (at the 5% level) in null-hypothesis significance testing as 'no effect' in conservation science. As per their recommendations, we also report Hedge's effect size and power for the results significant at the 10% level. As appropriate, original variables (both dependent and independent) were transformed to meet the assumptions of normality for parametric tests, and then back-transformed (dependent variables) to obtain the mean (\pm S.E.).

3. Results

3.1. Stingray condition and fitness metrics

Although size ranges overlapped ($\text{range}_{\text{tourist}} = 37\text{-}130$ cm; $\text{range}_{\text{non-tourist}} = 40\text{-}104$ cm), female stingrays were significantly larger, both in disc width and weight, at the tourist site than females sampled from the non-tourist sites for both the 2004 and 2005 years (25% -75% median quartiles_{tourist} = 99-100 cm, 32-33 kg; quartiles_{non-tourist} = 76.5-78 cm, 14.5-15 kg (Semeniuk and Rothley, 2008)). However, despite the larger size, growth trajectories (i.e., log-transformed disc width and weight relationship) were not significantly different between the two locations, indicating that tourist-fed rays are not significantly heavier for a given size. Body condition, however, measured as residuals of the logarithmic relationship between disc width and weight for the tourist and non-tourist sites combined, was lower for rays at the tourist site (Semeniuk and Rothley, 2008).

For the 2004 data year, a principle component analysis on the correlation between number of parasites, injuries (e.g. predator-detection/defense, susceptible-to-infection, and motility-impairment injury types), and conspecific bite marks (all corrected for stingray disc width) returned a significant factor with an eigenvalue > 1 that explained 44.6% of the original variation. This stingray fitness metric loaded positively for parasite load and injuries, but negatively for conspecific bite marks, so an intermediate score corresponds to a stingray simultaneously exhibiting intermediate amounts of parasites, injuries, and bite marks; a low score denotes a stingray in good condition, and a high score represents poor condition with respect to a stingray possessing high injuries and parasites. The 2005 PC analysis on the correlation between number of parasites, 'fresh injuries' (including open wounds from conspecific bite marks) and other, non-fresh injuries (e.g. predator-detection/defense and motility-impairment injury types; again, all corrected for disc width) returned a significant factor with an eigenvalue of 1.28 that explained 42.7% of the original variation. The 2005 stingray fitness metric loaded positively for both injury variables, and had a positive quadratic relationship with the parasite-load variable; therefore, an intermediate score denotes low parasites and an intermediate number of injuries, and a high score signifies a poor-condition stingray with a high number of parasites and injuries (open wounds and other).

3.2. Relationships between physiological indicators and tourism treatment, stingray fitness

Tourist rays had significantly lower hematocrit than non-tourist rays ($F_{1,102} = 9.13$, $P < 0.005$; $n_{\text{tourist rays}} = 67$, $\bar{x} = 0.294 \pm 0.004$ S.E.; $n_{\text{non-tourist rays}} = 37$, $\bar{x} = 0.312 \pm 0.005$ S.E.; fig. 1). There were no linear or quadratic effects nor second-order interactions of stingray size, body condition, or fitness metric 2004 on the proportion of packed red cell volume overall or within each treatment (all P 's > 0.143), and they were subsequently removed from the model.

There was a highly significant, negative relationship between leukocrit and disc width, even with other variables and their interactions included in the model which were not significant (i.e., treatment, body condition, fitness PC 2004 and their second order interactions; overall model: $F_{8,69} = 4.67$, $P < 0.0001$; $\beta_{\text{disc width}} = -0.167$, $t = -4.66$, $P < 0.0001$; all other variables $P > 0.18$). After taking the residuals of Lct standardized for stingray disc width, we found no effect of treatment, but a significant, negative linear effect of the fitness metric on residual Lct ($t = -2.03$, $P = 0.046$). Investigating this further, we found the relationship between Lct and fitness was driven by tourist rays solely, and displayed a significant, negative linear trend ($F_{1,53} = 5.21$, $P = 0.027$, $r^2 = 0.09$; Residual Lct = $-0.003 - 0.002 \times \text{fitness PC 2004}$; non-tourist rays: $P = 0.73$; fig. 2), denoting lowest Lct was associated with highest number of parasites and injuries.

Both treatment and stingray disc size had a significant effect on total serum protein (Tsp; overall model: $F_{2,108} = 6.57$, $P = 0.002$), with larger stingrays having

significantly higher concentrations of serum protein ($\beta_{\text{disc width}} = 13.25$, $t = 2.45$, $P = 0.016$), and tourist rays having significantly lower Tsp than non-tourist rays ($\beta_{\text{treatment (non-tourist rays)}} = 2.05$, $t = 3.49$, $P < 0.001$; $n_{\text{tourist rays}} = 70$, least-squared $\bar{x} = 41.2 \text{ mg/mL} \pm 0.67$; $n_{\text{non-tourist rays}} = 41$, least-squared $\bar{x} = 45.3 \text{ mg/mL} \pm 0.89$; fig. 3a). No other variables in the model were significant. Taking the residuals of Tsp standardized for disc width, we found a significant, non-linear effect of stingray fitness metric 2004 on residual Tsp for tourist rays only ($(F_{2,53} = 3.77$, $P = 0.029$, $r^2 = 0.125$; Residual Tsp = $-2.38 - 0.23 \times \text{fitness PC 2004} + 1.33(\text{fitness PC 2004} - 0.015)^2$), with animals which simultaneously exhibited parasites, bite marks and injuries having had the lowest total serum protein concentration (fig. 3b).

Overall, the proportion of summed white blood cells (lymphocytes, heterophils, eosinophils, monocytes and thrombocytes) out of the total peripheral blood cell count did not differ between treatments ($t = 0.12$, $P = 0.72$; $n_{\text{tourist rays}} = 46$, $\bar{x} = 0.183 \pm 0.008$; $n_{\text{non-tourist rays}} = 49$, $\bar{x} = 0.188 \pm 0.007$); however, this non-difference may be attributed to a higher proportion of thrombocytes in tourist ray peripheral blood, since when thrombocytes were excluded, the proportion of remaining leukocytes in the total white blood cell count was significantly lower at the 10% significance-level in tourist rays than in non-tourist rays ($t = 1.68$, $P = 0.09$, Power = 0.39, Effect Size = 0.35; $\bar{x}_{\text{tourist rays}} = 0.741 \pm 0.01$; $\bar{x}_{\text{non-tourist rays}} = 0.776 \pm 0.01$).

Lymphocytes There was a significant interaction effect of treatment and parasite load (overall model: $F_{3,91} = 5.78$, $P = 0.001$; $\beta_{\text{treatment} \times \text{parasite load}} = -0.045$, $t = -3.71$, $P < 0.001$), and a parasite load effect on the proportion of lymphocytes ($\beta_{\text{parasite load}} = -0.027$, $t = -2.25$, $P = 0.027$). Further within-treatment analysis revealed that while lymphocytes decreased with increasing parasites in non-tourist rays (linear regression: $F_{1,47} = 17.5$, $P < 0.001$, $r^2 = 0.27$), there was no relationship among tourist rays (fig. 4a), as they maintained a constant and lower (median_{tourist rays} = 0.475 vs. median_{non-tourist rays} = 0.52) proportion of these white blood cells ($F_{1,44} = 1.27$, $P = 0.27$, $r^2 = 0.03$).

Heterophils Heterophils were significantly and positively affected by stingray size and number of fresh injuries (overall model: $F_{3,91} = 5.72$, $P = 0.001$; $\beta_{\text{disc width}} = 0.34$, $t = 3.25$, $P < 0.001$; $\beta_{\text{fresh injury number}} = 0.11$, $t = 5.08$, $P < 0.001$), and tourist rays had a significantly lower proportion of these cell types ($\beta_{\text{treatment}} = 0.06$, $t = 3.81$, $P < 0.001$; back-transformed, least-squared $\bar{x}_{\text{tourist rays}} = 0.126 \pm 0.016$ S.E.; back-transformed, least-squared $\bar{x}_{\text{non-tourist rays}} = 0.219 \pm 0.025$ S.E.). In addition, there were significant interaction effects between treatment and disc width and fresh injury numbers ($\beta_{\text{treatment} \times \text{disc width}} = 0.403$, $t = 3.83$, $P < 0.001$; $\beta_{\text{treatment} \times \text{fresh injury number}} = 0.077$, $t = 3.51$, $P < 0.001$). A within-treatment analysis revealed that non-tourist rays were more responsive to an increase in the number of fresh injuries than tourist rays (non-tourist rays: $F_{1,47} = 4.53$, $P = 0.038$, $r^2 = 0.09$, proportion heterophils = $0.389 + 0.065 \times \text{fresh injury number}$; tourist rays: $F_{1,44} =$

3.48, $P = 0.069$, $r^2 = 0.07$; proportion heterophils = $0.35 + 0.036 \times \text{fresh injury number}$; fig. 4b).

Eosinophils The proportion of eosinophils significantly increased with both stingray size and parasite load (overall model: $F_{3,91} = 6.54$, $P = 0.0005$; $\beta_{\text{disc width}} = 0.204$, $t = 3.37$, $P = 0.001$; $\beta_{\text{parasite load}} = 0.021$, $t = 2.77$, $P = 0.007$); also, tourist rays had significantly lower proportion of eosinophils than did non-tourist rays ($\beta_{\text{disc width}} = 0.024$, $t = 3.27$, $P = 0.002$; back-transformed, least-squared $\bar{x}_{\text{tourist rays}} = 0.076 \pm 0.010$ S.E.; back-transformed, least-squared $\bar{x}_{\text{non-tourist rays}} = 0.105 \pm 0.009$ S.E.).

Monocytes There was a significant effect at the 10% level of treatment only on the proportion of monocytes, with tourist rays having a higher proportion of these cell types ($F_{1,93} = 3.56$, $P = 0.059$, Effect Size = 0.39, Power = 0.46; back-transformed, least-squared $\bar{x}_{\text{tourist rays}} = 0.027 \pm 0.010$ S.E.; back-transformed, least-squared $\bar{x}_{\text{non-tourist rays}} = 0.020 \pm 0.009$ S.E.).

Thrombocytes Thrombocyte proportion also had a significant treatment effect, with tourist rays having a higher proportion of cells significant at the 10% level than non-tourist rays ($F_{1,93} = 3.33$, $P = 0.067$, Effect Size = 0.38, Power = 0.44; back-transformed, least-squared $\bar{x}_{\text{tourist rays}} = 0.251 \pm 0.015$ S.E.; back-transformed, least-squared $\bar{x}_{\text{non-tourist rays}} = 0.214 \pm 0.015$ S.E.). Within-treatment analyses showed that for tourist rays only, there was a (non-linear) relationship

between the proportion of thrombocytes and the number of fresh injuries, corrected for stingray size, with lowest thrombocyte number corresponding to lowest injuries ($F_{2, 43} = 3.17$, $P = 0.05$, $r^2 = 0.129$; transformed proportion thrombocytes = $0.474 - 0.0016 \times \text{residual fresh injury number} + 0.054(\text{residual fresh injury number} - 0.366)^2$; fig. 4c).

There was a significant effect of treatment and body condition on the concentration of serum TAC (overall model: $F_{2,91} = 8.48$, $P < 0.001$; $\beta_{\text{treatment}} = 0.056$, $t = 3.69$, $P < 0.001$; $\beta_{\text{body condition}} = -0.631$, $t = -2.33$, $P = 0.022$), with animals from the tourist site having significantly lower concentrations of antioxidants ($n_{\text{tourist rays}} = 49$, least-squared $\bar{x} = 0.455 \pm 0.020$ S.E.; $n_{\text{non-tourist rays}} = 45$, least-squared $\bar{x} = 0.565 \pm 0.021$ S.E.). The negative relationship between TAC and body condition, although significant in the overall model, was driven entirely by rays from the non-tourist site ($F_{1, 43} = 6.48$, $P = 0.015$, $r^2 = 0.131$; $[\text{TAC}] = 0.566 - 0.820 \times \text{body condition}$; fig. 5a), since within-treatment analyses showed no relationship for tourist rays ($P = 0.96$). Instead, the fitness PC 2005 variable significantly explained a portion of the TAC concentration in a non-linear way for tourist rays only, with highest TAC corresponding to low parasite and intermediate injury numbers ($F_{2, 44} = 3.82$, $P = 0.03$, $r^2 = 0.148$; $[\text{TAC}] = 0.471 - 0.043 \times \text{Fitness PC 2005} - 0.028(\text{residual fresh injury number} - 0.052)^2$; fig. 5b). There was no effect of disc width or higher order interactions.

TOS concentrations were significantly higher among tourist rays (overall model: $F_{2,86} = 4.51$, $P = 0.014$; $\beta_{\text{treatment}} = 59.65$, $t = 2.99$, $P = 0.0036$; $n_{\text{tourist rays}} = 47$, least-squared $\bar{x} = 364.6 \pm 25.88$ S.E.; $n_{\text{non-tourist rays}} = 44$, least-squared $\bar{x} = 245.3 \pm 26.23$ S.E.), and also decreased with increasing fitness PC 2005 (i.e., highest score representing high parasites and injuries, both fresh and other; $\beta_{\text{fitness PC}} = -32.03$, $t = -1.82$, $P = 0.072$; fig. 5c). However, this relationship with stingray fitness metrics was driven solely by tourist rays ($F_{1,53} = 4.14$, $P = 0.048$, $r^2 = 0.09$; [TOS] = $368.8 - 36.1 \times \text{fitness PC 2005}$; non-tourist rays: $P = 0.51$). There was no effect of body condition, disc width, or higher order interactions.

4. Discussion

4.1. Interpretation of results

We explored whether the cumulative effects of the tourist stingrays' altered behaviours, non-natural diet, and associated grouping costs had any modifications indicating that there may be some significant physiological costs being incurred by rays in tourist-visited areas. Comparing the condition of rays from tourist and non-tourist sites, we found marked physiological differences. Tourist rays had lowered hematocrit, lowered total serum proteins, differential leukocrit and leukocyte reactions (adjusted for body size), and exhibited oxidative stress, all of which likely indicate that tourist rays are subjected to negative physiological consequences of visitation, and that their ability to persist has been

affected. Because the general variation in physiological responses of anthropogenic impacts is attributed to: differences in the predictability of the duration of the stressors, the number and temporal pattern of stressors, the damaged-induced mortality rate from inadequate homeostatic maintenance, the mortality rate from the stressor if no resources are allocated to combat it, and the ability of the organism to recover (Schreck, 2000; McNamara and Buchanan, 2005), it is important to take into account the ecological context of the study system. Accordingly, we also found that parasite loads and injuries (bite marks, fresh wounds and other types) explained a proportion of the variation in our hematological variables, suggesting that the physiological changes of tourist rays were in partial response to these stressors.

Stingrays were, on average, larger at the tourist site (although the minimum range overlapped); however, we do not believe size - as a proxy for age - to be the principle driving factor explaining the physiological differences. For hematological variables for which stingray disc width was a significant factor, controlling for size still resulted in significant effects of fitness PC's; moreover, if there was a significant linear relationship between the dependent variable and stingray size in non-tourist rays, the same relationship did not hold for tourist rays, and was in the opposite direction (for example, as Tsp increased with size in control rays, tourist rays had lower Tsp). Lastly, previous research by Semeniuk and Rothley (2008) demonstrated that SCS stingrays were equally injured across size categories, and that the largest females did not have the

highest number of conspecific bite marks. Therefore, we believe other factors, such as injuries and parasite loads, independent of stingray size, have more of an effect on our measured physiological variables. We acknowledge these variables could not completely explain the observed patterns, and other tourism-related causative factors, while not explored in this paper (e.g., internal parasites and bacterial pathogens, water pollution (fouled by boat fuel or sunscreens), and increased predation pressure), could also be responsible for the differences in stingray physiology.

The lowered hematocrit of tourist stingrays (hematocrit values of elasmobranchs are generally one-third total cell volume; Stoskopf, 2000) can be indicative of parasites and infection (Jones and Grutter 2005). In our model, however, there was no effect of body condition, ecto-dermal parasite load, or injuries on packed red blood cell volume (although this does not negate the possibility of internal parasites). Low Hct values can also be due to reproductive anemia (Williams, 2004), caused by reduced physical exercise (Gallauger et al., 1995); or conversely, increased through capture and handling (Wells, et al. 1986). We do not believe these alternative explanations can explain our results. Firstly, the female stingrays we examined were a mixture of sexually mature (> 75 cm disc width) and immature in both treatments (Henningesen 2000), and there was no effect of body size on Hct; therefore reproductive status had no bearing on the results. An acoustic tracking study of stingrays at the tourist site furthermore revealed that tourist rays have similar rates of movement ($\text{km} \cdot \text{h}^{-1}$) when

compared to stingrays from other areas around Grand Cayman (Corcoran, 2006), and consequently, the lowered Hct in tourist rays cannot be due to reduced physical activity. Lastly, although non-tourist rays required tracking before capture, studies of the capture and handling of sharks have found no evidence of hemodilution or hemoconcentration in response to capture and restraint (Hoffmayer and Parsons, 2001; Manire et al., 2001). Finally, lowered hematocrit can be caused by a scarcity of micronutrients such as iron, copper, and vitamin B12 (Cho, 1983, Sturkie and Griminger, 1986). Squid, the non-natural diet, is lower in iron and B12 and higher in copper than in shellfish (King et al. 1990; Kongkachuichai et al. 2002), the natural diet on which southern stingrays feed (Gilliam and Sullivan, 1993). Although we have no direct evidence, there is a significant possibility of diet-induced anemia in our system. Regardless of the cause, because lowered hematocrit is an aggregate, general indicator of poor health state and nutritional condition of animals in the wild (Verhulst et al., 2004, Huitu et al., 2007), we believe it also reflects the general, poorer state of tourist stingrays, as well.

Leukocrit is used as a general indicator to assess health and immunocompetence of a wide variety of animals, and low values can indicate stress-induced immunosuppression (e.g., McLeay and Gordon, 1977). Given the significantly higher numbers of ectodermal parasites and injuries of tourist rays compared to control, non-tourist animals (Semeniuk and Rothley, 2008), the negative relationship between Lct (corrected for the stingray size) and increasing

injuries and parasite load (fitness PC 2004) for tourist rays only (fig. 2) is not surprising. Similarly, the lower total serum protein concentration of tourist rays was also partially explained by stingray fitness (2004), with individuals simultaneously possessing parasites, injuries and bite marks demonstrating lowest Tsp (fig. 3b). Total serum protein is also a general indicator, with low values indicative of a range of health issues such as dietary inadequacies, immune deficiency and disease (e.g., Adams et al., 2003). The low values of Lct and Tsp associated with 'poor' fitness scores, coupled with the incidence of hypoproteinaemia (e.g., Ots et al., 1998), suggest sub-optimal health and a downregulation in the defense mechanism of tourist rays.

Further substantiation of altered physiological defenses was found in the white blood cell differentials. The differences in the proportion of the various leukocytes (including thrombocytes) was influenced by stingray size, parasite load, and fresh-injury numbers. Interestingly, the direction and magnitude of these covariates differed between treatments. For instance, the proportion of lymphocytes, which play a role in cell-mediated immunity and antibody production, decreased with increasing parasite loads in non-tourist rays, perhaps in favour of the corresponding measured rise in heterophils - phagocytic and pinocytic cells - which increased with fresh injuries (figs. 4a and 4b, respectively). In tourist rays, however, this same relationship did not hold: the percentage of lymphocytes, while marginally smaller than in non-tourist rays, was relatively unresponsive to parasites, and heterophils, which were significantly lower in

proportion than in non-tourist rays, were not as responsive to the number of injuries. Differences in immune response continued with the other cell types: eosinophils which play a role in parasite and antigen control, expectedly increased with parasite load regardless of treatment, but were still significantly lower in tourist rays; and monocytes and thrombocytes (both involved in non-specific immune responses, although the latter has more of a role in blood clotting) were proportionally higher (at the 10% significance level) in tourist rays. Within this latter group, thrombocytes were lowest when individuals displayed the lowest number of parasites (fig. 4c). To sum, it appears that with regards to cell-mediated immunity, the responses of tourist rays do not match the suite of responses of control stingrays when exposed to similar, albeit fewer, stressors. There is evidence that some of the physiological responses are indicative of suppression (i.e., low and unresponsive - lymphocytes and heterophils), up-regulation (monocytes and thrombocytes), and down-regulation (eosinophils). Variations in differential cell counts suggestive of immunosuppression have been shown in other studies (see Barker et al., 1994 and Lepak and Kraft, 2008 for examples in teleosts); and in addition to the differential reaction between treatments, the lower ratio of leukocytes to thrombocytes in tourist rays (at the 10% level) also suggest that cell-mediated immunity has been attenuated in tourist rays.

The final evidence of compromised defenses in tourist stingrays come from the oxidative stress findings. A rise in reactive oxygen species is not necessarily

problematic if cells are able to defend themselves against ROS damage through a compensatory increase in antioxidant potential. In particular, ROS can play a positive role in the activation of protective signaling pathways provided they are not produced in excess, i.e., beyond the capacity of anti-oxidants to counteract their production (Finkel and Holbrook, 2000). However, tourist rays not only exhibited a significantly higher concentration of total oxidative species, but significantly lower total antioxidant capacity as well (figs. 5c and 5b, respectively). The assay used in this study measures small molecule antioxidants (AO) such as ascorbic acid, uric acid, glutathione, and polyphenol AO. Nonetheless, cells in many vertebrates also defend themselves through the use of enzymes such as superoxide dismutases and catalases. Elasmobranchs, however, have a limited enzymatic antioxidant system in their sera, and compensate for this deficiency by relying on small molecular AO instead, such as vitamin K, urea, and glutathione (Rudneva, 1997). Therefore, our results should reflect an accurate assessment of the degree of oxidative stress experienced. Oxidative stress in fish can be caused by nutritional deficiencies, environmental factors, xenobiotics, immune responses to injury, parasite infestations, and increased energy demand and workload (see Martínez-Álvarez et al., 2005 for a review). At the non-tourist sites, animals in the best body condition had lowest TAC; this relationship did not hold for rays from the tourist site. Instead, animals that simultaneously possessed the lowest number of parasites (and intermediate number of injuries – fitness PC 2005) had the highest TAC. Additionally, the TOS decrease with a rise in ‘poor’ fitness PC (i.e., higher parasites, and fresh and other injuries) for tourist rays may

be speculatively explained by the significant reduction in circulating heterophils (unlike for the non-tourist rays) that usually remain in chronic wounds for longer than they do in acute wounds and which produce reactive oxygen species and enzymes (Schönfelder et al., 2005). Regardless, TOS concentrations were still higher overall - suggesting additional sources of oxidative damage, such as ischemia, a lack of oxygen from being removed from the water which can also be a contributing factor to the higher oxidative status of the rays (Hermes-Lima and Zenteno-Savin 2002). In combination with lowered TAC, the TOS findings demonstrate a cumulative effect of oxidative stress which can presumably lead to premature cellular ageing and shortened stingray lifespan.

4.2. Sources of Physiological Costs at 'Stingray City Sandbar'

McNamara and Buchanan (2005) modeled the optimal tradeoff of resource allocation between competing demands of combating a stressor and bodily maintenance, and predicted that the longer the stress period is expected to last, damage to self maintenance (e.g., reduced physiological reserves of essential nutrients, minerals or energy; increased levels of oxidative stress; or reduced condition of protective body covering) will build up to high and unacceptable levels unless resources are put into maintenance and thus fewer into combating the stressor. Consequently, as the duration of the stressor increases, the probability of death from both poor condition and the stressor increase at an accelerating rate, with the stressor becoming proportionately more important as a

threat of mortality. This is because the longer the stress period lasts, the more resources are allocated toward maintaining condition.

Our findings provide evidence that in tourist rays, which are continually exposed to the impacts of tourism, both self-maintenance and protection from the stressor may be compromised due to their novel environmental conditions: unnatural food, high injury rates and increased parasite loads. Energy and nutrient pools are used by the organism for maintenance, repair, and growth and reproduction. If a stressor degrades the quality or quantity of available food, it may compromise maintenance and repair processes as well as limit the energy available for growth or reproduction (Adams, 1990). Squid, the predominant diet item of fed stingrays, is a non-natural food with a different composition of minerals and vitamins than the natural shellfish diet; and the tourist rays have a drastically different ratio of dietary omega-3:omega-6 fatty acids when compared to the ratio found in non-tourist stingray serum (Semeniuk et al., 2007). Essential fatty acid requirements for different fish species reflect dietary and metabolic adaptations to distinctive habitats and ecosystems (Sargent et al., 1999; Bell and Sargent, 2003). The imbalance of essential nutrients and fatty acid ratios from the tourist ray's diet –important for disease resistance, stress-management and gamete quality - may be hindering the capability of stingrays to allocate their resources into proper maintenance. The low hematocrit, serum protein, and total antioxidant capacity, all influenced by diet, also support this hypothesis.

Likewise, chronically high injury rates and increased parasite loads have influenced, to a certain extent, the majority of the physiological traits measured. The incidence of oxidative stress coupled with dampened physiological responses may resultantly increase the rays' vulnerability to additional or future stressors such as modified physicochemical regimes, changes in food and habitat availability, increased predation risk, and increases in infectious pathogens (Schreck, 2000; Barton et al., 2002). The tourist rays' altered defense system may also enhance their susceptibility to impacts arising from changing environmental conditions such as oil spills, increased hurricane intensity, and climate change, which may ultimately prove lethal.

4.3. Physiological Change and Fitness Costs

The question remains as to whether the physiological differences detected in this system will translate into negative consequences for reproduction and/or survival. There are few studies that have evaluated the correlations between physiological parameters and fitness components, but the available research supports this likelihood (e.g., Romero and Wikelski, 2001; Verhulst et al., 2004, Cabezas et al., 2007). In our system, while direct evidence is still unknown, the probability of reduced survival seems likely to be quite high. The tourist system may therefore act as an "ecological trap" by enticing the rays to exploit an attractant with an immediate payoff (i.e., an easily exploitable food source) that may generate relatively greater fitness costs longer term (Schlaepfer et al., 2002). Alternatively, stingrays can be allocating the surplus resource to faster growth rates and/or

reproduction, in which case, the fitness benefits would outweigh the costs. This may certainly explain why stingrays are larger at the tourist site, but would not explain why for a given size, tourist rays had smaller mass. In addition, since larger females have larger litter sizes (Henningesen, 2000), females could also be trading off the physiological costs incurred with higher fecundity, although we would have again expected residuals of the length-weight relationship for tourist rays to be positive, not negative (Semeniuk and Rothley, 2008). The potential positive impacts of tourism consequently cannot be supported at this time. Accordingly, we purport that based on previous research and current physiological evidence, wildlife tourism for the current Cayman Island stingrays frequenting SCS acts as an ecological trap – i.e., maladaptive decisions resulting in lowered fitness. Furthermore, should the following generations of stingrays born from SCS rays seek out the tourist site themselves, the site may then not be sustainable. From a management perspective, long-term monitoring and management of the Stingray City Sandbar is essential.

4.4. Conclusion

Education and awareness of the risks posed to stingrays are a key tactic in mitigating the negative impacts of tourism (Semeniuk et al. *in press*).

Furthermore, measures should be taken to alleviate crowding conditions (leading to injuries and parasite transmission) at SCS by limiting the number of people and boats, or by expanding the site into nearby areas to accommodate the current level (although this decision would have to be adaptively monitored).

Less food provisioned to the rays would also alleviate the stingray aggregation, and ensure that the rays resume foraging naturally and solitarily, further away from the tourist site. Additionally, safety devices on boat propellers, such as cages and guards, can also aid in reducing injuries. We explore how these management plans can affect stingray population size and life expectancy in a forthcoming simulation study on the system dynamics of the tourist-stingray relationship (unpubl. data).

The discrepancies detected among different physiological indicators when assessing the physiological and condition-related indicators of environmental impacts emphasize the importance of using multiple single indicators (Adamo, 2005; Matson et al., 2006) and of an appropriate control (Barton et al., 2002) when defining best measures for fitness. This undertaken in our study, we also employed indicators that varied in their ease of collection and interpretation, and those that are fairly robust to capture and handling, to allow for the reproduction of our methods by managers for monitoring purposes. Future assessment should consider baseline (control) as well as tourism-induced parameters for key monitoring purposes, integrating both physiological and general fitness (injury rates, open wounds, parasite loads) indicators as a basis for limits of acceptable change. We duly acknowledge that while we tout the advantages of investigating stress-physiology in marine wildlife over behavioural studies, we understand that there exist some complications involved in procuring the data. Whenever possible, however, finer scale and multi-level analyses of disturbance effects will

provide a more complete understanding of the actual costs to the animal, especially in the absence of long-term population data.

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Figure 5.1 Bar graph showing significant difference (*) in mean (+ S.E.) hematocrit between tourist and non-tourist rays.

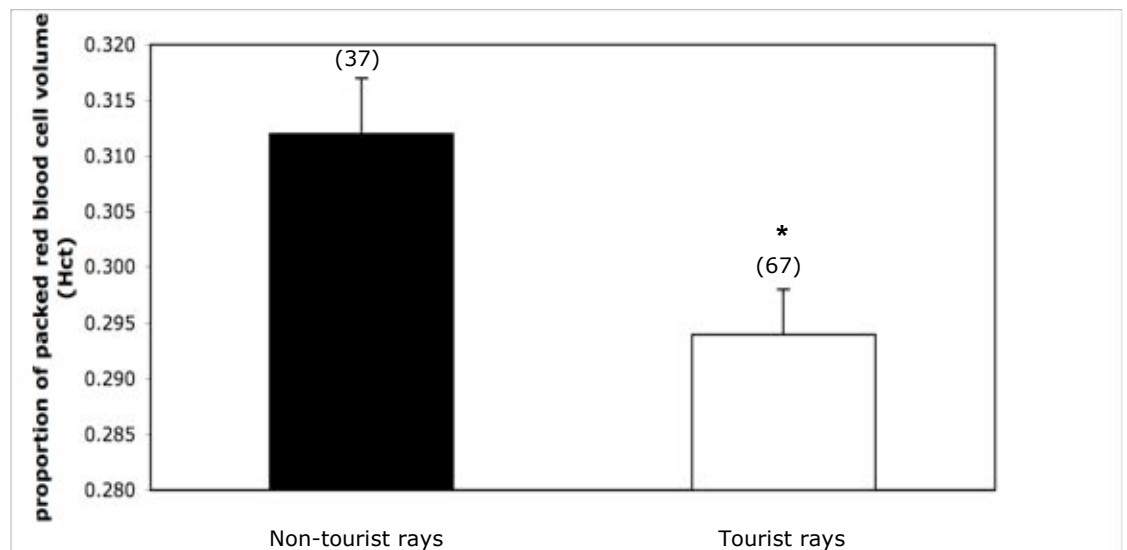


Figure 5.2 Negative linear relationship between Fitness PC 2004 (a high score denotes high injury and parasite load and low conspecific bite marks) and leukocrit (controlled for stingray size) for tourist rays only. No relationship found for non-tourist rays. ■ = non-tourist rays; O = tourist rays; (--) = tourist ray trendline.

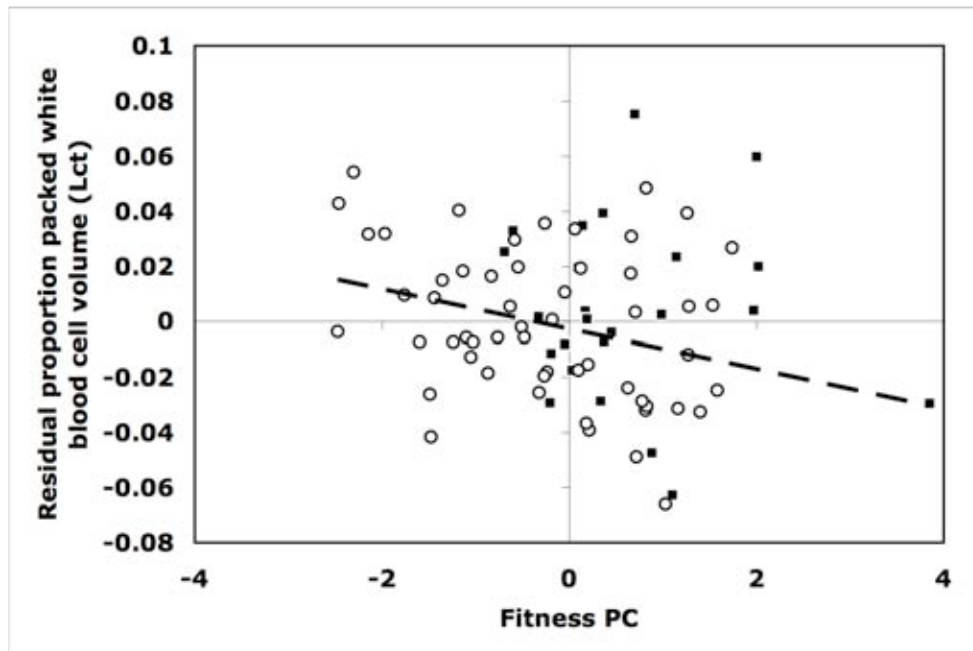
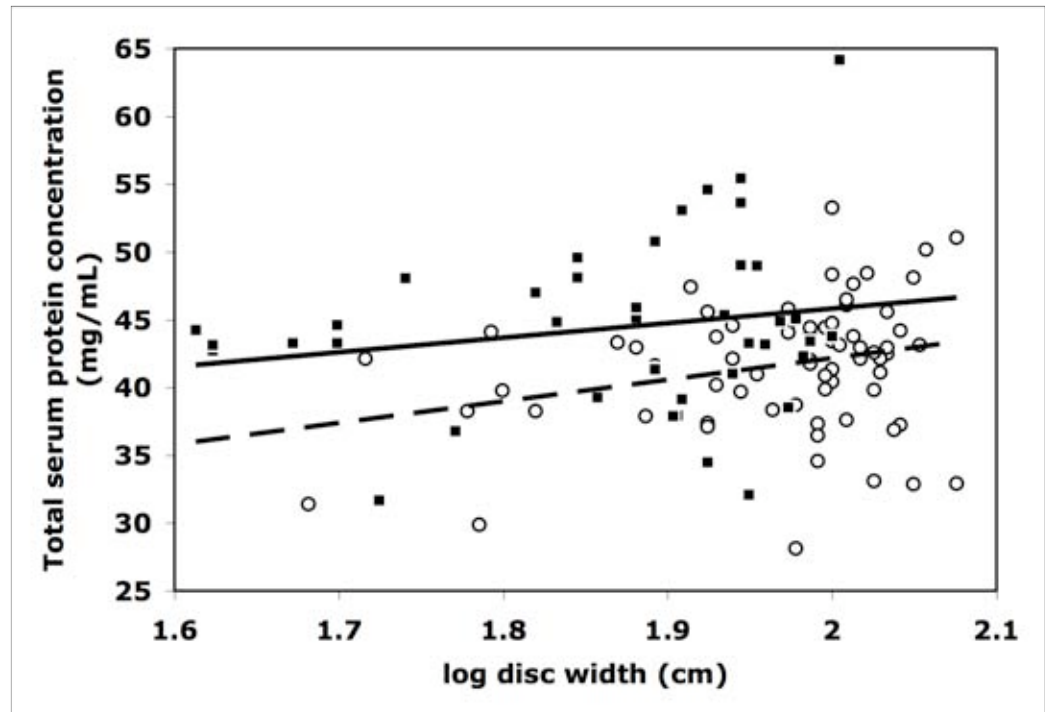


Figure 5.3 a. Negative linear relationship between (\log_{10}) disc width (cm) and total serum protein concentration (mg/mL) for both tourist and non-tourist rays. b. Nonlinear relationship between Fitness PC 2004 (an intermediate score denotes intermediate parasite load and injuries and high conspecific bite marks) and total serum protein concentration (corrected for stingray size) for tourist rays only. No relationship found for non-tourist rays. ■ = non-tourist rays; ○ = tourist rays; (–) = non-tourist ray trendline; (--) = tourist ray trendline.

5.3a.



5.3b.

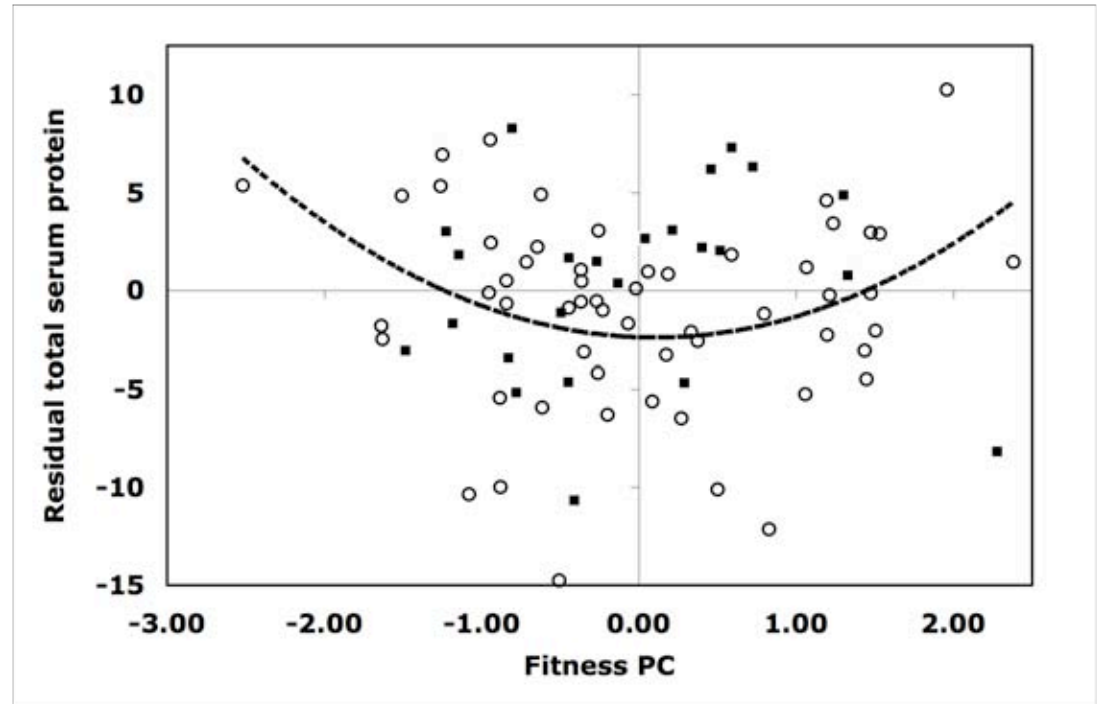
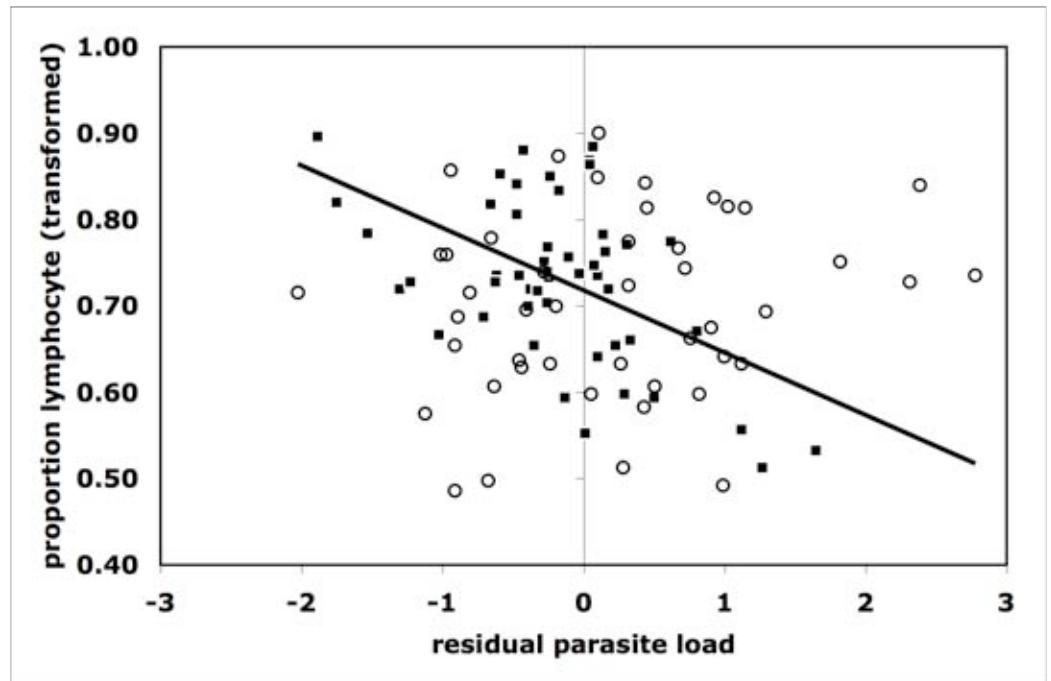
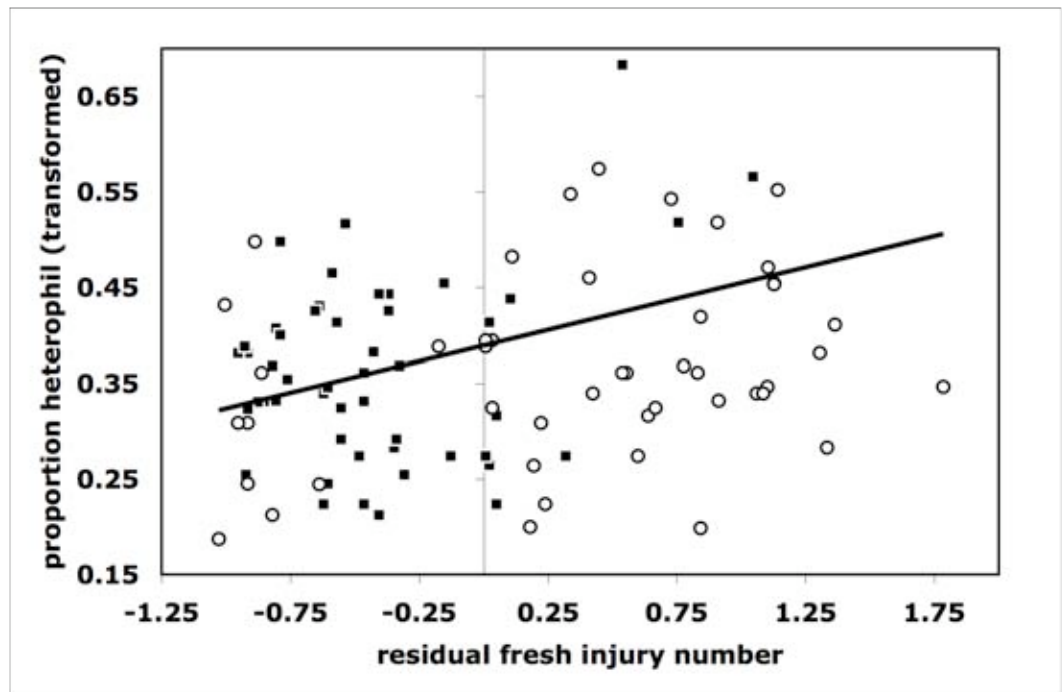


Figure 5.4 a. Negative linear relationship between parasite load (corrected for stingray size, 2005) and proportion of lymphocytes for non-tourist rays only. No relationship found for tourist rays. b. Positive linear relationship between injury number (corrected for stingray size) and proportion of heterophils for non-tourist rays only. No relationship found for tourist rays. c. Nonlinear relationship between fresh injury number (corrected for stingray size, 2005) and proportion of thrombocytes for tourist rays only. No relationship found for non-tourist rays. ■ = non-tourist rays; ○ = tourist rays; (–) = non-tourist ray trendline; (--) = tourist ray trendline.

5.4a.



5.4b.



5.4c.

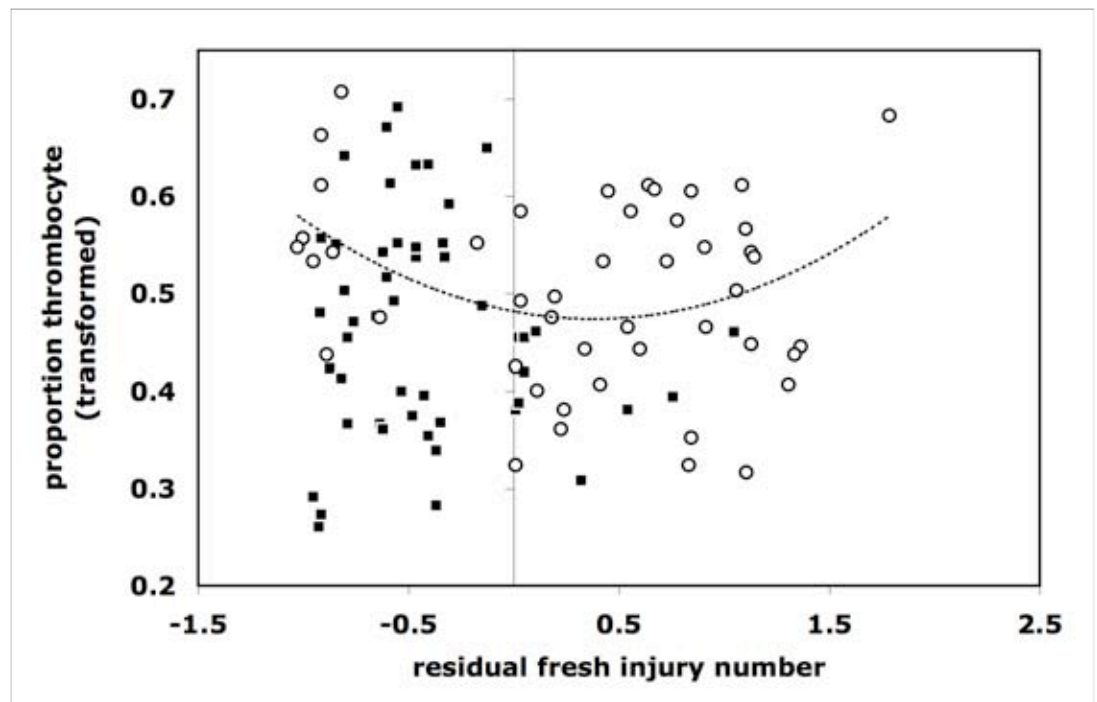
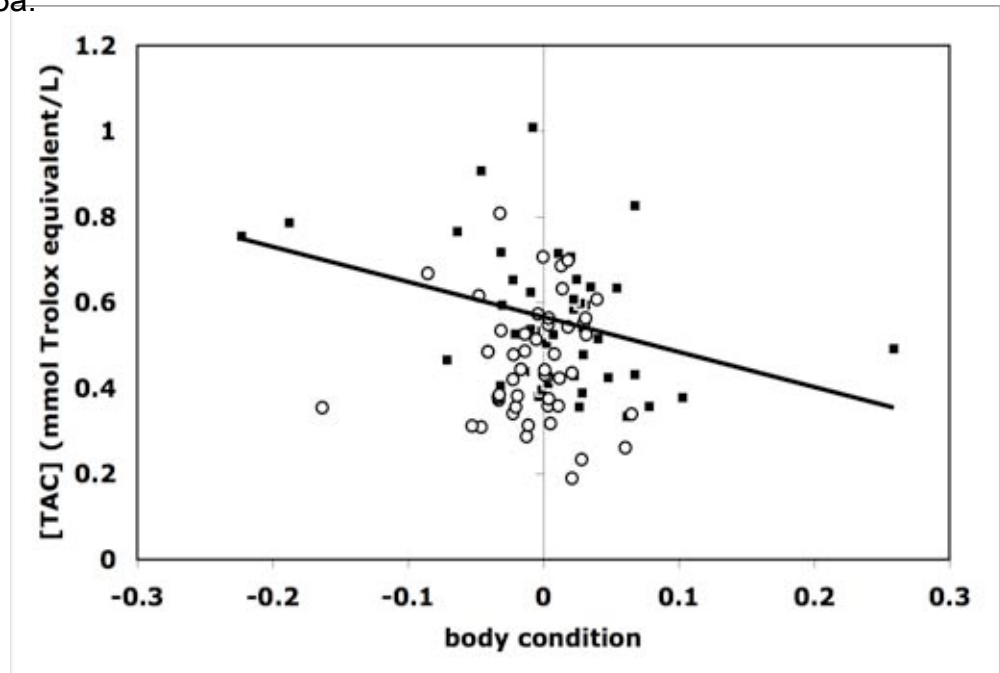
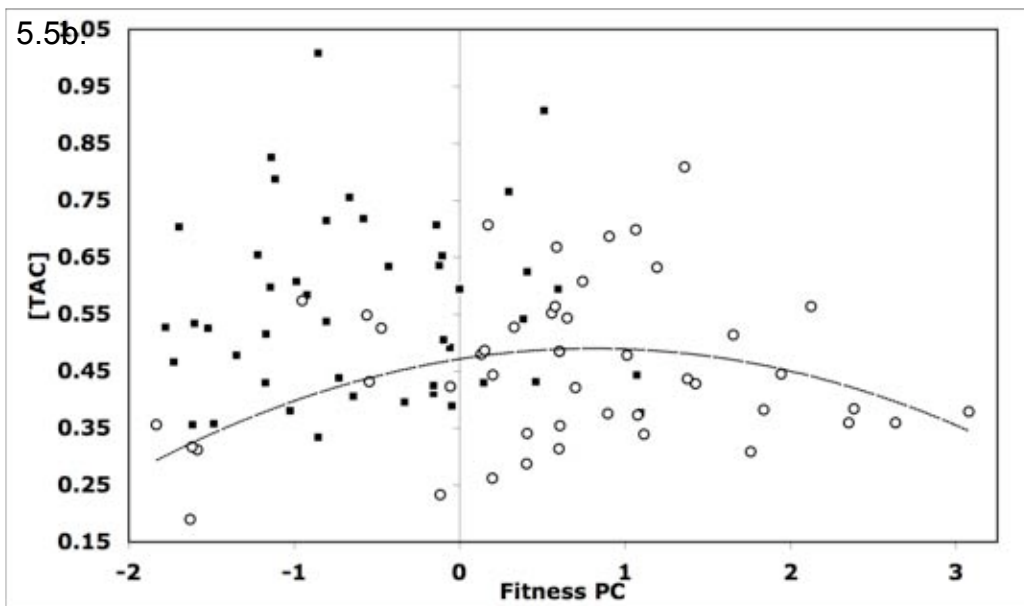


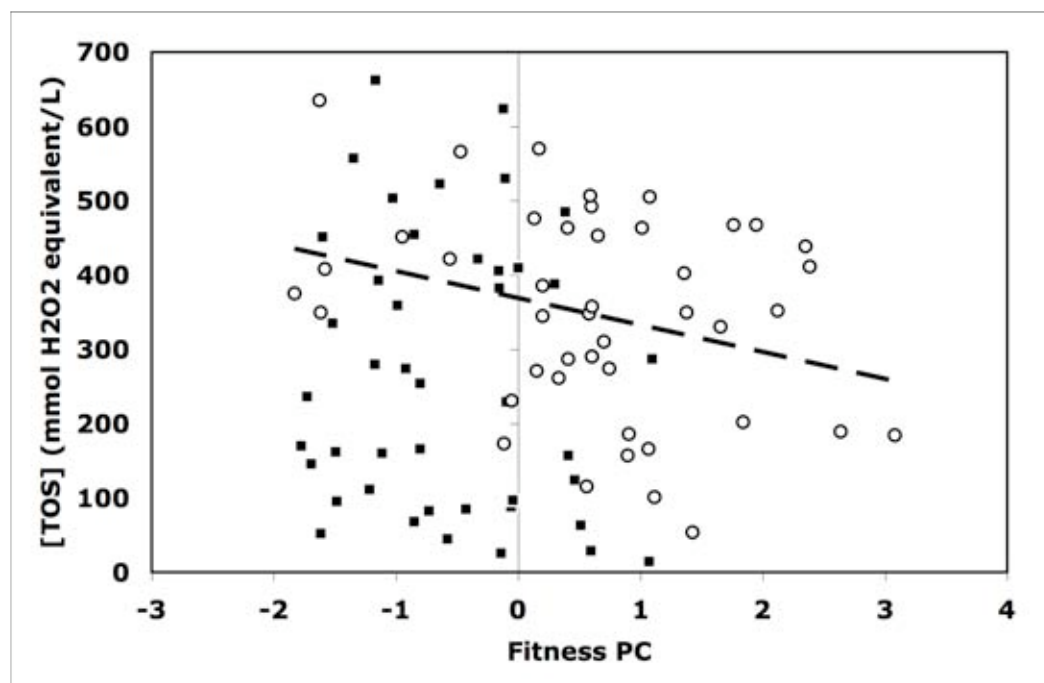
Figure 5.5 a. Negative linear relationship between body condition (residuals of length-weight relationship) and total antioxidant capacity (TAC). No relationship found for tourist rays. b. Nonlinear relationship between Fitness PC 2005 (intermediate score denotes low parasites and intermediate number of injuries, fresh and other) and TAC for tourist rays only. c. Negative linear relationship between Fitness PC 2005 (high score denotes high injuries (fresh and other) and high parasite load) and total oxidant status for both tourist and non-tourist rays. ■ = non-tourist rays; ○ = tourist rays; (–) = non-tourist ray trendline; (– –) = tourist ray trendline.

5.5a.





5.5c.



CHAPTER 6: UNIFYING THE ECOLOGICAL AND SOCIAL SCIENCES INTO A PREDICTIVE SYSTEM DYNAMICS MODEL FOR THE MANAGEMENT OF WILDLIFE TOURISM

This manuscript is intended and formatted for *Ecological Modelling*.

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ABSTRACT

As marine wildlife tourism attractions increase in popularity, managers need an understanding of the tourist-resource relationship to protect the wildlife base and safeguard the tourism experience. We used ecological- and social-trap theories to explain the evolution of the wildlife-tourism lifecycle. We then created a systems-dynamic model for the feeding of stingrays at 'Stingray City Sandbar' (SCS), Cayman Islands, to predict the state of the marine tourism attraction; specifically, tourist population numbers, stingray population size, and stingray life expectancy, over time. The null model of no management was contrasted against five differing management scenarios with varying levels of congestion control, stingray interaction regulations, ecological outcomes, and a conservation access fee. Social data incorporated in the model included utility preferences of latent tourist segments for the different management options as well as for stingray- and tourist- densities, along with actual tourist population trends, arrival and departure rates. Ecological data included stingray population growth rates and survival estimates (from mark-recapture data), and estimates of mortality caused by tourism which varied under the divergent management scenarios. The model's predictions were sensitive to the stingray population growth rate, relative contributions of different tourism-mortality estimates, as well as the different management options. A lack of SCS management is predicted to yield the lowest tourist and stingray population and stingray life-expectancy over time, providing evidence of ecological and social traps. The best management strategy, according to our model, is, instead, a reduction in visitor density, restriction of

stingray interactions to the tour operator only, and an imposition a 5\$ conservation access fee. Over time, tourists favouring this management would replace those favouring no management; tourist satisfaction would be maximized, and although fewer stingrays would remain at SCS, they would live longer, on average, and experience fewer stochastic disease events. Our model is useful for understanding the interlinkages between the social and ecological components of the system, the processes affecting stingray and tourist population dynamics, and the prediction of wildlife tourism management on both the tourism experience and wildlife fitness.

INTRODUCTION

As wildlife tourism attractions increase in popularity, management is required to protect the resource base and safeguard the tourism experience. However, values of conservation, animal welfare, visitor satisfaction, and economic profitability are often in conflict within wildlife tourism, and tradeoffs are necessary (Reynolds and Braithwaite 2001). Accordingly, a thorough investigation combining both the ecological and social aspects of wildlife tourism can provide a greater understanding of the recreational system than considering either alone, and offer insights to address potential conflicts (Newsome et al. 2005). Consequently, we must consider humans and animals as a system to make predictions about the effects of management alternatives. While ostensibly reasonable, there are few case-study examples guiding the amalgamation of these two disciplines in terms of what questions should be asked, and how answers can be incorporated into effective management plans.

We chose the concept of ‘traps’, both ecological and social, to link the human dimension features of the wildlife tourism setting to the natural science issues. In an ecological context, a trap occurs when human-driven environmental change decouples the cues that animals use to assess habitat quality from the true quality of the environment (Schlaepfer *et al.* 2002). Animals mistakenly rely on false or altered environmental cues to maximize their fitness, but do not immediately receive the necessary feedback to inform them that their choices are wrong – i.e., no longer adaptive. The consequence can be reduced survival,

reproduction, or even local population extinction compared to the probable outcome if the true high-quality habitat had been selected (Battin 2004). An example is hotel night lights which disorient sea turtle hatchlings from finding the shore (for other examples, see Schaeffer et al 2002). In a social context, a trap could occur when over time, visitor typologies shift from the specialist to the more novice generalist, and tourists, in their quest to maximize satisfaction with their wildlife experience, possess values, motivations and actions that unwittingly cause impacts to the wildlife system (Higginbottom et al., 2003). These tourists do not perceive the negative impacts of their actions and desires, and a social trap transpires when the resource base deteriorates to such a point that tourist satisfaction is affected. In time, tourist populations too, may decline. The ultimate outcome is site fatigue, gains by competitors, and the reduction of environmental quality (Butler 1980; see Patullo 1996, Akama 1997 and Holden 2003 for examples). Therefore, in the absence of deliberate management intervention, wildlife tourism attractions containing ecological and social traps can evolve to the detriment of both the visitor experience and the focal wildlife species (Duffus & Dearden 1990; Higham, 1998).

Based on the arguments above, we maintain that best management practices for wildlife tourism attractions should incorporate animal ecology and tourism dynamics, as well as the economic, social and institutional frameworks within which these systems operate. Given the complexity of this decision-making environment, integrated models of natural and human systems can support or

may even be essential for policy makers (Costanza and Voinov, 2001). In particular, dynamic models are increasingly being used in environmental, biological, and socio-economic systems to simulate the various ecological and social outcomes of different management and policy directives (Hernández and León 2007). The basic approach is to create flow diagrams relating the dynamic structure of the system through feedback loops, and to represent this structure with mathematical equations. Dynamic models can also test the leverage of each modeling assumption, prioritize variables for data collection, and identify the most sensitive attributes that require long-term monitoring (Faust et al. 2004). In an environmental-management context, models can become a useful tool for assessing the importance of precaution in decision-making, acceptable levels of additional risk, estimates of how long it may take for mitigating measures to take effect, whether effects are reversible, and efficient allocation of conservation resources (Thompson et al. 2000, Faust et al. 2004).

Here, we describe the formulation of a dynamic model for the ‘Stingray City Sandbar’(SCS) in the Cayman Islands as an archetypal social-ecological system in wildlife tourism. Our model assimilates quantitative social-science data (tourist stated-preferences for management options) with biological data (animal’s health and population indices) to predict the outcome of various management policies on tourist population size, wildlife population size and wildlife life-expectancy after a 25-yr time span. By linking stakeholder input, and social and ecological data and theory, we account for and explore feedback loops between the two

most important agents involved in wildlife tourism at SCS. Our goal for the SCS model is to find management strategies to protect both the resource base and tourist experience over the long-term, by looking for evidence of ecological and social traps that could be degrading the system as a whole. We then consider the implications of this specific modeling exercise to the field of wildlife tourism management at large.

THE SOCIAL-ECOLOGICAL SYSTEM

The Wildlife Attraction

Stingray City Sandbar (SCS) is a warm, shallow water (1.6 m maximum depth) sandbar approximately 7,740 m² area located roughly 300 meters inland from the fringing reef in the North Sound in Grand Cayman Island. Southern stingrays (*Dasyatis americana*) congregate here to be fed frozen squid by tourists and tour-boat operators. A daily occurrence which first began in the mid 1980's (Shackley, 1998), up to 2500 tourists can now be simultaneously present at the shallow sandbar, engaged in unsupervised feeding, touching, and holding of stingrays as part of their marine tourism experience. Tourist numbers have more than doubled between 1999 and 2002 (CI MoT, 2002). Without management or codes of practice, the site has become congested, and government officials, tour operators, tourists and locals have expressed concern about the long-term sustainability of the attraction (Gina Ebanks-Petrie, CI Director of the Environment, pers. comm.; C.A.D.S., pers. obs.). In 2003, the stakeholders

convened a committee to agree upon a set of detailed rules for crowding alleviation and stingray protection for SCS. There was no means to predict the effect, if any, of these plans on both stingray fitness and visitor response. While each proposed regulation considered alone would be expected to redress the known problems (e.g., limits on boat density would be likely to reduce congestion), the outcome of the simultaneous application of these regulations was uncertain. Additionally, as argued above, the tight human/animal interdependence necessitated that the effects of proposed management scenarios be evaluated on the integrated SCS system rather than on individual components (e.g., handling rules could reduce stingray injuries but also dissuade visitors).

The Tourist Experience

To understand and predict tourist preferences for various regulations and fees at SCS, Semeniuk et al. (in press) conducted a social-science survey on cruiseline passengers visiting SCS in 2004, and developed a decision support tool that quantified visitor support for varying regulation/fee scenarios. The results indicated that SCS tourists could be divided into (1) a 'pro-management' group (68% of respondents), preferring actions that reduce congestion, impacts on stingrays, and the number of stingrays present, and being amenable to a conservation fee; and (2) a 'pro-current' group supporting a small access fee but strongly desirous to continue direct interactions with the stingrays. Not surprisingly, these visitor groups were particularly at odds with respect to a

proposed rule to restrict the handling and feeding of rays to 'the tour operator only'. Opposition to this regulation by the 'pro-currents' was so strong that no other feasible attribute levels could compensate for it, while 'pro-managements' were willing to trade handling and feeding restrictions for the reduction in risk of stingray injury. It is likely, then, that the proposed SCS management plan in SCS would lead to a shift in the tourist mix over time, with 'pro-current' typologies being usurped almost completely by 'pro-management' visitors.

The Wildlife

Although the southern stingray inhabits all shallow bays around the Cayman Islands, only in the vicinity of SCS can stingrays be found year-round in a dense mixed-sex aggregation of individuals. An assemblage of over one hundred tagged and identified rays can now be found at SCS at a given time, attracted by the unregulated quantity of provisioned squid (*Illex* and *Loligo* spp.), a non-natural diet item shipped in from the North Atlantic and North Pacific. Squid is now the major food diet item of tourist-fed stingrays and may be inadequate in supplying the proper, balanced nutrition for proper maintenance (Semeniuk et al. 2007). Corcoran (2006) showed that the tourist-fed stingrays have reduced activity space, strong and persistent site fidelity, and a shift to diurnal behaviors in comparison to stingrays from non-tourist sites in Grand Cayman. Additionally, the tourist-fed stingrays are more likely to be in lower body condition, be injured by boats and predators, be susceptible to ecto-dermal parasites, and be engaged in intense interference competition (in the form of conspecific bite marks). Tourist

rays also have significantly higher mean numbers of injuries, parasites and median bite marks in comparison to stingrays from non-tourist sites (Semeniuk and Rothley 2008). As a result of the unnatural diet in combination with the physical stresses at the SCS site, stingrays display physiological responses indicative of sub-optimal health and attenuation of the defense system, including oxidative stress (Semeniuk et al. unpubl. data) and, over the long term, the SCS stingray population may not be sustainable.

THE MODEL

We used a systems dynamics approach to describe the relationships of the ecological and social components of the SCS (fig. 1), and translated our flow diagram (figs. 2-4) to a set of difference equations with STELLA 9.03 (isee Systems, Inc.). Our null model of no management was contrasted against five differing management scenarios which consisted of varying levels of congestion control, stingray interaction regulations, ecological outcomes, and a conservation access fee (Table 1), and we predicted the management plans' effects on tourist preferences and stingray fitness (Table 2). The three state variables were 'Pro-Management Tourist Population' (PM), 'Pro-Current Tourist Population' (PC), and 'Female Ray Population'. The auxiliary variables are listed in Table 3. The driving variables of the system were management policies and stingray immigration rate.

Tourist Module

Initial state variable stocks of PM and PC were set at 552 000 and 260 000, respectively, based on the total number of cruise-ship passengers docked at Grand Cayman in 2006 (pers. comm., CI Director of Tourism). It is estimated that 50% of cruise-ship passengers disembark on the island, and from these, the majority visit SCS. The calculated population estimates used in the model are in agreement with those estimated for SCS (CI Department of Environment (DoE), pers. comm.). We chose the initial population sizes of PM and PC tourists based on the heterogeneous probability classification of these two groups from the latent class model of tourist preferences (i.e., 68% and 32%, respectively of 812 000 visitors in 2006; Semeniuk et al. *in press*).

Tourist population growth rate was calculated from actual data supplied by DoT's Port Authority of cruise-ship tourist numbers from 1984 until 2006 (again, estimating the proportion to actually visit SCS). Assuming a logistic discrete growth with a carrying capacity of two million visitors to SCS, R_{\max} - the net discrete per capita rate of growth - was estimated using the solver tool in Microsoft excel to find the R that minimized the sum of the squares of the differences between the mean and the actual population-size values over time. A carrying capacity of two million people was chosen as the maximum the site could potentially accommodate should the Port Authority allow eight cruise ships to dock each day throughout the year; at present, during the off-season, a maximum of four boats are docked at any given time and for a maximum of 5 days/week. The value obtained for R_{\max} was 0.231. Since R_{\max} represents the

fastest rate of growth at small population sizes, this value was converted to R_{now} to reflect current conditions:

$$R_{\text{now}} = R_{\text{max}}(1 - N_{\text{Pm+PC}}/K); \quad (\text{eq. 1})$$

therefore, R_{now} was calculated as 0.137.

Both PM and PC stocks change with tourist arrivals and departures. The departure rate, d_{now} , was estimated from Semeniuk et al. (*in press*), in which only 11% of the tourists partaking of the survey were return visitors. Moreover, the authors' decision-tree analysis revealed that of the 11% returning, just over half are PC tourists (54.5%, or 6% of the 11%), while the rest (45.5%, or 5% of the 11%) are PM tourists. From these data, we assumed that PM tourists do not return at a rate of -0.9265 (i.e., 0.05/0.68), and PC tourists do not return at a rate of -0.8125 (0.06/0.32).

Knowing the per capita rate of growth of the population as well as the departure rate allowed for the calculation of the rate of arrival (i.e., arrival rate + departure rate = R) as 1.064 and 0.950 for PM and PC tourists, respectively. Other variables influencing the number of arrivals to SCS were tourist preferences for the management options (PM/PC Plan Prefs), preferences for the number of stingrays in the population (PM/PC Ray Pop Prefs), and preferences for the density of tourists (PM/PC People Pop Prefs). These preferences are presumed to represent intended visitation behaviours; the theory of reasoned action posits there exists a link between intended behaviour and actual behaviour

(Ajzen and Fishbein 1980); therefore, we are allowing visitor preferences to affect visitor arrival and departure rates. To quantify preferences in common units, relative scores - called utilities - were used. Utility can be measured in many ways, including monetary units; however, it can also represent scores that describe the relative preferences of different management scenarios. We estimated utilities from the stated preference choice model (Semeniuk et al. *in press*) using a conditional mixed logit model to analyze the frequencies of choices, and produced regression estimates, known as part-worth utility (PWU) parameters, for each attribute - the sum of which represents respondent preferences as a whole:

$$P(i | i \in M) = \frac{\exp(X_i, \beta)}{\sum_{j \in M} \exp(X_j, \beta)} \quad , \quad (\text{eq. 2})$$

where the probability of choosing scenario alternative i from all scenarios included (M) equals the exponent of all the measurable attributes of alternative i (i.e., X , the vector of explanatory variables, and β , the parameter vector to be estimated) over the sum of the exponent of all measurable elements of all alternatives, j .

Tourist preferences for the management options (PM/PC Plan Prefs) were estimated as the percent relative change in support of PM/PC tourists when management shifts from 'no-management' (set to a value of 1) to an alternate scenario. As an example, suppose a scenario in which only the tour operator can

feed stingrays, all else being equal to status quo. This scenario is less preferred by PM tourists and changes relatively by (–) 8.74%. Therefore, we assumed that the arrival rate of PM tourists would decrease by a value of 0.0874. Table 1 lists all the management plans tested in the model and Table 2, their associated percent relative change.

Because tourists respond to the number of surrounding stingrays they encounter on their visit, the population size of rays will also independently influence the arrival of visitors to the site (PM/PC Ray Pop Prefs). For instance, we know from the PWU's that PC tourists prefer encountering a higher density of rays than PM tourists, all else being equal. We therefore used the change in relative support for 10, 24, 40 and 55 (current) surrounding rays (from the choice experiment in Semeniuk et al. *in press*) and allowed these values to equal changes in preferences for total stingray population sizes at SCS of 27, 68, 110 and 150 (current) rays, respectively, all other attributes being set to the 'no management' scenario. Next, we extrapolated the (non-linear, negatively quadratic; eq. 3) relationship between proportion relative change in PWU and ray population size for PM tourists, and the (non-linear exponential; eq. 4) relationship for PC tourists, and used these numeric relationships to predict tourist preferences for population sizes ranging from 20 rays to 250 – the imposed stingray carrying capacity. Note that at the current ray population estimate of 150, the relative change in support is set to 0:

$$\text{PM: Ray Pop Prefs} = -5\text{E-}05 * (\text{ray population size})^2 + 0.0093(\text{ray population size}) - 0.27; \quad (\text{eq. 3})$$

and

$$\text{PC: Ray Pop Prefs} = 0.2778 * \ln(\text{ray population size}) - 1.392. \quad (\text{eq. 4})$$

Lastly, although less people were preferred by both tourist types, they were not significant in comparison to the PWUs for the other attributes (Semeniuk et al., *in press*). However, crowding issues were still an expressed concern in the survey, and as the population of tourists is increasing (as evidenced from *R*), the number of people will most likely have an affect on tourist arrivals (PM/PC People Pop Prefs). Therefore, similarly to the method above, we scaled the number of surrounding people used in the choice experiment (500, 750 and 1000) to an annual population of 812,000, 1,200,000, and 1,600,000, respectively, and used the corresponding proportion of relative change in preferences to derive an equation of the relationships (eq.'s 5 and 6). Again, we set the change in support for 812 000 people (the current estimate) to 0:

$$\text{PM: People Pop Prefs} = -3\text{E-}07 * (\text{tourist population size}) + 0.2436; \text{ and} \quad (\text{eq. 5})$$

$$\text{PC: People Pop Prefs} = -3\text{E-}07 * (\text{tourist population size}) + 0.244. \quad (\text{eq. 6})$$

Tourist arrivals into the population were summarily calculated as follows and assumed no interactions:

$$(\text{Tourist Population} * \text{arrival rate} * (\text{Plan Prefs} + \text{Ray Pop Prefs} + \text{People Pop Prefs})). \quad (\text{eq. 7})$$

Similar to affecting tourist arrivals, the three auxiliary variables presented above are presumed to affect tourist departures as well over and above the departure rate determined from the survey. More specifically, we have assumed they will affect the tourist's likelihood of return. Tourist departures are calculated as follows:

$$(\text{Tourist Population} * \text{PM/PC Departure Rate}) + (\text{Tourist Population} * ((1 - \text{PM/PC Departure Rate}) * (1 - (\text{Plan Prefs} + \text{Ray Pop Prefs} + \text{People Pop Prefs}))))). \quad (\text{eq. 8})$$

In this instance, if a management scenario is perceived positively, the summed value of the preferences will be greater than one, resulting in a negative value (i.e., 1-preferences), denoting fewer people will depart.

Stingray Population Module

The initial state variable stock of Female Stingrays was set at 150 based on the number of female stingrays tagged and identified at SCS and estimates from tour operator and marine research officer inputs. Only female rays are modeled in this

paper since just 18% of the tagged rays at the tourist site are males; as such, females will be the major recipients of any management actions.

The rate of stingray population growth (λ) was estimated from mark and recapture data. From 2002 to 2005, stingrays at SCS were captured, identified or tagged (with a passive integrated transponder – PIT), and released and recaptured on subsequent sampling efforts. We used open-population Pradel models in program MARK (White and Burnham 1999, Cooch and White 2002) to estimate realized population growth rate (λ) and apparent survival rates (ϕ). Model parameters also included capture probability (p).

The data supported models with variable λ over time, with two of the three final models with $\Delta AIC_c < 4.0$ (Burnham and Anderson 1998) having λ decrease linearly over time. Model averaging produced a λ of 0.88 (95% CI = 0.682-0.977), indicating that the size of the female component of the tourist-stingray population was, on average, decreasing during the study period (2002-2005). We decided to subject this parameter to a sensitivity analysis because over a four- year study period in such a long-lived animal, a decreasing population growth rate may not necessarily reflect the long-term trend. The λ 's = 1 and 1.15 were consequently used as well. Models of both time invariance and variance were supported for ϕ (survival) rate estimates, with a model average value of 0.85 (95% CI = 0.780-

0911). This estimate was fairly robust in the different models analyzed and was not subjected to sensitivity analysis.

Stingray Population Recruitment

We let realized λ (0.88) and apparent ϕ (0.85) parameters represent projected λ and annual survival rates, and used these values to estimate R_{now} , the net geometric per capita rate of growth (from MARK), for the purposes of determining mortality (d) and recruitment rates (f). Since $\lambda = (R + 1)$, $R_{\text{now}} = -0.12$, and we used an R of 0 and 0.15 for the different sensitivity λ 's. Mortality probability is simply calculated as $1 - \phi$, and therefore 0.15 was used for d . The recruitment rate into the population by births (b) and immigration (imm) was calculated as 0.03, 0.15, and 0.3 (for the different λ 's), using: $f = R - d$.

The total mortality-rate parameter was unchanged in the various sensitivity permutations of λ , as it represented the cumulative tourism-induced and natural mortality impacts. We did, however, vary the relative contributions of different tourism-mortality sources (more below). Based on previous research on stingray fitness metrics at SCS (Semeniuk and Rothley 2008; Semeniuk et al. unpubl. data), changes in stingray population size are likely to occur through immigration into the population, and not through an increase in birth rate nor a decrease in mortality rate. We therefore let b and imm both equal 0.015 (i.e, for *recruitment* =

0.03) under $\lambda < 1$, but we varied *imm* (0.135 and 0.285) and kept *b* at 0.015 (although density-dependent) for the λ sensitivity analyses.

Rays immigrate into population based on food available (Semeniuk and Rothley 2008). Available food is influenced by deliberate management directives, and the number of tourists. To simplify the model, we made the immigration rate of stingrays influenced primarily by the number of tourists ("Imm Rate based on Tourist#"). This relationship is modeled as a positive decelerating curve (eq. 9), constraining immigration rate to 0.015 at current tourist volume and at a $\lambda < 1$ (it will also equal 0.135 and 0.285 at the different λ 's). We also included a variable "net immigration scalar" to represent the immigration consequences of managing the amount of provisioned food. This latter variable slows down the immigration rate and also causes it to become negative (i.e., emigration) when the amount of provisioned food is no longer in excess, as dictated by management. However, an increasing tourist population will cancel out these effects. Furthermore, we also made immigration rate density-dependent, but only for when $\lambda \geq 1$ so as not to surpass the carrying capacity of 250 rays. The relationship between ray immigration rate and tourist density is:

$$\text{Imm_Rate_based_on_Tourist\#} = -3\text{E-}15(\text{Tourist } N_{\text{PM} + \text{PC}})^2 + 2\text{E-}08(\text{Tourist } N_{\text{PM} + \text{PC}}) - 0.0012. \quad (\text{eq. 9})$$

In sum, recruitment into the ray population was then:

$$(b * N_{\text{fem}}) + ((\text{Imm_Rate_based_on_Tourist\#} + \text{net_imm_scalar}) * N_{\text{fem}}).$$

(eq. 10)

Stingray Population ‘Mortality’

Stingray populations decline through emigration, natural mortality, and via tourism-induced mortality. The emigration rate was incorporated into the ‘recruitment’ portion of the model. Natural mortality rate (d_{nm}) was derived from the lifespan calculation based on average annual survival rates after Brownie et al. (1985):

$$\text{Lifespan} = 1 / -\ln(\text{survival}).$$

(eq. 11)

There are conflicting values of *Dasyatis americana* longevity estimates. García et al. (2007) cites a maximum lifespan of 18 years, while a captive study (Henningsen 2002) suggests 26 years. We used the shorter, more conservative lifespan to represent the average, and back calculated a natural mortality estimate (Brownie et al. 1985). Although the Hoenig (1983) formula is typically used to estimate natural mortality from longevity values in fish and reptiles, this formulation is not recommended for elasmobranchs (sharks and rays) as they return relatively high and implausible values (Frisk et al. 2001; Rodríguez-Cabello and Sánchez 2005). Elasmobranchs typically have low fecundity which is compensated for by investment in large offspring with high survival. They also have higher adult survival than the average teleost fish. The natural mortality-rate

estimate used in the model was therefore 0.054. This rate was held constant in the model, and represents natural sources of disease, predation and ageing.

Because the overall mortality rate was calculated from MARK as $1 - \phi$ (i.e., 0.15) and emigration at present scenario is assumed to be 0 and natural mortality is 0.054, tourism-induced mortality is consequently set to 0.096. Tourism-induced mortality is assumed to originate from three sources: direct mortality via predation and boat collisions (d_{PB}), indirect mortality via disease (d_D), and indirect mortality from sustained injuries (d_I). To account for increased predation risk (from shark predators), higher boat collisions, injuries, and disease caused by dense aggregation (Semeniuk and Rothley 2008), we have included a 'negative' density dependence of 50 rays to these mortality estimates, denoting that these mortality rates will decrease as stingray density declines to one-third its present population estimate.

With regards to mortality caused by increased predation (d_P), management plans which reduce the amount of provisioned food directly or indirectly (e.g., through a reduction of people and boats at any given time), will cause stingrays to forage for prey in their surrounding environment and away from the tourist site, thereby decreasing the probability of being detected and preyed upon by predators.

Mortality arising from boat collisions (d_B) can be reduced by management plans that reduce the number of boats allowed at the site at any given time, and also by

reducing the amount of food provisioned, as stingrays will then forage away from boats to find naturally-occurring prey (see Appendix 1 for equations).

Stingrays also sustain injuries from either conspecifics (d_{lc}) or heterospecifics (d_{lh} ; i.e., predators and boats). Stingrays at SCS display a large number of open wounds from bite marks from other rays as they aggressively compete for the food provisioned by tourists. The rays also exhibit wounds and scarring from predators, boat propellers, anchors and chains (Semeniuk and Rothley 2008). These injuries affect the rays by representing a source of stress to which they must devote energy and resources for repair, and therefore divert energy away from homeostatic maintenance which will eventually affect longevity (McNamara and Buchanan 2005). Therefore, we assume that any management plan which alleviates the crowding conditions (e.g., amount of provisioned food), improves the quality of food to aid the ray's repair system, and reduces collision risk with boats will reduce the mortality rate of stingrays caused by their injuries (see Appendix 1 for equations).

The last component of tourism-induced mortality, disease (d_D), is composed of two sources: disease caused through handling (d_{Dh}) and via crowding conditions (i.e., transmission; d_{Dc}). In the first instance, excessive handling of rays by tourists and tour operators can remove the protective mucous coating on the ray's skin which serves as a barrier to pathogen infection. Next, crowding conditions increases the virulence of infectious agents and transmission rate of

parasite loads; ectodermal isopod-parasite loads are higher in SCS rays than those not experiencing tourism (Semeniuk et al. 2008). These parasites are known to cause gill and skin lesions and blood loss; and heavy infections may cause osmotic imbalance, deleterious metabolic demands, and may open lesions facilitating invasion by opportunistic pathogens (Benz & Bullard 2004). These two sources of disease have a random component built in, to reflect the stochasticity of outbreaks of disease-inducing events such as hurricanes, oil spills, and environmental perturbations (e.g., algal blooms, etc.). Any management plan, therefore, which attempts to reduce people, or has explicit handling rules (i.e., touching, holding, and lifting the ray free of the water), or improves the quality of provisioned food to aid the ray's defense system will reduce the ray's likelihood of succumbing to disease (see Appendix 1 for equations).

In sum, 'mortality' of the ray population was then:

$$N_{\text{fem}} * (d_{nm} + d_P + d_B + d_{Ic} + d_{Ih} + d_D + d_{Dc}). \quad (\text{eq. 12})$$

As we do not know the relative contribution of each source of mortality on stingray mortality rate, we subjected tourism-induced mortality to sensitivity analysis. In the first instance, we assumed equal contribution of each mortality source; i.e., $PB=I=D$. Next, we assumed that predation and boats contributed the majority of mortality: $PB>I=D$; then injury: $I>PB=D$; disease: $D>I=PB$; and finally,

we assumed an equal and high contribution of both injury and disease to mortality rate: $PB \leq I = D$.

Stingray Life Expectancy Module

While the stingray population may increase or decrease, it is of equal importance to model the stingray's average life expectancy over the 25-year time series. Life span using eq. 10 was calculated at each time interval using the sum of mortality estimates for d_{nm} , d_{PB} , d_I and d_D .

APPLICATION

We began by calibrating the model to reproduce the measured data, and then ran each module separately to look for inconsistencies in behaviours. We used a yearly time step over a period of 25 years to investigate the evolution of the tourist life-cycle model of SCS which is presently approaching its 'consolidation' phase (Butler 1980). The six management plans were each simulated multiple times: each tourism-mortality sensitivity was run 10 times within the six management plans for the three different stingray population growth rates (i.e., 10x5x6x3 runs). Tourist- and stingray-population final values, and average stingray life expectancy along with its coefficient of variation (as a proxy for stability) were compared for each sensitivity within a management plan, then averaged to compare findings across management plans for each stingray λ .

Tukey-Kramer HSD was used to statistically compare the outputs of the various plans while protecting the overall error rate.

RESULTS

The tourist and stingray systems converged to a stable equilibrium (except for when periodic disease outbreaks took place); and tourist populations mostly fluctuated in response to the stingray population variable. Predictions of final outputs differed according to the management plan scenario, stingray population growth rate (λ) used, and relative contribution of tourism-induced mortalities (Tables 4-6). Regardless of λ , the current scenario of 'no management' results in the lowest total tourist population size while the feasible management plan ('5') results in the highest total tourist population size with PM-tourists completely replacing PC-tourists (Tables 4-6).

Under the scenario with a stingray population growth rate that is less than parity (Table 4) and where management did not address the food quality (i.e., plans 0-2, 4), the smallest stingray residual population size and the lowest life expectancy occurred when both disease and injury were the most important sources of mortality ($PB < I = D$). Conversely, the Feasible management plan "5" resulted in the largest ray population size and the longest lifespan when both injury and disease predominated. The next largest stingray population size and

longest average lifespan that occurred in the remaining plans were when either mortality from predation and boat collisions ($PB > I = D$) or injuries ($I > PB = D$) was the major source, possibly due to the minor impact stochastic disease processes would have on the relatively smaller contribution of this mortality variable. As such, while the Feasible plan ('5') resulted in the highest number of rays on average under the varying mortality sensitivities after 25 years, the plan controlling food quality predicted the second-largest mean population size and the second-highest average lifespan. Finally, under all sensitivities and management plans, PM-tourists replaced PC-tourists, with the PM tourist population reaching its maximum size under the Feasible management plan, and its lowest size under no management.

Under the scenario of a stable stingray population growth rate (Table 5), the differential mortality sensitivities had no effect on stingray population size under no management ('0'), when management controlled the amount of boats and people per visit ('1'), and when management restricted the handling of rays to tour operators ('4'; Table 5). Alternatively, controlling food quality (under management plans '5' and '3') had a differential effect on mortality sensitivities, resulting in positive effects when mortality was derived equally from injury and disease ($PB < I = D$). The outcome was the largest stingray population size and longest average lifespan given that all other mortality sensitivities were lower and relatively insensitive to these two management plans. Controlling the amount of food (management plan '2') also differentially affected stingray numbers under

different mortality sensitivities, with rays that were predisposed to succumbing to their injuries ($I > PB = D$) having the highest lifespan and population size, likely because controlling the food supply decreases the tendency of rays to aggregate, thereby reducing the rays' injury rates from conspecific aggression and boat collisions (the effects of food quantity on mortality from predators, boat collisions and disease are already low with this sensitivity). Under the remaining management plans, high injury mortality rates resulted in the lowest average lifespan. Finally, in contrast to when the ray population is assumed to be in decline, both the Feasible management plan ('5') and that controlling the amount of food provisioned ('2') resulted in similarly low population sizes under the varying mortality sensitivities; controlling the amount of food provisioned also predicted the second-highest average lifespan (after plan '5').

Interestingly, tourist population trends differed with ray mortality sensitivities and management plans under the scenario of a stable stingray population growth rate. For example, for all mortality sensitivities, both no management ('0') and crowd-control management ('1') resulted in PC-tourists out-competing PM-tourists due to the latter's lack of preference for these plans. Additionally, when tourism-induced mortality sensitivity was primarily driven by disease or at least disease was equal to the other sources (i.e., $D \geq (PB = I)$), PM-tourists were also replaced under the management plan of food quality control (plan '3'), likely given that PC-tourists have the highest preference for this plan, coupled with the resulting high number of rays remaining in the population, since with improved

food quality, fewer deaths occur due to disease, and emigration is unaffected (as proportion of food remains in excess). Similar to the scenario of a decline in the stingray population growth rate, the largest PM-tourist population size was predicted under the Feasible management plan.

Lastly, under the scenario of a stingray population growth rate that is greater than parity (Table 6), stingray population size under management plans 0, 1 (crowd control) and 2 (amount of food) was insensitive to differential sources of tourism mortality; however, lifespan was not, with high injury incidence ($I > PB = D$) resulting in shortest average lifespan for plans '0' and '1' (Table 6). Although the Feasible management plan resulted in the smallest stingray population size regardless of tourism-mortality sensitivities, it nonetheless predicted the longest average lifespan. In addition to the Feasible management plan, the plans controlling the quality of provisioned food ('3') and stingray handling conditions ('4') predicted the largest ray population sizes and longest lifespan when stingray mortality was derived mainly from the combined effect of equal and high prevalence of injury and disease ($PB < I = D$). With regards to tourist population numbers, PC tourists consistently replaced PM-tourists regardless of tourism-mortality sensitivities when no management ('0'), crowd control ('1'), and 'provisioned food quality control' ('3') plans were enacted. In contrast, the Feasible management plan always resulted in highest PM-tourist numbers, followed by the plan controlling the amount of provisioned food ('2').

With respect to how management affected the stochasticity in stingray lifespan, management plans '5' (feasible plan) and '2' (control of amount of provisioned food) offered the least amount of variation, regardless of what mortality sensitivity and stingray population trajectory were used (Tables 4-6). Likewise, for scenarios where stingray population growth rates were not stable (i.e., λ 's <1 and >1), no management plan ('0') and controlling the quality of provisioned food ('3') resulted in the greatest stochasticity, again irrespective of the tourism-mortality sensitivity. Under a stable population growth rate scenario ($\lambda = 1$), the plan which restricted handling the rays to tour operators (plan '4') resulted in a similarly large coefficient of variation. Importantly, coefficients of variation were internally consistent within each management plan for the differing mortality sensitivities.

DISCUSSION

Our findings indicate that the 'Stingray City Sandbar' attraction is currently caught in a social and ecological trap, and we discuss each one in turn.

Model predictions of social data

We predict that without site management, SCS tourist population numbers will fail to reach their potential maximum because too few stingrays will remain at the site (an undesirable attribute). In this instance, the ratio of tourists favouring

management to tourists favouring the status quo will remain constant, or tip toward pro-status quo tourists, depending on stingray λ . These outcomes will also contribute to producing the lowest stingray fitness, with populations being sustained through recruitment rather than increased survival. As a result, tourist population size (as a proxy for satisfaction since population dynamics are partly based on preferences) is not as high compared with other proposed management scenarios, suggesting a social trap. Although at first glance these results seem contradictory to one of the primary goals of management which is to reduce congestion, our intent was to show exactly how unfavourable this management plan is. If, in fact, a carrying capacity of one million tourists is imposed in the model for plans '1' (crowd-control) and '5' (feasible plan), the total tourist population will stabilize at this equilibrium point. Summarily, under a feasible management plan (i.e., '5'), while tourist population size would not increase should a visitor carrying capacity be implemented at the site, our findings predict that visitor satisfaction with their tourist experience would. Indeed, it has been suggested that in most wildlife tourism activities, the development goals of new markets should not be to increase numbers but rather to maximize the per unit value of each tourist (Dearden et al. 2006), both fiscally and non-market.

Model predictions of ecological data

'Stingray City Sandbar' also exhibits the traits required for the habitat to be classified as an ecological trap. For a trap to occur, habitat alteration must (1)

alter the cue set with which the animal assesses habitat quality (i.e., increase its attractiveness), (2) decrease the suitability of a habitat, or (3) do both simultaneously (Robertson & Hutto 2006). Firstly, rays clearly show a preference for the tourist-fed habitat: their high site fidelity, demonstrated through acoustic-telemetry tracking studies (Corcoran 2006) and an averaged yearly recapture rate of 0.925 (0.03 S.D.; C.A.D.S., unpubl. data), demonstrate non-random habitat use. Secondly, tourist-fed rays show indications of physiological costs of wildlife tourism (Semeniuk et al. unpubl. data); and exhibit evidence of nutritional deficiencies and reduced general health compared with un-fed rays (Semeniuk et al. 2007; Semeniuk and Rothley 2008), thus suggesting a compromised life expectancy. Indeed, the survival estimates from the mark-and-recapture work presented here (i.e., less than the average estimated lifespan of 18 years) further supports this finding. Lastly, the model predicts that management plans which do not address the major causes of stingray mortality (i.e., provisioned food quality and quantity) will not maintain or increase stingray numbers via increased survival but instead through new migrants, an exhaustible resource.

Tourism-induced mortality sensitivities

A high mortality predominance from both injuries and disease often resulted in the smallest population size and shortest average lifespan when management plans, regardless of the ray population growth rate, did not address the quality of food provisioned. Mortality sensitivities had less of an impact under a stable and positive stingray population growth rate, but again, a high mortality prevalence

stemming from both injuries and disease, when adequately addressed (i.e., management plans '3' and '5'), did result in larger population sizes and longer average lifespan. In addition, mortality from injury dominance ($I > PB = D$) predicted the lowest average ray lifespan for $\lambda \geq 1$ when the amount of food was not explicitly controlled (as in plans '2' and '5'). In our model, the quality and quantity of provisioned food have a pervasive effect on mortality sources, but not without sound reasoning. We believe these impacts on mortality to be a great contributor to stingray survival based on our previous research. Firstly, the amount of provisioned food at SCS is such that the southern stingray, a typically solitary forager, has transitioned to novel grouping behaviour and now forms a dense aggregation of individuals. In addition to the increased transmission of ectoparasites, over 80% of rays at SCS have injuries which stem from predator attacks, aggressive encounters with conspecifics, and from collisions with boat propellers and anchors (Semeniuk and Rothley 2008). These injuries can be categorized as having three effects: predator detection/defense, mobility-impairment, and susceptible-to-infection injuries. Indeed, the physiological indicators of wildlife-tourism costs measured in this population were partially influenced by both injuries and parasites (Semeniuk et al. unpubl.). Secondly, the results by Semeniuk et al. (2007 and unpubl.) suggest nutrition (i.e., quality) to play a very important role in the overall fitness of the southern stingray. For instance, the higher levels of oxidative stress, low serum protein concentrations, and low packed red blood cell volume can be influenced by a poor diet. Therefore, it is logical that a management plan addressing both the quality and/or

quantity of food would have the greatest effect on stingray survival when mortality stems primarily from resultant sustained injury and disease.

Management plan alternatives

Because of the sensitivity of the model to the different net per capital growth rates of the stingray population and the relative sources of stingray mortality, the most robust and consistent management plan in being able to: reduce stingray populations to levels without detriment to the tourist experience, increase the average lifespan of the ray, ensure visitor satisfaction is maximized, and promote the arrival and return of Pro-Management tourists is the 'Feasible' management plan. Perhaps unsurprisingly, this is because the plan addresses all sources of mortality, and was drastically preferred by pro-management tourists over those preferring the status-quo. In the absence of finer resolution of the data, this management option, the actions of which dictate reducing the density of boats and people at a given time, reducing the amount of provisioned food and simultaneously improving the quality of this supplemental diet, and restricting handling the rays to only the tour operator and preventing the removal of rays from the water for photographic opportunities will ensure an amelioration of the stingrays' well-being as well as an increase in visitor satisfaction.

What was unexpected from our model predictions, however, was the effects of controlling the quality and quantity of provisioned food. Although controlling food

quality ('3') might prove a reasonable strategy in terms of stingray population size and lifespan with a stingray $\lambda < 1$, this is not the case with higher stingray population growth rates under the majority of mortality-source sensitivities; for example, average lifespan ranks third or worse when assuming equal, high disease, high injury, or high direct (PB) relative mortality contributions. Additionally, the coefficient of variation (CV) is consistently high for this management plan regardless of λ and mortality sensitivities, denoting a less stable system. A possible reason for this result is that while the quality of food is improved, the plan still does not address mortality which occurs from most other sources such as boat collisions, predation, and density-related issues. Furthermore, in certain cases (particularly at $\lambda \geq 1$), PC-tourists are predicted to replace PM-tourists under this management plan, an unfavourable outcome.

Controlling the amount of provisioned food ('2') seems a more robust management plan under the differing sensitivities, consistently providing a second rank stingray lifespan and low associated CV, and although it also predicted low stingray population sizes at $\lambda's \geq 1$, this result is, in fact, favourable in alleviating the crowding conditions of stingrays at SCS, thus resulting in higher preferences for PM-tourists (i.e., fewest PC-tourists remaining after 25 years).

No management, simply controlling boat and tourist densities ('1'), or only restricting stingray handling to tour operators ('4') consistently predicted the

lowest stingray average lifespan regardless of the tourism-mortality sensitivities. Therefore, these management plan alternatives are not recommended.

Wildlife tourism as a source for ecological and social traps

Few studies have investigated both the social aspects of the wildlife tourism attraction alongside the ecological impacts. However, a key component to effectively managing wildlife is an understanding of the tourist's relationship to the resource. As Duffus and Dearden (1993: 151) suggest: "...both human and ecological dimensions must be understood, and balanced, in the planning stages for management. To ignore either is to invite conflict that will result in the degradation of the resource base...and/or degradation of the recreational experience." Generally stated, mitigating negative and promoting positive impacts of wildlife can only be achieved by bridging the gap between the social and natural sciences (Berkes and Folke 1998). Using the framework of how the evolution of the wildlife tourism life-cycle as a social trap can produce an ecological trap for wildlife can help bridge this gap. While conceptually perceptive, there has also been empirical support for this dynamic.

In a diver specialization study by Dearden et al. (2006), satisfaction with underwater environmental features in Phuket, Thailand, decreased as specialization increased, and the decline in the number of dive companies operating out of Phuket suggested the limits of acceptable environmental change

of coral-reef quality for both specialists and generalists had been exceeded. Higham's 1998 review of Royal Albatross (*Diomedea epomophora sanfordi*) tourism at Taiaroa Head, New Zealand, also demonstrates various dimensions of change over time: site users have transitioned from wildlife experts to novices, and the unique status of the small breeding colony of Albatrosses has become insufficient to guarantee visitor and tour guide satisfaction. Moreover, the nesting distribution of albatrosses has gradually shifted away from human presence and into sub-optimal nesting areas with a proportion of birds requiring breeding assistance. In another example, along the Gulf Coast of Central Florida, the doubling of visitation rates to manatee (*Trichechus manatus latirostris*) winter sanctuaries has compelled stakeholders to identify water quality, harassment, density and crowding, visitor displacement, need for education, and enforcement as causes of concern for management (Sorice et al. 2006). Impacts on the manatees involve changes in their behaviour presumed to have negative effects due to increased energetic expenditures of the animals which are already at the limit of their temperature-tolerant ranges in wintering habitats (King and Heinen 2004). In a last example, the wild dolphin-feeding program in Shark Bay, Western Australia, is currently at its stagnation level of the tourist lifecycle model, and plans are underway to increase site capacity and diversify the tourism product (Smith et al. 2006). However, respondents were unwilling to support further managerial development such as viewing platforms as they felt it would detract from their experience. Moreover, a study of the population of Shark Bay dolphins has revealed that the abundance of dolphins exposed to tourism vessels

(different from the feeding program) has decreased due to a long-term shift in habitat use, and that the decline is unlikely to be sustainable for local dolphin tourism (Bejder et al. 2006).

We believe that our results in addition to those from other tourism systems provide compelling evidence that wildlife tourism can act as both social and ecological traps. Due to the shift over time in behaviors and expectations, tourists are engaging in activities that have the ability to affect the long-term fitness of the focal animals. Animals are either using their traditional breeding and foraging sites (now deteriorated), are attracted to novel ones (in the case of supplemental feeding) or, equally, attracted to sub-optimal habitat to avoid disturbances, all without necessarily perceiving the long-term costs associated with their behaviours. Consequently, biodiversity can be lost, reproductive success reduced, animal welfare compromised, abundance in decline, and life expectancy lowered. These tourist actions will also eventually undermine and spoil the tourist experience whether it be via the deterioration in the quality of the environment, fewer wildlife to observe or to interact with, a resistance to management plans, or concern about animal welfare and conservation. In essence, wildlife tourism can cause social traps that in turn result in ecological traps, affecting the sustainability of the tourism product.

Value of integrating ecological and social data

Overall, our model illustrates the predictive power of combining interactions between social and ecological/biological systems which have often proven difficult to quantify. A model, which can be considered somewhat unwieldy, but which integrates the human/animal system is possible and gives useful predictions. System dynamics models which have accomplished such feats are found in studies on nature-based tourism and its associated industry sectors (van den Belt et al. 1998, Patterson et al. 2004, Hernández and León 2007), water resource management (Stave 2003; Tidwell et al. 2004), and rangeland management and policy (Janssen et al. 2000). Modelling in general can help clarify inter-linkages between different sectors, and can be used as a background for development of policies and a forum for discussion (van den Belt et al. 1998). Our SCS model predicts which management option is best (and second-best, etc.), and suggests that social and ecological traps are indeed occurring, and in the absence of management, will lead to declines in both tourist experience and ray population. This is the first instance we know of which has attempted to relate quantitative visitor preference data to tourist and wildlife population dynamics. We believe our model can provide a valuable tool for the synthesis of data and theories of alternative policies on both the ecological and social science front. New data can be incorporated as it becomes available, and other modules can be added to expand the system beyond that of the tourist and wildlife (for instance, tour operators, local businesses, competing sites, etc.). For the present time, the results of this integrative model can be used by Caymanians to explore more than one potential socio-ecological outcome in a transparent fashion for

their management-related mandate, and will represent an analysis of alternative policies or management actions for policy makers to choose from (Noss 2007, Scott et al. 2007). These considerations can then feed into the policy-process and, ultimately, become part of institutional analysis and iterative public dialogue.

Our model is not without its limitations. The sensitivity of our results to the different λ 's and mortality estimates highlight the need to accumulate long-term population census data sets. In addition, the continuous collection of fitness metrics such as parasite loads and injuries, as well as physiological general-health parameters of oxidative stress and immune function, etc., can allow one to differentiate between the contribution of disease- and injury- induced mortality and collision- and predator-induced mortalities to the overall mortality estimate in the mark-and-recapture programs. This would help reduce the uncertainty in the model as to sources of mortality which we were unable to accommodate other than through a sensitivity analysis, since different indicators were collected in different years. We were relatively unconcerned, however, with adjusting our carrying capacity variables for both tourists and stingrays as we were more interested in exploring the relative differences between management plans than in determining absolute final output values. We acknowledge that data gaps exist in our model (e.g., stage-based stingray population structure, individual optimization behaviours), but its purpose nonetheless was to provide a model to adequately assess different management practices at a broad, simplified scale, and to provide low-resolution data for interpretations of general trends.

Furthermore, our model does not attempt to make absolute predictions but relative ones, by ranking different management options, a practice encouraged in simulation modeling (Grimm and Volker 2005). The idea here is to provide wildlife tourism managers with the tools to predict how and why key wildlife and tourist variables will interact to impact the ecological and social continuance of this tourism experience.

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Table 6.1 Management plans compared in the STELLA simulation model.
Bolded levels represent changes from the current scenario (0) of
‘No Management’.

Management Plans	Management Attributes						
	Number of Boats	Number of Surrounding People	Stingray Feeding	Stingray Handling	Number of Surrounding Rays	Ray Risk of Injury	Conservation Access Fee
‘0’ - No Management	40	1000	Operator & Tourist	Operator & Tourist	55	High	None
‘1’ - Congestion Control	20	500	Operator & Tourist	Operator & Tourist	40	Medium	5\$ USD
‘2’ – Amount of Food	40	1000	Operator only	Operator & Tourist	40	Medium	None
‘3’ – Food Quality Control	40	1000	Operator & Tourist	Operator & Tourist	55	Medium	5\$ USD
‘4’ – Handling Rules	40	1000	Operator & Tourist	Operator only	55	Medium	None
‘5’ – Feasible Plan	20	500	Operator only	Operator only	40	Low	5\$ USD

Table 6.2 Relative change in support over status quo (No Management) of pro-management (PM) and pro-current (PC) tourists and the associated stingray fitness effects for different management plans.

Management Plans	Relative Change of Part-Worth Utility Support		Effects on Stingray Fitness
	PM	PC	
'0' - No Management	1	1	Boat-collision mortality, predation mortality; disease caused via handling stress, inadequate maintenance due to injuries, crowding conditions, inadequate food quality; excess food and no emigration
'1' - Congestion Control	1.498	1.395	Fewer collision mortalities, reduced handling by tourists
'2' - Amount of Food	1.371	0.450	More natural foraging; immigration decreased and emigration increased; less ray congestion – lower predation, injury and disease caused by crowding
'3' - Food Quality Control	1.333	1.179	Food quantity kept constant; quality through specially-formulated diet is improved; immigration and emigration not affected; disease and injury caused by inadequate diet is reduced
'4' - Handling Rules	1.389	0.900	Disease caused by excessive handling by tourists is reduced
'5' - Feasible Plan	1.513	0.392	Combined effects of plans 1-5

Table 6.3 Parameters and values used in Stingray City Sandbar Management Model.

Parameter	Value	Source
State Variables		
Pro-Management Starting Population	552 000	2006 Cayman Islands Port Authority (68% from latent class analysis)
Pro-Current Starting Population	226 000	2006 Cayman Islands Port Authority (32% from LCA)
Female Stingray Starting Population	150	tour operator input and tagging study
Auxiliary Variables		
<i>Tourists:</i>		
Carrying Capacity	2 000 000	estimated maximum cruise ship capacity
Per capita rate of growth (R_{now})	0.137	calculated as value that minimized the sum of the squares of the differences between the mean and actual population-size values over time
PM departure rate	0.9265	calculated from the proportion of PM tourists in the population and proportion of returning visitors (from survey)
PC departure rate	0.8125	calculated from the proportion of PC tourists in the population and proportion of returning visitors (from survey)
density-dependent PM arrival rate	1.064	calculated from tourist population growth rate (R_{now}) and PM departure rate
density-dependent PC arrival rate	0.950	calculated from tourist population growth rate (R_{now}) and PC departure rate
PM/PC Plan Prefs	see Table 2	calculated as the percent relative change in support over status quo from a stated preference, discrete choice experiment.
PM/PC Ray Pop Prefs	see eq.s 3 and 4	population-level estimate extrapolated from relationship of tourist preferences for number of immediate, surrounding rays per trip
PM/PC People Pop Prefs	see eq.s 5 and 6	population-level estimate extrapolated from relationship of tourist preferences for number of people allowed per trip

<i>Stingray</i>		
Carrying capacity	250	an estimate allowing stingray population to grow
Per capita rate of growth (R)	-0.12, 0, 0.15	sensitivity values calculated from population growth rate ($\lambda = 0.88$ (from Pradel model), 1, and 1.5)
Overall mortality probability (d_{total})	0.15	calculated as (1- survival) from Pradel model
Birth Rate (b)	0.015	one half the recruitment rate, calculated from (recruitment = $R - d$)
net immigration scalar	0, \geq (- <i>imm</i> sensitivity)	considers magnitude of immigration/ emigration under different management plans
Imm_Rate_based_on_Tourist#	see eq. 10 (max: 0.031, min: 0)	estimated positive decelerating curve
Natural mortality rate (d_{nm})	0.054	based on average life-expectancy of 18 years using eq. 12.
Mortality rate of predation and boat collision (d_{PB})	0.008, 0.016, 0.032 each	sensitivity values for direct tourism-induced mortality; mortality estimated as a proportion of overall mortality rate calculated from Pradel survival estimate
Mortality rate of conspecific and heterospecific injury ($d_{lc, lh}$)	same as above	sensitivity values for indirect tourism-induced mortality; mortality estimated as a proportion of overall mortality rate calculated from Pradel survival estimate
Mortality rate of handling- and crowding-disease	same as above	sensitivity values for indirect tourism-induced mortality; mortality estimated as a proportion of overall mortality rate calculated from Pradel survival estimate
Driving Variables		
stingray population growth rate (λ) via immigration rate (<i>imm</i>)	λ : 0.88 (1.0 and 1.15 sensitivity); <i>imm</i> : 0.015, 0.135, 0.285	0.88 value calculated from Pradel model; <i>imm</i> values calculated from recruitment: $b - imm = R - d$
stingray tourism-induced mortality estimates	values of 0.16, 0.32, 0.64 used in sensitivity analyses to total 0.096 ($d_{total} - d_{nm}$)	PB=I=D; PB>I=D; I>PB=D; D>PB=I; PB<I=D see text and Appendix for details
Management scenario	see Tables 1 and 2	Caymanian stakeholder input

Table 6.4 Model predictions with stingray $\lambda = 0.88$ (from Pradel model).

		Management Plans*					
Model Output after 25 years**		'0' – No Management	'1' - Congestion Control	'2' – Amount of Food	'3' – Food Quality Control	'4' – Handling Rules	'5' – Feasible Plan
Female Ray Population Size (current: 150 rays)	Equal:	21 ¹	29 ¹	26 ¹	40 ^{1,2}	33 ¹	55 ¹
	PB:	34 ²	43 ²	36 ²	41 ^{1,2}	42 ^{2,3}	56 ¹
	I:	34 ²	40 ²	38 ²	46 ¹	45 ²	52 ¹
	D:	20 ^{1,3}	37 ²	24 ¹	34 ²	37 ^{1,3}	44 ²
	I&D:	14 ³	19 ³	13 ³	40 ^{1,2}	17 ⁴	64 ³
	Mean:	25 ^a	34 ^b	27 ^a	40 ^c	35 ^b	54 ^d
Mean Ray Life Expectancy (years)	Equal:	9.5 ¹	9.5 ¹	9.7 ¹	11.4 ¹	9.6 ¹	14.6 ¹
	PB:	11.3 ²	11.2 ²	11.5 ²	11.9 ¹	10.9 ²	14.6 ¹
	I:	11.1 ²	11.0 ²	11.6 ²	12.4 ²	11.1 ²	14.2 ²
	D:	9.0 ^{1,3}	9.9 ³	9.4 ³	10.0 ³	10 ³	12.6 ³
	I&D:	7.5 ⁴	7.6 ⁴	7.6 ⁴	11.4 ¹	7.5 ⁴	12.6 ⁴
	Mean:	9.6 ^a	9.8 ^a	10.0 ^a	11.4 ^b	9.8 ^a	14.4 ^c
Coefficient of Variation in Life Expectancy	Equal:	0.244 ¹	0.212 ^{1,2}	0.152 ¹	0.235 ^{1,2}	0.191 ^{1,2}	0.128 ¹
	PB:	0.250 ¹	0.225 ^{1,2}	0.198 ²	0.279 ¹	0.224 ¹	0.334 ¹
	I:	0.265 ¹	0.252 ¹	0.166 ¹	0.277 ¹	0.231 ¹	0.161 ²
	D:	0.224 ¹	0.181 ^{2,3}	0.141 ¹	0.198 ²	0.189 ^{1,2}	0.127 ¹
	I&D:	0.169 ²	0.152 ³	0.136 ¹	0.199 ²	0.161 ²	0.104 ³
	Mean:	0.230 ^a	0.204 ^b	0.159 ^c	0.238 ^a	0.199 ^b	0.131 ^d
PM Tourist Population Size (current: 552 000)	Equal:	869 647 ¹	1 253 009 ¹	1 176 973 ¹	1 200 214 ^{1,2}	1 211 506 ¹	1 318 670 ¹
	PB:	923 239 ²	1 288 151 ²	1 207 232 ²	1 202 564 ^{1,2}	1 236 948 ²	1 320 461 ¹
	I:	919 417 ²	1 280 680 ²	1 218 629 ²	1 216 908 ¹	1 243 571 ²	1 315 756 ¹
	D:	867 106 ¹	1 274 385 ²	1 174 523 ¹	1 184 043 ²	1 221 843 ¹	1 299 543 ²
	I&D:	864 840 ¹	1 240 625 ¹	1 169 914 ¹	1 201 046 ^{1,2}	1 181 382 ³	1 331 046 ³
	Mean:	888 850 ^a	1 267 370 ^b	1 189 454 ^c	1 200 955 ^c	1 219 050 ^d	1 317 095 ^e
PC Tourist Population Size (current: 260 000)	Equal:	29	385	0	35	0	0
	PB:	52	598	0	32	0	0
	I:	57	527	0	30	0	0
	D:	35	525	0	21	0	0
	I&D:	22	228	0	45	0	0
	Mean:	39	453	0	33	0	0
Total Tourist Population Size		888 889	1 267 823	1 189 454	1 200 988	1 219 050	1 317 095

* different superscript letters represent significant differences between management plans within each trait.

** different superscript numbers represent significant differences between mortality sensitivities within each plan. Statistical differences are omitted for PM or PC tourist values that are relatively insignificant to the total tourist population size.

Table 6.5 Model predictions with stingray $\lambda = 1.0$ (sensitivity analysis)

		Management Plans*					
Model Output after 25 years**		'0' – No Management	'1' – Congestion Control	'2' – Amount of Food	'3' – Food Quality Control	'4' – Handling Rules	'5' – Feasible Plan
Female Ray Population Size (current: 150 rays)	Equal:	158 ¹	182 ¹	129 ^{1,3}	178 ¹	173 ¹	135 ¹
	PB:	157 ¹	183 ₁	132 ^{1,2}	171 ¹	168 ¹	128 ^{1,2}
	I:	156 ¹	175 ¹	137 ²	171 ¹	166 ¹	122 ²
	D:	153 ¹	177 ¹	125 ^{3,4}	173 ¹	173 ¹	122 ²
	I&D:	155 ¹	174 ¹	121 ⁴	191 ²	174 ¹	144 ³
	Mean:	156 ^a	178 ^c	129 ^b	177 ^c	171 ^d	129 ^b
Mean Ray Life Expectancy (years)	Equal:	5.9 ^{1,2}	6.0 ¹	7.7 ¹	6.6 ¹	5.8 ¹	12.5 ¹
	PB:	5.9 ¹	6.1 ²	8.0 ²	5.8 ²	5.6 ²	12.1 ²
	I:	5.75 ²	5.5 ³	8.3 ³	5.8 ²	5.4 ³	11.0 ³
	D:	5.9 ¹	6.2 ²	7.6 ¹	6.1 ³	6.0 ⁴	10.8 ⁴
	I&D:	5.9 ¹	5.9 ¹	6.9 ⁴	8.2 ⁴	5.9 ¹	14.6 ⁵
	Mean:	5.9 ^a	5.95 ^a	7.7 ^b	6.5 ^b	5.75 ^b	12.2 ^d
Coefficient of Variation in Life Expectancy	Equal:	0.167 ¹	0.159 ¹	0.121 ¹	0.171 ¹	0.165 ¹	0.110 ¹
	PB:	0.153 ¹	0.144 ¹	0.120 ¹	0.163 ¹	0.162 ¹	0.115 ¹
	I:	0.150 ¹	0.157 ¹	0.123 ¹	0.156 ¹	0.170 ¹	0.107 ¹
	D:	0.167 ¹	0.157 ¹	0.125 ¹	0.162 ¹	0.167 ₁	0.101 ¹
	I&D:	0.151 ¹	0.155 ¹	0.119 ¹	0.181 ¹	0.152 ₁	0.111 ¹
	Mean:	0.158 ^a	0.154 ^a	0.122 ^b	0.167 ^a	0.163 ^a	0.109 ^b
PM Tourist Population Size (current: 552 000)	Equal:	487 109 ¹	128 716 ¹	1 258 439 ^{1,2}	340 318 ¹	1 123 149 ¹	1 317 774 ¹
	PB:	427 993 ¹	80 987 ¹	1 252 080 ²	782 219 ²	1 136 695 ¹	1 323 000 ¹
	I:	510 231 ¹	232 833 ²	1 241 286 ³	695 676 ²	1 153 826 ¹	1 332 283 ²
	D:	455 994 ¹	81 185 ¹	1 262 738 ^{1,4}	517 645 ³	1 118 484 ¹	1 332 388 ²
	I&D:	421 220 ¹	140 870 ¹	1 270 751 ⁴	68 694 ⁴	1 125 535 ¹	1 293 492 ³
	Mean:	460 509 ^a	132 918 ^b	1 257 059 ^c	470 231 ^a	1 131 538 ^d	1 319 787 ^c
PC Tourist Population Size (current: 260 000)	Equal:	430 495 ¹	1 128 098 ¹	0	758 665 ¹	330	0
	PB:	494 430 ¹	1 183 745 ¹	0	372 640 ²	246	0
	I:	407 154 ¹	1 014 709 ²	0	404 427 ²	183	0
	D:	461 688 ¹	1 180 757 ¹	0	576 772 ³	480	0
	I&D:	496 015 ¹	1 114 220 ¹	0	1 054 855 ⁴	467	0
	Mean:	457 956 ^a	1 124 306 ^b	0 ^c	633 472 ^d	342 ^c	0 ^c
Total Tourist Population Size		918 465	1 257 224	1 257 059	1 103703	1 131 880	1 319 787

* different superscript letters represent significant differences between management plans within each trait.

** different superscript numbers represent significant differences between mortality sensitivities within each plan. Statistical differences are omitted for PM or PC tourist values that are relatively insignificant to the total tourist population size.

Table 6.6 Model predictions with stingray $\lambda = 1.15$ (sensitivity analysis).

		Management Plans*					
Model Output after 25 years**		'0' – No Management	'1' - Congestion Control	'2' – Amount of Food	'3' – Food Quality Control	'4' – Handling Rules	'5' – Feasible Plan
Female Ray Population Size (current: 150 rays)	Equal:	202 ¹	216 ¹	167 ¹	211 ^{1,2}	198 ^{1,2}	165 ¹
	PB:	199 ¹	216 ¹	168 ¹	206 ²	199 ^{1,2}	164 ¹
	I:	199 ¹	210 ¹	169 ¹	204 ²	194 ²	158 ²
	D:	202 ¹	215 ¹	167 ¹	205 ²	198 ^{1,2}	160 ²
	I&D:	204 ¹	213 ¹	166 ¹	219 ¹	203 ¹	173 ³
	Mean:	201 ^a	214 ^b	167 ^c	209 ^d	199 ^a	164 ^c
Mean Ray Life Expectancy (years)	Equal:	5.1 ¹	5.5 ^{1,2}	6.9 ¹	5.7 ¹	5.2 ¹	11.6 ¹
	PB:	4.8 ²	5.4 ²	7.0 ¹	4.9 ²	4.9 ²	11.1 ²
	I:	4.7 ³	4.7 ³	7.3 ²	4.9 ²	4.7 ³	9.8 ³
	D:	5.1 ¹	5.6 ^{1,4}	7.0 ¹	5.3 ³	5.5 ⁴	10.0 ⁴
	I&D:	5.4 ⁴	5.6 ⁴	6.6 ³	7.6 ⁴	5.6 ⁴	14.1 ⁵
	Mean:	5.0 ^a	5.4 ^{a,c}	6.95 ^b	5.7 ^c	5.2 ^a	11.3 ^d
Coefficient of Variation in Life Expectancy	Equal:	0.169 ¹	0.158 ¹	0.143 ¹	0.203 ¹	0.171 ¹	0.165 ^{1,2}
	PB:	0.171 ¹	0.169 ¹	0.143 ¹	0.171 ^{1,2}	0.162 ¹	0.122 ^{1,2}
	I:	0.188 ¹	0.169 ¹	0.139 ¹	0.180 ^{1,2}	0.143 ¹	0.134 ¹
	D:	0.161 ¹	0.153 ¹	0.138 ¹	0.161 ²	0.158 ¹	0.114 ²
	I&D:	0.171 ¹	0.165 ¹	0.143 ¹	0.169 ^{1,2}	0.126 ¹	0.126 ²
	Mean:	0.172 ^{a,c}	0.163 ^{a,c}	0.139 ^b	0.177 ^a	0.158 ^c	0.122 ^d
PM Tourist Population Size (current: 552 000)	Equal:	13	31	1 130 623 ¹	126	788 416 ¹	1 232 315 ¹
	PB:	28	35	1 134 435 ¹	397	866 949 ²	1 233 600 ¹
	I:	63	126	1 130 662 ¹	551	905 655 ²	1 253 536 ²
	D:	10	22	1 138 224 ¹	189	685 753 ³	1 248 098 ²
	I&D:	5	30	1 147 360 ¹	6	683 728 ³	1 200 364 ³
	Mean:	24 ^a	49 ^a	1 136 261 ^b	254 ^a	786 103 ^c	1 233 583 ^d
PC Tourist Population Size (current: 260 000)	Equal:	1 005 038 ¹	1 301 730 ^{1,2}	0	1 150 718 ¹	143 509 ¹	0
	PB:	1 000 640 ¹	1 302 133 ^{1,2}	0	1 150 981 ¹	76 740 ²	0
	I:	997 340 ¹	1 295 450 ²	0	1 147 397 ¹	68 862 ²	0
	D:	1 003 200 ¹	1 302 932 ¹	0	1 150 318 ¹	207 183 ³	0
	I&D:	1 006 652 ¹	1 299 133 ^{1,2}	0	1 163 085 ²	211 598 ³	0
	Mean:	1 002 574 ^a	1 300 276 ^b	0 ^c	1 152 500 ^d	141 578 ^e	0 ^c
Total Tourist Population Size		1 002 598	1 300 325	1 136 261	1 152 754	927 681	1 233 583

* different superscript letters represent significant differences between management plans within each trait.

** different superscript numbers represent significant differences between mortality sensitivities within each plan. Statistical differences are omitted for PM or PC tourist values that are relatively insignificant to the total tourist population size.

Figure 6.1 Conceptual diagram of the interlinked ecological and social system of SCS.

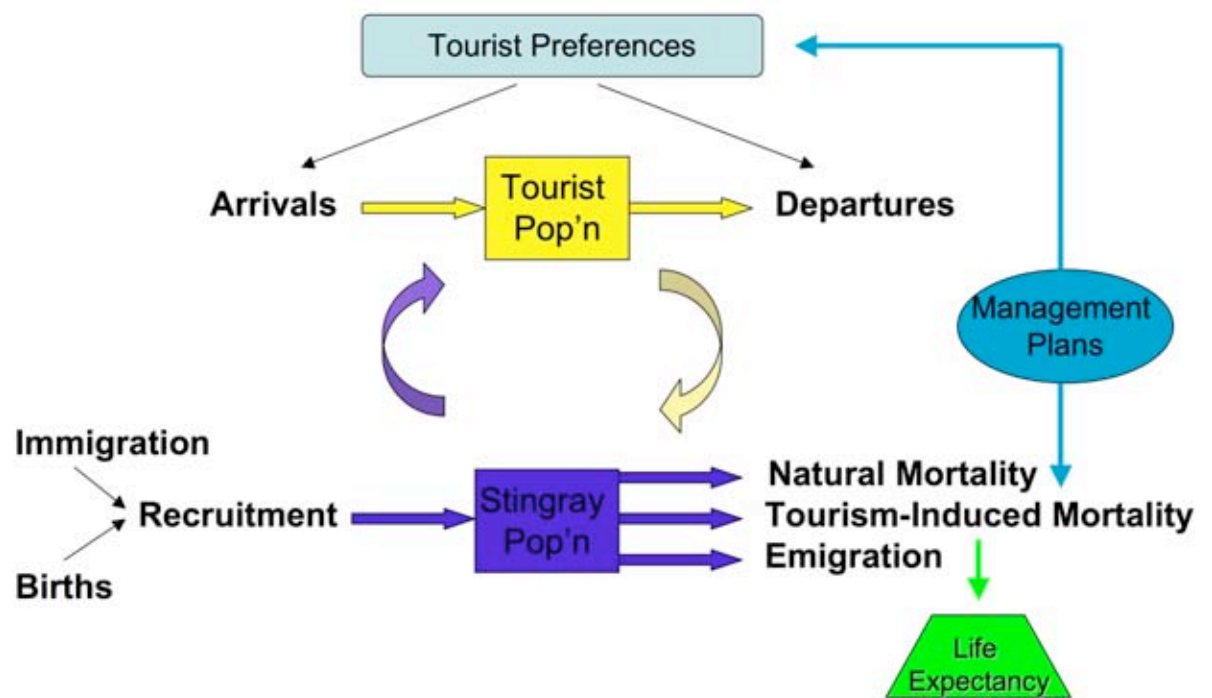


Figure 6.2 STELLA diagram of the ‘Tourist Module’ of Stingray City Sandbar Model. PM and PC tourists had their own module each with segment-specific inputs.

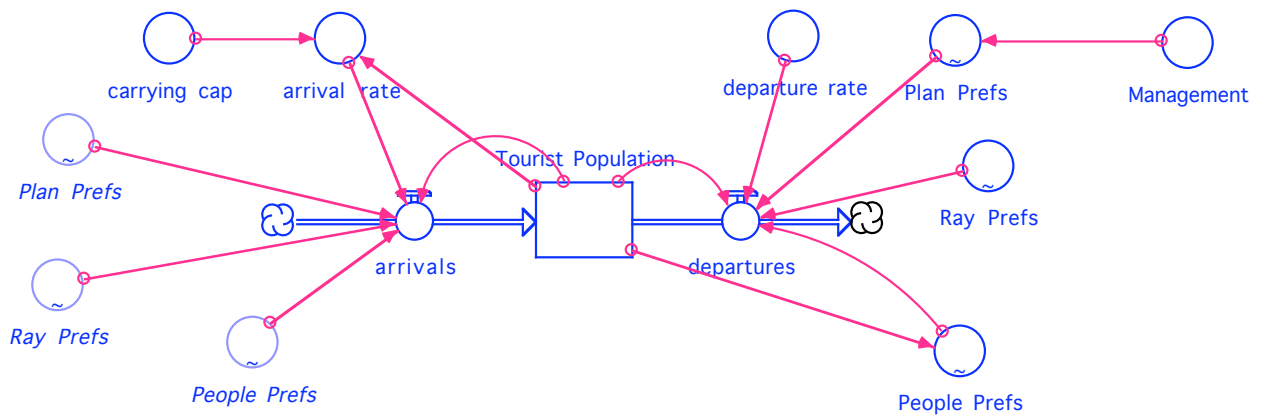


Figure 6.3 STELLA diagram of the ‘Stingray Recruitment Module’ of Stingray City Sandbar Model.

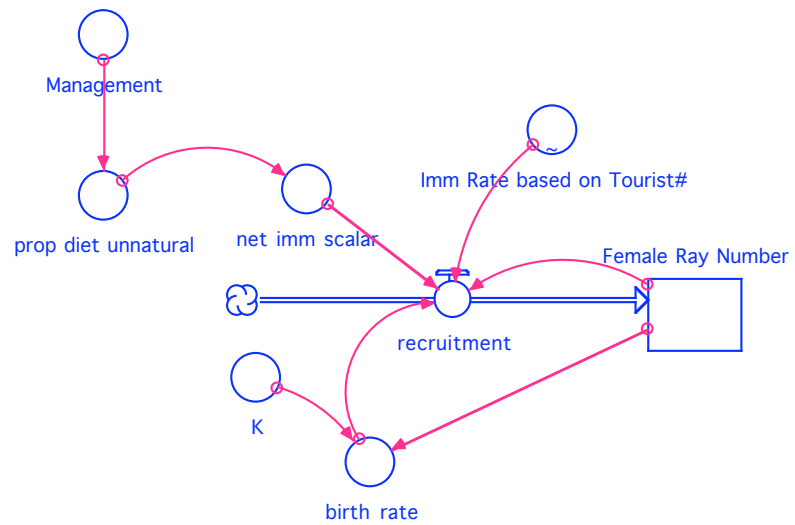
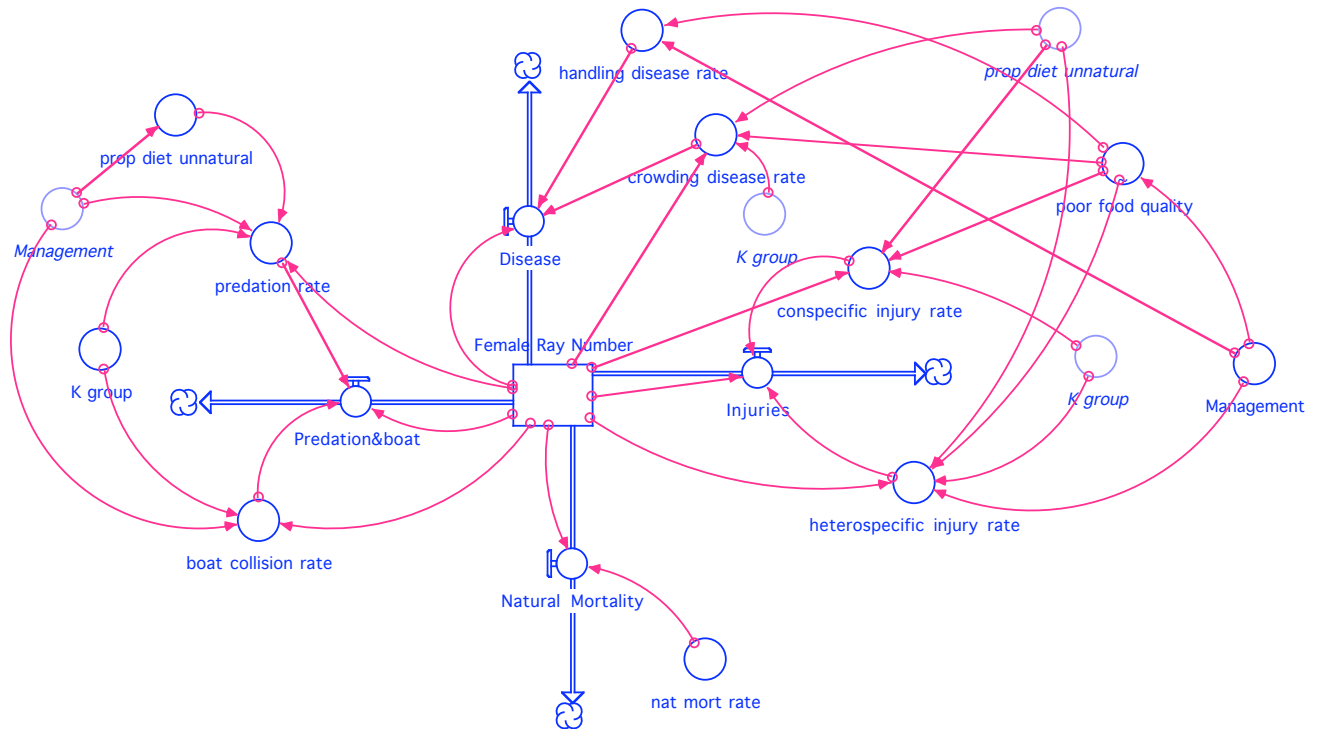


Figure 6.4 STELLA diagram of the ‘Stingray Mortality Module’ of Stingray City Sandbar Model.



APPENDIX. Equations used to calculate the different tourism-induced stingray mortality estimates.

Mortality rate by predation (d_P) = IF(prop_diet_unnatural>1 OR (Management = 0 OR Management = 3 OR Management = 4)) THEN(-0.008*(1-(Female_Ray_Number/K_group))) ELSE (IF(Management = 2) THEN (-0.006*(1-(Female_Ray_Number/K_group))) ELSE(IF(prop_diet_unnatural<1.0 OR (Management = 1 OR Management = 5))THEN (-0.004*(prop_diet_unnatural)*(1-(Female_Ray_Number/K_group)))ELSE 0.016))

(eq. 1)

Mortality rate by boat collisions (d_B) = IF(Management=0) OR (Management=4) OR (Management=3) THEN(-0.008*(1-(Female_Ray_Number/K_group))) ELSE IF(Management=2) THEN (-0.006*(1-Female_Ray_Number/K_group))ELSE IF(Management=1) OR (Management=5)THEN(-0.004*(1-Female_Ray_Number/K_group)) ELSE(0.016)

(eq. 2)

Mortality rate by conspecific injuries (d_{lc}) = IF(prop_diet_unnatural>1.0)THEN ((poor_food_quality_mortality_rate)+(-0.004*(1-(Female_Ray_Number/K_group)))) ELSE (IF(prop_diet_unnatural<=1.0)THEN ((poor_food_quality_mortality_rate)+(-0.002*(1-(Female_Ray_Number/K_group))))ELSE (-0.008*(1-(Female_Ray_Number/K_group)))).

(eq. 3)

Mortality rate by heterospecific injuries (d_{ih}) = IF(prop_diet_unnatural>1.0 OR
(Management = 0 OR Management = 3 OR Management = 4))THEN
((poor_food_quality_mortality_rate)+(-0.004*(1-
(Female_Ray_Number/K_group)))) ELSE (IF((prop_diet_unnatural<=1.0) OR
Management = 1 OR Management = 2 OR Management = 5) THEN
(poor_food_quality_mortality_rate)+(-0.002*(1-
(Female_Ray_Number/K_group))))ELSE (-0.008*(1-(Female_Ray_Number/
K_group)))).

(eq. 4)

Mortality rate by disease through handling (d_{Dh}) = IF(Management=0 OR
Management = 2 OR Management = 3) THEN (IF (RANDOM(0,100)<2) THEN
0.25 ELSE ((poor_food_quality_mortality_rate)+0.008)) ELSE
(IF(Management=4 OR Management = 1 OR Management = 5) THEN (IF
(RANDOM(0,1000)<2)THEN 0.25 ELSE
((poor_food_quality_mortality_rate)+0.004)) ELSE 0.016).

(eq.5)

Mortality rate by disease through crowding (d_{Dc}) = IF(prop_diet_unnatural>1.0)
THEN (IF(RANDOM(1,100)<6)THEN 0.25 ELSE
((poor_food_quality_mortality_rate)+(-0.004*(1-(Female_Ray_Number/

```

K_group)))))) ELSE (IF(prop_diet_unnatural<=1.0)THEN
(IF(RANDOM(1,1000)<6)THEN 0.25 ELSE
((poor_food_quality_mortality_rate)+(-0.002* (1-(Female_Ray_Number/
K_group)))))) ELSE (-0.008*(1-(Female_Ray_Number/K_group))))).

```

(eq. 6)

N.B. The variable “poor_food_quality_mortality_rate” ranges from 0 (for management plan 5) and 0.002 (management plan 3) to 0.008 (for plans 0, 1, 2 and 4). Under the different tourism-induced mortality sensitivities, the relative impact from poor food quality was kept constant for each variable it influenced; instead mortality arising from the express effects of handling, crowding, conspecific injuries and heterospecific injuries were allowed to differentially vary.

CHAPTER 7: THESIS SUMMARY

INTRODUCTION

Natural resource management systems are complex systems distinguished by multiple scales and sectors that make them context specific; they are characterized by various feedback processes, time delays and non-linearities; and typically possess stakeholders of divergent and conflicting values and goals (Campbell et al. 2001). Natural resource management therefore requires the integration of diverse sources and types of knowledge into the decision-making process. To be successful, this approach must first develop conceptual models that simplify the system and make explicit the key components and interactions; ensure careful social and ecological indicator selection that allows for their amalgamation; and then subsequently create simulation models to understand system performance, while acknowledging the propensity for systems to behave in unpredictable ways (Campbell et al. 2001; Neff 2007). According to Daily (1999), scientists must be able to translate such possible trajectories into meaningful social terms, concerning basic economic, health, and other aspects of human well-being. Nonetheless, while applied ecologists recognize the importance of social processes within ecological systems, they seldom address them with the analytical or intellectual rigor with which they address ecological processes. Similarly, social scientists address environmental issues, but seldom

examine specific connections between social and biophysical processes (Grant et al. 2002). Although there is a recognized need for integrated (physical, biological, social) models to address a variety of natural resource management issues, relatively few truly integrated quantitative models exist that synthesize current theories in the natural and social sciences (Grant et al. 2002; Deconchat et al. 2007).

FINDINGS SUMMARY

This thesis has attempted to synergize the natural and social sciences using a compatible theory of social and ecological traps for the management of wildlife tourism systems and the conflict they engender. To reiterate, this theory posits that in an attempt to maximize their tourism experience, visitors at wildlife-tourism attractions can potentially engage in activities and/or possess behaviours that can alter the environment for the focal species. Wildlife, faced with changes in their environment, can then make maladaptive decisions about foraging or breeding habitats which will negatively impact their survival and/or reproduction. Consequently, this reduction in fitness will translate into reduced wildlife numbers, and in some cases, unhealthy animals, which will cause the visitor site to become less attractive. As a result, tourist numbers will begin to decline in turn, or equivalently, the tourist experience will not be maximized. The 'trap' framework necessitates the choosing of appropriate indicators to reflect the condition of and relationship between the ecological and social aspects of the human-wildlife interaction that could lead to a deteriorated wildlife experience and actual wildlife fitness; and the incorporation of the ecological and social

findings into an integrated model to simulate the impact of alternative management policies on the various ecological and social system components. How each thesis data chapter contributes to the trap framework is discussed in turn.

To begin, chapter 2 comprised the social component of the thesis, and strove to determine tourist typology and preferences for the management of the stingray-feeding tourist attraction, so that Caymanian stakeholders would have an idea of how tourists would react to any management proposed. The indicators in this chapter revealed that while tourists are very satisfied overall with their wildlife interaction at SCS, they nonetheless: would like to learn more about the natural history of stingrays and the surrounding environment; and require education and/or interpretation regarding the consequences of their actions/desire as they still prefer to feed and handle stingrays themselves. However, the majority are willing to have activities regulated to a certain extent, and are willing to pay a conservation access fee to the site. From these data there was the suggestion of the possibility of a trap occurring: just over half of the tourists expressed 'mild' concern for potential negative impacts arising at the attraction and 22% felt 'low' concern. Research on the stingrays at the site reveals serious harmful implications of tourist interactions with these animals; therefore, visitors at Stingray City Sandbar, in their quest to maximize their satisfaction, are engaging in activities that are unsafe to the health of the stingrays. Further evidence from the discrete choice survey suggests that realization of this high risk of injury to

the stingrays would result in significant diminishment of trip experience (expressed as reduced preference for this management outcome), again intimating that a social trap, in which reduced satisfaction is followed by tourist population declines, is a distinct possibility. The suggestion of a social trap is later confirmed by the system dynamics model (discussed more below).

Tour operators believed prior to this research that the stingrays were still foraging predominantly naturally, and that if there were negative repercussions, then the stingrays, being wild and not captive, would no longer remain in the area. The ecological chapters therefore served two purposes: to determine if the stingrays would be impacted by the proposed management options (i.e., reduced food and restricted handling), and to investigate whether the tourist attraction can act as an ecological trap. In the former case, Chapter 3, the fatty acid profile differences between tourist and non-tourist stingrays, demonstrated that the diet of the fed-stingrays was predominantly composed of squid, revealing these animals are habituated to the constant supply of provisioned food. My findings additionally show that the diet to which the stingrays are habituated is unnatural and out of balance with respect to the lipid nutrition stingrays require in tropical habitats. Chapter 5 also demonstrates diet-induced physiological changes (e.g. lowered hematocrit, serum proteins, anti-oxidant capacity); therefore any management plan designed to restrict or improve stingray feeding would indeed have an impact. Restricting handling would also positively impact stingray health: touching and holding stingrays whether in or out of water can remove the

protective mucosal coat on the stingray skin used to reduce parasite and pathogen transmission (fed stingrays had higher parasite loads but exhibited down-regulation of eosinophil concentration that is required to combat this stressor), and the stress of being removed from the water can also be a contributing factor to the higher oxidative status of the rays (Hermes-Lima and Zenteno-Savin 2002).

With regards to examining whether the stingray-feeding attraction can act as an ecological trap, the chapters were designed to build on one another. For a trap to occur (i.e., maladaptive decision making), habitat alteration must simultaneously alter the cue set with which the animal assesses habitat quality (i.e., increase its attractiveness), and decrease the suitability of a habitat. It is therefore necessary to assess the ability of the animal to adjust to and persist in these novel conditions. In Chapter 3, I demonstrated non-random habitat use by revealing stingrays were incorporating the tourist-supplemented food as the major item in their diet and had very high yearly recapture rates suggesting strong site fidelity. I then demonstrated the novel grouping behaviour around the provisioned resource imposed costs in the form of increased aggression, parasite load, and injury. What was still lacking was definitive evidence of long-term costs that would reveal the occurrence of an ecological trap. Using stingrays from non-tourist sites about Grand Cayman as a basis for comparison, I showed in this natural experiment that tourist-exposed stingrays exhibited hematological changes indicative of physiological costs of wildlife tourism in the form of sub-

optimal health and attenuation of the defense system. Taken together, and situated within ecological context of the stingrays' injuries and parasite loads, the primary data from my doctoral research indicate that the long-term health and survival of tourist stingrays, a long-lived marine species, have a significant probability of being affected. Again, the suggestion of an ecological trap is later confirmed by the system dynamics model.

Finally, it was essential to be able to combine the data to explore the future well-being of the ecological-social system under differing management regimes. The development of the model was guided by the belief that sound ecological management occurs only when social values and concomitant behaviours and preferences are equally integrated. System dynamics modeling facilitates the understanding of system behaviour with the assistance of the dynamic simulation of system components, thus providing insight as to how a system changes over time. It is an ideal platform as it provides modelers and process participants a transparent, user-friendly, and icon-based technique (Beall and Zeoli 2008). The model created for Stingray City Sandbar provides illustrative results of how tourist numbers, stingray population size and stingray life-expectancy would change over time under different restrictive management plans. It incorporates social data on tourist preferences for management that was assumed to link with behavioural intentions regarding future visitation rates. Ecological primary data from mark and recapture work was incorporated in the form of survival and population growth estimates, and tourism-induced mortality parameters were

based on secondary data and estimated from the ecological and biological data from chapters 3-5. The most notable conclusions from the model are that the most restrictive plan corresponds to higher arrival and return rates of the desired tourist segment, and although fewer stingrays remain at SCS, they are healthier. Secondly, without any management, the model predicts lower tourist numbers of both tourist segments, larger stingray population size (mainly through immigration), but poorer health, all classic hallmarks of social and ecological traps.

MANAGEMENT IMPLICATIONS

Each chapter has a devoted 'management implications' section, and so I will briefly summarize them here: the existence of divergent preferences from the social survey study suggests several implications for the Caymanian resource managers charged with the responsibilities of protecting the environment and providing satisfactory recreational opportunities: (1) different groups may require different management practices; (2) communication and education through various forms of media will play a key role in resolving behaviours or actions which prove harmful to stingray health; and (3) the wildlife tourism attraction will need to undergo marketing and promotional restructuring in order to implement the desirable changes, as at the moment, most visual and written advertisements for SCS promote the feeding and holding of stingrays. Ecological management measures that should be taken are the alleviation of stingray crowding conditions at SCS by limiting the number of people and boats, or by expanding the site into

nearby areas to accommodate the current level. Less food provisioned to the rays will also alleviate stingray competition and subsequent aggression-injuries, and ensure that the animals resume foraging naturally and solitarily, further away from the tourist site. If food is still to be provisioned, care must be taken to ensure that as natural a diet is provided, either through locally-caught food or a formulated diet which can be monetarily compensated for by the conservation access fee. Restriction of handling to the tour operator only is also recommended; and safety devices on boat propellers, such as cages and guards, will also aid in reducing injuries.

Since the inception of the North Sound Committee in 2003, charged with the planning and management of SCS, new developments have transpired. Recently enacted legislation has resulted in the creation of Wildlife Interaction Zones, including the North Sound of Grand Cayman where SCS is located. This zoning act contains a regulation that no marine life may be taken out of the water, including the stingrays, and the Department of Environment will be enforcing the new regulation. Also, while feeding is allowed within these designated zones, the food must be approved by the Marine Conservation Board. Plans are to have a permanent officer for the Wildlife Interaction Zones, with a vessel bought specifically for that job as well as the hiring of an officer whose main responsibilities will be to patrol these areas.

In addition, all commercial boat operators are now required to have a license to visit SCS. Approved by the Minister for Tourism, Environment, Investment and Commerce, licenses are valid for three years and will cost \$300 for vessels 50 ft. or shorter in length and \$600 for vessels longer than 50 ft. The licensing and registration regulations are designed to help control the number of passengers that may be carried to any of the designated zones, and will also regulate the mooring or anchoring of boats. Issues that still to be addressed are the nature and collection mechanisms for a proposed access fee, and the pricing structure for trips to SCS, particular for trips that are sold on-board cruise ships which charge their passengers approximately USD45.00 – USD60.00 while the local operators who provide the trips receive only around USD20.00. Resolving these issues would improve incomes for dive and snorkel tour operators and provide revenues to contribute to management and conservation actions.

My work has informed these decisions: stakeholders are now aware of how Stingray City Sandbar poses a threat to the overall health and longevity of the stingrays and have requested I create a protocol and equipment list for them to be able to carry on the research; they are pleasantly surprised at the amount tourists are willing to pay for a conservation access fee; the decision support tool of the tourist segment preferences has been distributed amongst government officials, and brochures and educational tools will be provided to tour operators for the purposes of increasing the knowledge content of the stingray tours.

CONCLUSION

I began this thesis with a chapter on the role of today's conservation biologist in the mitigation of human-wildlife conflict. Such a global scientist should address conservation in a human-dominated landscape by including the human dimensions of wildlife; go beyond the insights of biology and ecology by incorporating analyses from the social sciences and humanities; and suggest conservation measures based on limited knowledge that recognize effects on humans. However, is it realistic to presume conservation biologists should be proficient in social theory? Should they also be collecting primary social-science data themselves? After all, if expertise is spread amongst various disciplines, how qualified can one truly be in any one field? The complexity of caring for an ecosystem exceeds the capacity of any one individual (Ewel 2001), and so why should a conservation biologist not simply collaborate with others, instead? What it means to be a conservation biologist, however, is rapidly evolving and broadening. Conservation biologists are not only finding themselves having to work across a natural-science scale reaching from molecular genetics to landscape-level processes, but also across social-science ranges such as attitude-behaviour theory to stakeholder participation and institutional change.

Accordingly, there has been a call for research be performed transdisciplinarily – that is, “joint work using a shared conceptual framework drawing together disciplinary-specific theories, concepts, and approaches” (Lund et al. 2006), as opposed to working still within a disciplinary-specific base. Working from this

framework, research would then be problem oriented, with discipline-related outputs less central to the project design, and with less focus on further development within a discipline (Quinlan and Scogings 2004). And during the policy process, actions would entail both social and natural scientists ideally combining their thoughts and actions throughout each stage - from design, to field work and analysis (Fox et al. 2006). One way to achieve this transdisciplinarity for conservation biologists is through proper resource-management training.

There have long been criticisms that traditional conservation biology curricula focus solely on scientific and technical aspects of species or ecosystems (Jacobson 1990; Jacobson & McDuff 1998), resulting in conservationists lacking integrative, interdisciplinary and problem-solving skills for the real world (Clark 2001). Indeed, offered suggestions on ways to improve this dearth in training include incorporating human dimensions research, conflict management, fiscal management, and socio-politics into the curriculum at the university level, as well as at the in-service level for current professionals. Organizing workshops and seminars involving university faculty, students and external agencies, and encouraging student internships with agencies and organizations are other ways in which to ensure tight collaboration. Lastly, coordinating joint, interdisciplinary conferences, promoting internet discussion groups on human dimensions of wildlife, and creating additional academic journals that publish original work comprising both the natural and social sciences of resource management are

avenues which should also be pursued (Jacobson and McDuff 1998, Clark 2001, Perez 2005).

For the research I undertook, the project was of a manageable size that I was able to become immersed in all aspects of inquiry, and it was therefore unnecessary for the work to be divided amongst various teams working in concert. However, it was crucial that I still involve other, experienced researchers in the various fields of discipline this work required: physiologists, resource modelers, and social scientists. Drawing on their advice and/or skills, I was assured that the research questions I had devised were legitimate and would stand up to peer review. During the course of my research, I would at times feel like a ‘jack-of-all-trades, master-of-none’ - a figure of speech used in reference to a person who is competent with many skills but is not outstanding in any one. However, now at the completion stage of my degree, I feel differently. Still using the same figure of speech to describe myself, I now believe that a Jack of all trades may also be a master of integration, as the individual knows enough from many learned trades and skills to be able to bring these disciplines together in a practical manner. Which is exactly as a doctoral graduate at Simon Fraser University’s School of Resource and Environmental Management should do.

FUTURE DIRECTIONS

This is certainly not to say that the research is impervious to critique. Although I concentrated my efforts on stingrays and tourists as the primary stakeholders, there are other important ones in the system that are equally embroiled in conflict: locals and tour operators, tour operators and government, and government and cruiseline industries. For instance, the discrete choice model presented to the tourists represented a bounded reality that concerned mainly the ecological outcomes on stingrays. If an attribute had been added which consisted of different levels of employment loss of tour operators under various management regimes, this may have altered preferences for the more social capital-centric respondents. It would also have been interesting to include an economic module in the STELLA model to determine economic fallout (or possible windfall) to the tour operators from the different management alternatives (e.g., boat restriction and compensatory fee).

As for ecological directions, I believe it is of importance to determine the relatedness of the stingrays at SCS. Should future generations of SCS stingrays be attracted to the site rather than disperse, then there exists the potential for inbreeding to occur. Also, physiological tests can determine whether these younger, related rays are poorer in health than young, non-related stingrays at SCS. With regards to the future monitoring of stingrays, I have established for the Cayman Islands Department of Environment a control baseline from unfed stingrays, as well as a pre-management baseline of the SCS stingrays

themselves. I have taught Caymanian marine research officers my stingray examination techniques (including blood collection) for their future monitoring, have created a protocol as to the analyses officers can do themselves, and have established relationships with laboratories which can perform the remaining analyses commercially.

While the social and ecological indicators I chose to investigate for the doctoral research were system specific, I believe the 'trap' theory presented in this thesis is transferable and can serve as a guiding framework for other wildlife-tourism attractions. By examining tourist behaviours and attitudes which have the potential to affect the tourism experience as well as wildlife fitness, and by selecting the appropriate indicators that reflect this relationship between humans and wildlife, one can then suggest management options (and explore the alternatives) which will prevent both traps from occurring, thus leading to a healthier resource base and a highly satisfactory wildlife experience.

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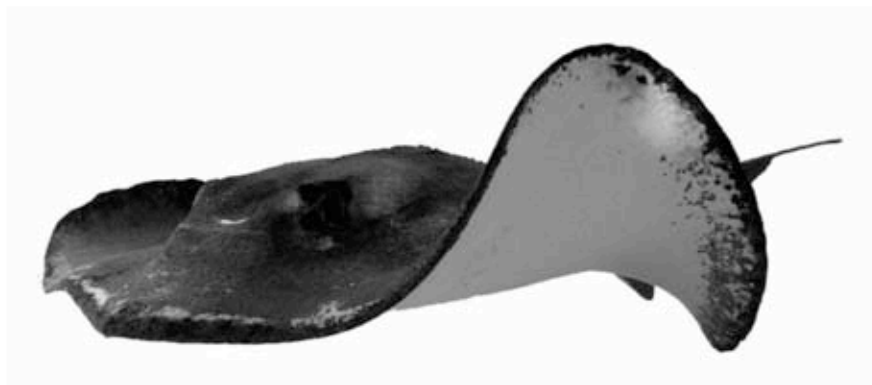
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APPENDICES

Appendix 1: The Survey Implement

1

STINGRAY CITY SANDBAR QUESTIONNAIRE 2004



Southern stingray
Dasyatis americana



SOUTHERN STINGRAY PROJECT

Introduction

The Southern stingray is the fish you encountered on your trip to Stingray City Sandbar. This stingray has been fed by tourists in these waters since the early 1980's. Growing numbers of people are currently traveling out to the Sandbar in the North Sound to touch and feed the stingrays. We would like to ensure that visitors have high quality experiences while making certain the stingrays are as healthy as possible. **We would like to know your opinions about different ways of managing future visits with stingrays at this site.** The information we gather will assist with the planning and management of feeding stingrays as a marine tourism attraction both locally and in other areas.

All of the personal information that you provide will be kept strictly confidential. However, it will be combined with that of many other visitors to provide a fuller picture of how tourists feel about the management of this special experience with stingrays. Participation is entirely voluntary, and you may discontinue your participation at any time during the survey should you wish. This questionnaire will take approximately 15 minutes to complete. If you can help by completing this questionnaire it would be greatly appreciated. Please answer all questions as best you can. We look forward to your comments.

When you have completed this questionnaire, please return it to the people administering the survey.

You are welcome to tear off and keep this cover page.

Thank you for your participation.

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Section 1:

YOUR EXPERIENCE

Q1. Please circle the number which best reflects the extent to which your expectations were met at the Stingray City Sandbar with respect to each of the following factors:

Characteristics	Satisfaction				
	Worse than Expected		Expectations Met		Better than Expected
Visual attractiveness	1	2	3	4	5
Adequate safety	1	2	3	4	5
How close you could get to a stingray	1	2	3	4	5
Touching a stingray (if applicable)	1	2	3	4	5
Feeding a stingray (if applicable)	1	2	3	4	5
Learning about the stingray	1	2	3	4	5
Learning about the marine environment	1	2	3	4	5
Reasonable prices	1	2	3	4	5
Providing quality experience worth the money paid	1	2	3	4	5
	Less than Expected		Expectations Met		More than Expected
The number of people in the water	1	2	3	4	5
The number of boats in the water	1	2	3	4	5
The number of stingrays seen	1	2	3	4	5
The amount of information about Stingray City Sandbar	1	2	3	4	5

Q2. Please check the time of day during which you visited the Sandbar:

☐ 8:00 – 10:00 a.m. ☐ 10:00 a.m.-12:00 p.m. ☐ 12:00-2:00 p.m. ☐ 2:00-4:00 p.m.

Q3. Is this your first visit to Stingray City Sandbar? ☐ YES ☐ NO....

If NO, number of previous visits? _____ Year(s) visited? _____, _____

Q4. Please circle the number which best captures how satisfied you were overall with your visit to Stingray City Sandbar:

Extremely dissatisfied							Extremely satisfied
1	2	3	4	5	6	7	

Section 2: ***ABOUT YOUR VIEWS ON WILDLIFE CONSERVATION & STINGRAY CITY SANDBAR IMPACTS***

Please place a check in the box which best reflects the extent to which you agree or disagree with each of the following statements:

Q1. *"I feel that conservation of wildlife and the natural environment is very important"*

<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Strongly disagree	Somewhat disagree	Neutral	Somewhat agree	Strongly agree

Q 2. *" I consider myself to be very informed about current conservation issues concerning wildlife and the natural environment"*

<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Strongly disagree	Somewhat disagree	Neutral	Somewhat agree	Strongly agree

Q3. Do you belong to any organizations that are primarily concerned with the conservation of wildlife or the natural environment ? ☐ NO ☐ YES....if yes, could you please list those organizations.

Q4. Please place a circle around the number which best reflects how important or unimportant you feel each of the following activities is to a satisfying wildlife tourism experience:

	Not important at all	Somewhat <u>un</u> important	Somewhat important	Very important	Don't know
Seeing animals in their natural environment	1	2	3	4	5
Seeing wildlife without the need for binoculars	1	2	3	4	5
Photographing wildlife	1	2	3	4	5
Touching wildlife	1	2	3	4	5
Feeding wildlife	1	2	3	4	5
Learning about the wildlife	1	2	3	4	5
Minimizing tourist activity impacts on wildlife	1	2	3	4	5
Contributing effort to wildlife conservation activities	1	2	3	4	5

Q.5. Please place a circle around the number which best reflects how concerned or unconcerned you feel about the following potential effects of tourism at Stingray City Sandbar?

	Not concerned at all	Somewhat <u>un</u> concerned	Somewhat concerned	Very concerned	Don't know
The number of tourists in the water	1	2	3	4	5
The risk of injury to tourists by boats	1	2	3	4	5
The amount of unsightly litter in water	1	2	3	4	5
The health of surrounding coral reefs	1	2	3	4	5
The risk of injury to stingrays by boats	1	2	3	4	5
The effects of feeding squid on stingray health	1	2	3	4	5
The change in behaviour of stingrays by the presence of tourists & boats	1	2	3	4	5
The health of stingrays being held out of water	1	2	3	4	5

Section 3: ***PREFERENCES FOR MANAGEMENT OPTIONS***

INSTRUCTIONS

- Four sets of possible management scenarios are presented on the following pages.
- We would like to know which management scenario you prefer out of each set of three scenarios, if these were the only options available.
- Each scenario is described in terms of 7 features, comprised of the following management strategies and outcomes:

Congestion Control, Tourist Conduct Rules, Ecological Outcomes, Conservation Fee

- In each set of options, the first scenario is the 'current' option, which corresponds to no management of the Sandbar tourist experience.
- You'll find some of the management components more appealing than others, and you may have to give up attractive features of one scenario (eg. feeding the rays) to get some other features you like more in a second scenario (e.g. less crowding).
- Should the presented scenarios not meet your expectations, please still choose amongst the options.

SET 1 – Please answer the following:

Q. 1 A

If you had the opportunity to return to Stingray City Sandbar, please choose the one management scenario that would maximize your experience if there were only these 3 options:

Please check one box only:

☐
☐
☐

Site Characteristics	Current	Scenario #1	Scenario #2
# Boats allowed	40	40	20
# People allowed	1000	750	250
Stingray Feeding By:	Operator & Tourist	No feeding of rays at all	Operator & Tourist
Stingray Handling By:	Operator & Tourist hold <u>out</u> of water	Operator & Tourist hold <u>out</u> of water	Operator only hold <u>in</u> water
Number of surrounding stingrays	55	25	55
Risk of Injury to Stingrays	High	Low	High
Conservation Access Fee	No fee	No fee	20\$US

Q. 1 B



*If your chosen management scenario from question 1A was being followed, would you return to Sandbar:
(please check one box)*

If I had the opportunity, I would return

☐

If I had the opportunity, I would not return

☐

SET 2 – This is a different question. Please answer the following:

Q. 2 A

If you had the opportunity to return to Stingray City Sandbar, please choose the one management scenario that would maximize your experience if there were only these 3 options:

Please check one box only:

☐
☐
☐

Site Characteristics	Current	Scenario #1	Scenario #2
# Boats allowed	40	20	10
# People allowed	1000	250	500
Stingray Feeding By:	Operator & Tourist	Operator only	No feeding on this trip
Stingray Handling By:	Operator & Tourist hold <u>out</u> of water	Operator only hold <u>in</u> water	No holding of ray
Number of surrounding stingrays	55	40	10
Risk of Injury to Stingrays	High	Medium	Low
Conservation Access Fee	No fee	10\$ US	No fee

Q. 2 B



*If your chosen management scenario from question 2A was being followed, would you return to Sandbar:
(please check one box)*

If I had the opportunity, I would return

☐

If I had the opportunity, I would not return

☐

SET 3 – This is a different question. Please answer the following:

Q. 3 A

If you had the opportunity to return to Stingray City Sandbar, please choose the one management scenario that would maximize your experience if there were only these 3 options:

Please check one box only:

☐
☐
☐

Site Characteristics	Current	Scenario #1	Scenario #2
# Boats allowed	40	30	40
# People allowed	1000	500	750
Stingray Feeding By:	Operator & Tourist	Operator & Tourist	Operator only
Stingray Handling By:	Operator & Tourist hold <u>out</u> of water	No holding of ray	Operator & Tourist hold <u>out</u> of water
Number of surrounding stingrays	55	10	40
Risk of Injury to Stingrays	High	None	None
Conservation Access Fee	No fee	20\$US	10\$ US

Q. 3 B



*If your chosen management scenario from question 3A was being followed, would you return to Sandbar:
(please check one box)*

If I had the opportunity, I would return

☐

If I had the opportunity, I would not return

☐

SET 4 – This is a different question. Please answer the following:

Q. 4 A

If you had the opportunity to return to Stingray City Sandbar, please choose the one management scenario that would maximize your experience if there were only these 3 options:

Please check one box only:

☐
☐
☐

Site Characteristics	Current	Scenario #1	Scenario #2
# Boats allowed	40	10	30
# People allowed	1000	1000	1000
Stingray Feeding By:	Operator & Tourist	No feeding on this trip	No feeding of rays at all
Stingray Handling By:	Operator & Tourist hold <u>out</u> of water	Operator & Tourist hold <u>in</u> water	Operator & Tourist hold <u>in</u> water
Number of surrounding stingrays	55	55	25
Risk of Injury to Stingrays	High	High	Medium
Conservation Access Fee	No fee	5\$ US	5\$ US

Q. 4 B



*If your chosen management scenario from question 4A was being followed, would you return to Sandbar:
(please check one box)*

If I had the opportunity, I would return

☐

If I had the opportunity, I would not return

☐

Section 4:

ABOUT YOU

A reminder: Your answers to the survey will remain completely confidential and will be released only as summaries in which no individual answers can be identified.

Please have only one person complete this section. Thank you.

Q1. What is your gender ?

☐ Male

☐ Female

Q2. Name of your usual country of residence? _____

Q3. Which of the following age categories describes you ?

☐ 18 - 29

☐ 30 - 39

☐ 40 - 49

☐ 50 - 59

☐ 60 - 69

☐ 70 or over

Q4. What is the highest level of education you have completed?

☐ Completed elementary school

☐ Some high school

☐ Completed high school

☐ Technical training

☐ Some university

☐ Completed university

☐ Graduate study

Q5. What was your household income for the year 2003?

☐ Under 30 000

☐ 30 000 – 49 999

☐ 50 000 – 69 999

☐ 70 000 – 89 999

☐ 90 000 or over

Please indicate which currency:

☐ US

☐ CDN

☐ EURO

☐ £

☐ OTHER _____

Q6. How would you best describe your employment status (*Please check only one box*).

- ☐ Student
- ☐ Homemaker
- ☐ Unemployed
- ☐ Employed, not self-employed
- ☐ Self-employed
- ☐ Retired, not self-employed
- ☐ Retired, self-employed

Q7. What Cruise Line are you traveling on? _____

Q8. Which Tour Operator company brought you to the Sandbar? _____

Q9. Are there any other comments you would like to make about the issues covered by this survey?

*If you would like further information about our Stingray City Sandbar research,
Please contact the addresses listed at the start of the questionnaire.*

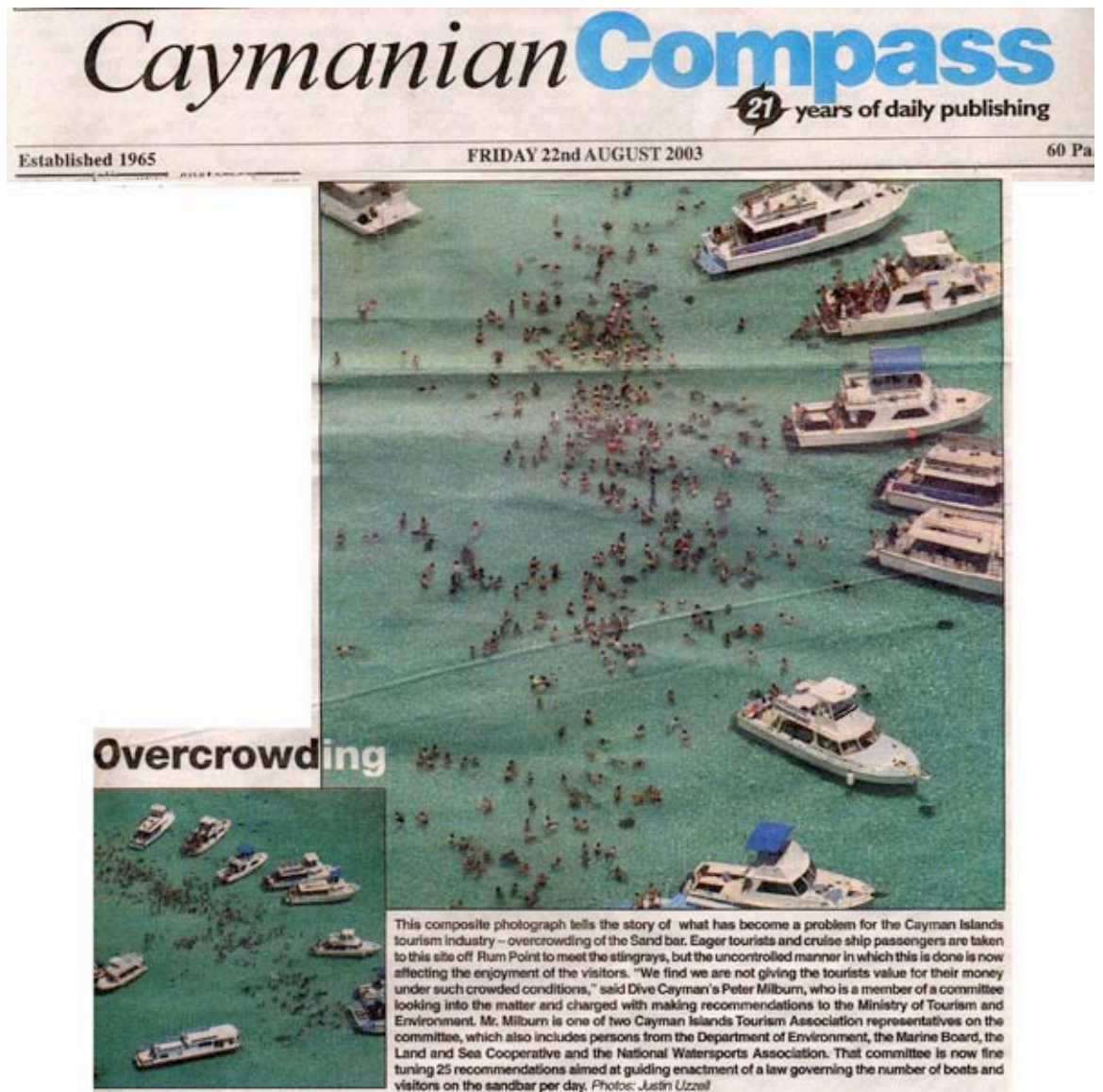
THANK YOU FOR YOUR HELP WITH THIS RESEARCH!

Appendix 2: Research System Photographs



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A2. Figure 1. Examples of the iconography of stingrays in Caymanian culture.



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A2. Figure 2. Headline from Caymanian Compass Newspaper, August 22, 2003, depicting current situation at Stingray City Sandbar, Grand Cayman.



© CAD Semeniuk

A2. Figure 3. Tour boat at Safehaven Dock, CI, with tourists disembarking from trip (top photo). Tour buses waiting to bus tourists back to Georgetown, CI, on which intercept surveys were administered (bottom photo).



© CAD Semeniuk

A2. Figure 4. Photos depicting stingray physical exam: a. tarp set-up for width measurement; b. weighing scale; c. checking parasite and counting bite marks; d. recording wounds; e. scanning for identification; f. tagging newly-captured stingrays; g. blood sampling from the caudal vein (in the stingray's tail); h. preparing blood smears.



A2. Figure 5. Photos of tourist and stingray activities: a. Stingray City Sandbar with tourists and boats; b. close-up of Stingray City Sandbar (from boat perspective); c. tourist interacting with stingray; d. tour operator holding stingray out of water for photo opportunity; e. informative in-water session by tour operator; f. non-natural food (squid) fed to stingrays by tourists and operators; g. increased water turbidity from stingray activity; h. propeller hazards. Photos (with exception of h.) were made available under a Creative Commons Attribution-Noncommercial license. Photo h. courtesy of Matthew Potenski, MDP Photography.