MINI REVIEW

Potential for spatial management of hunted mammal populations in tropical forests

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Abstract

Unsustainable hunting in tropical forests threatens biodiversity and rural livelihoods, yet managing these harvests in remote forests with low scientific capacity and funding is challenging. In response, some conservationists propose managing harvests through spatial management, a system of establishing no-take zones where hunting is not allowed. Spatial management was commonly used in customary management and is increasingly used for fisheries management today, but is not yet widely implemented in tropical forests. Through this review, we trace the development of spatial management and examine its proposed benefits in tropical forests. We find that while spatial management offers promise for managing the complex, multispecies harvests common in tropical forests, designing no-take zones will require more investment in ecological research and monitoring. Given these challenges, a reasonable first goal of no-take zones is to protect resident wildlife populations, not enhance harvests through dispersal. A greater understanding of socioeconomic impacts will also be required to ensure successful implementation. Past work in marine fisheries offers valuable insights for management in tropical forests, and greater integration between the bodies of literature should be pursued.

Introduction

Over the past few decades, hunting has emerged as a threat to wildlife populations in tropical forests, threatening a vital source of food for rural people, biodiversity, and ecosystem functioning (Robinson & Bennett 2000). Although wildlife management is a priority in tropical forests, quota-based management typically used in developed countries may not be appropriate in tropical forests. Quotas limit the number of animals harvested, sometimes in conjunction with regulations on harvester effort (e.g., hunting season). Regulations are developed separately for individual species of economic or recreational value, which requires resources for intensive scientific research and enforcement (Williams *et al.* 2002). In contrast, harvests in tropical forests are multispecies assemblages, which makes limits on individual species' harvests impractical. In addition, in tropical forests there is a lack of information on species' demographic rates, low research funding, and limited capacity, which complicates efforts to develop regulations (Milner-Gulland *et al.* 2003).

To address these challenges, some conservationists propose managing tropical forest hunting through spatial management or no-take zones, designating areas where hunting is not allowed (Novaro *et al.* 2000; Milner-Gulland *et al.* 2003). Spatial management has a long history of use, often combined with other restrictions on equipment or species. Past uses of no-take zones include customary resource management by preindustrial societies (Johannes 1978), early wildlife management in North America (McCullough 1996), and modern fisheries (Gell & Roberts 2003).

Spatial management is proposed to have several advantages over quota-based management, which has led to its resurgence in marine systems and its desired use in tropical forests. No-take zones are expected to protect against overharvest by isolating a proportion of the population from harvesting (McCullough 1996; Gell & Roberts 2003). No-take zones are proposed to contribute to offtake by providing dispersing animals from no-take zones to surrounding hunted areas (McCullough 1996; Novaro *et al.* 2000). Spatial management is also considered easier to implement and enforces for the multi-species harvests and complicated social and institutional settings typical of tropical forests (Milner-Gulland *et al.* 2003).

Proponents of spatial management also hope that no-take zones will formalize or harness the source-sink dynamics that may already be sustaining hunting offtake in tropical forests (Novaro *et al.* 2000; Naranjo & Bodmer 2007). Over the past two decades, researchers in tropical forests have repeatedly noted that high, presumably unsustainable, localized rates of offtake were continuing unabated for long periods. Researchers proposed that offtakes were sustained by wildlife populations in de facto no-take zones, areas either isolated by distance from hunters or culturally or legally defined as off-limits from harvesters (Alvard *et al.* 1997; Novaro *et al.* 2000; Naranjo & Bodmer 2007). Dispersal from these "source" areas into the "sinks" created by high hunting pressure (often localized around a village) was thought to maintain hunting offtake (Novaro *et al.* 2000; Salas & Kim 2002).

Although the rationale for no-take zones in tropical forests stems from both empirical observations and source-sink theory, no-take zones are not yet widely implemented or studied in tropical forests. In contrast, there has been a dramatic increase in research on no-take zones for fisheries management over the past two decades (Worm *et al.* 2009), along with a growing interest in the spatial dimensions of wildlife harvesting in temperate regions (Laudré & Clark 2003; Diefenbach *et al.* 2005). This review pulls together these disparate bodies of research on spatial management to inform research and implementation of no-take zones in tropical forests. Below, we first describe uses of no-take zones and compare their management goals in different settings (Table 1). We then draw upon theoretical and empirical research to generate recommendations for the design and implementation of no-take zones in tropical forests.

Past use of no-take zones

While the theoretical basis for no-take zones has developed over the past two decades, no-take zones have been used for resource management for at least a millennia (Johannes 1978; Colding & Folke 2001). No-take zones were widely used as informal or customary management regulations, developed by communities to regulate the use of common-pool resources, those resources available to more than one person and vulnerable to degradation as a result of overuse (Ostrom 1990). Over the past 200 years, no-take zones have also been used in formal management, those regulations mandated by government (Ostrom 1990).

In the terrestrial realm, informal spatial management included rotating hunting grounds over space among Cree groups in Canada (Berkes 1986) and protecting forests ("sacred groves") in India for their religious and cultural significance, providing refugia for biodiversity and harvested resources (Gadgil 1987). Formal use of no-take zones in North America arose from widespread declines of many game species in the 1880s (Dunlap 1988). For most species, no-take zones were supplanted by quotas once populations recovered (McCullough 1996). However, no-take zones are still used for management of hunted species in North America and Europe, including waterfowl and carnivores (Beringer *et al.* 1998; Brochet *et al.* 2009) (Table 1). Research also shows that de facto no-take zones are critical to maintaining hunting offtake in a variety of species in temperate ecosystems (Slough & Mowat 1996; Laudré & Clark 2003; Diefenbach *et al.* 2005; Kaltenborn & Andersen 2009).

In tropical forests, spatial management has been formally implemented in several places. In Congo, the Congolaise Industrielle des Bois logging company, in collaboration with Wildlife Conservation Society, designated sections of the Kabo concession as no-hunting zones, in combination with other restrictions on harvesting (Poulsen *et al.* 2007). No-take zones protect a central area of the concession as well as dispersed forest clearings important for large mammals. In the Amazon Basin, reserve management conducted in collaboration with communities often includes the use of a core no-take zone, along with more specific restrictions for use of fish, wildlife, and plants (e.g., Tamshiyacu Tahuayo Communal Reserve and Pacaya-Samiria Reserve in Peru) (Bodmer *et al.* 2009).

In marine systems, spatial management was common in informal resource management (Johannes 1978) and has recently emerged as a formal mechanism for fisheries management because past methods focused on quotas and maximum sustainable yield often led to overharvest and did not address habitat damage caused by fishing (Table 1) (Worm *et al.* 2009). Marine no-take zones have been implemented in a range of settings, from local or community-based initiatives for near-shore fisheries (Prince 2010) to larger regional networks of no-take zones. For example, over one-third of the 345,400 km^2 Great Barrier Marine Park in Australia is zoned as no-take, in order to enhance fisheries and minimize environmental impacts of fishing (McCook *et al.* 2010)).

Table 1 Comparison of the rationales for establishing no-take zones for small-scale, commercial, and recreational harvesting in the marine and terrestrial realms. For each potential rationale for using no-take zones we indicate if this reason cited as a factor motivating the use of no-take zones

	Marine harvesting		Terrestrial harvesting	
Rationale for establishing protected area:	Small-scale or near-shore	Commercial	Small-scale or subsistence in tropics	Recreational hunting in temperate areas
Protect a wide range of harvested species	Yes. A wide range of species are typically harvested.	Depends. Harvesting often focuses on those species of commercial value, but bycatch species are also protected by reserves.	Yes. A wide range of species are typically harvested.	No. Although reserves could protect other species, most reserves are set up for one focal species (often carnivores).
Protect biodiversity and ecological functioning	Yes	Yes	Not often considered, but certainly a potential benefit.	Not often considered, but certainly a potential benefit.
Prevent habitat destruction	Yes, destructive practices include dynamite and poison fishing.	Yes, commercial fisheries damage habitat through bottom trawling.	No	No
Shelter sizeable populations in reserves as a buffer against overharvest	Yes	Yes	Yes	Yes
Increase reproductive productivity in reserve	Yes, by sheltering the biggest females and protecting high-density breeding events.	Yes, by sheltering the biggest females and protecting high-density breeding events.	No	No, not likely for mammal populations. For waterfowl, reserves protect high-density breeding events.
Provide dispersers for harvesting outside reserves	Yes, though planktonic larvae and dispersal (spillover) of juveniles and adults.	Yes, though planktonic larvae and dispersal (spillover) of juveniles and adults.	Yes, through dispersal of mammals (juveniles or adults, depending on life history).	Yes, through dispersal of mammals (juveniles or adults, depending on life history).
Provide a natural link to community monitoring and enforcement	Yes	No	Yes	No. Possible depending on community size and composition, but is rarely considered.

Connections between marine and terrestrial use of no-take zones

While there is therefore a rich history of no-take zone use to inform management, differences in the characteristics of marine and terrestrial species alter the applicability of past work to tropical forest hunting. For example, because female fish become more fertile with age and size, protection from harvest in no-take zones can have large effects on populations dynamics and the production of potential dispersers (Carr *et al.* 2003). In tropical forests mammals are the most important prey species (Fa & Brown 2009), and they have lower reproductive productivity than marine species. Marine organisms are often highly mobile, which enhances populations outside no-take zones, through both the dispersal of larvae and the "spillover" movement of juveniles and adults (Botsford *et al.* 2009). In contrast, terrestrial species have no equivalent larval phase and their juvenile and adult dispersal abilities are generally more limited than marine species (Carr *et al.* 2003), with the exception of some migratory bird species. Differences in physical settings also alter the use of no-take zones. For example, marine no-take zones are often located in coastal areas, giving rise to population models based on linear landscapes (e.g., Le Quesne & Codling 2009), a configuration not likely to be applicable in terrestrial systems.

Social and institutional settings where spatial management is used often vary widely, which also determines applicability of past work to tropical forests (Milner-Gulland *et al.* 2003; Prince 2010). For example, near-shore fisheries and tropical wildlife hunting are fairly similar in their governance and technical characteristics: both have many actors harvesting a large variety of species, each of which might have limited commercial value (Milner-Gulland *et al.* 2003). In contrast, experience from commercial fisheries or recreational hunting may be less applicable to tropical forests. Commercial fisheries operate over a large-scale and produce considerable revenue from single species, generating more resources for management (Prince 2010). Recreational hunting and fishing in temperate areas typically also receive substantial government investment in management, produced from fees and taxes levied on participants (Mahoney 2009).

Design considerations for no-take zones

Although ecological and institutional settings vary, careful examination of past theoretical and empirical research offers valuable guidance for design of no-take zones in tropical forests. Thus far, advocates of spatial management in tropical forests have not critically examined no-take zone design (size, shape, location). Existing no-take zones have usually been designated as a central area within a reserve. No-take zone shape and size follow from landscape features that can be used as boundaries, such as past management uses, coarse information on vegetation distribution, and social concerns (Poulsen *et al.* 2007; Bodmer *et al.* 2009). In Amazonia, no-take zones are expected to conserve multiple resources (wildlife, fish, and plants) (Bodmer *et al.* 2009). In contrast, over the past two decades marine researchers have devoted substantial attention to no-take zone design. However, robust, generalizable guidelines remain rare because model simulation outcomes vary widely with species studied, and empirical data on design features have been slow to accumulate (Botsford *et al.* 2009). In general, marine models provide conceptual understandings of no-take zone effectiveness through simulations, not exact management prescriptions (Gerber *et al.* 2003; Moffitt *et al.* 2009). This past work in marine settings, combined with theoretical and empirical research in terrestrial systems, yield three main themes for no-take zone design in tropical forests. No-take zone design requires (1) a tradeoff between protection and dispersal (yield); (2) explicit selection of no-take zone goals; and (3) recognition of fine-grained spatial variation in harvests and resources. We address each theme in turn below.

No-take zones tradeoff protection and dispersal

Spatial management in both terrestrial and marine settings has two main objectives: protecting against overharvest by safeguarding the portion of the population that falls within no-take zones and enhancing yield through dispersal from no-take zones (McCullough 1996; Gell & Roberts 2003; Botsford *et al.* 2009). However, theoretical and empirical research reveals an inherent tradeoff between protection and dispersal. Many of the features that enhance protection within a no-take zone will diminish dispersal, and therefore yield, while those that promote dispersal decrease the protective capabilities of the no-take zone (Salas & Kim 2002; Botsford *et al.* 2009).

Features which enhance protection within no-take zones include relatively larger no-take zone size, smaller ratio of no-take zone to edge, and less mobile target species (i.e., less likely to move outside no-take zones) (Salas & Kim 2002; Gerber *et al.* 2003; Roberts *et al.* 2003; Claudet *et al.* 2008; Botsford *et al.* 2009; Claudet *et al.* 2010). Conversely, the features that threaten protection within no-take zones enhance dispersal. Dispersal increases with relatively smaller no-take zones, a larger ratio of edge to no-take zone, and greater mobility among resident wildlife (Salas & Kim 2002; Gerber *et al.* 2003; Claudet *et al.* 2008; Botsford *et al.* 2009; Claudet *et al.* 2010). Theoretical models demonstrate that maintaining a balance between protection and yield is challenging, as there are sudden transitions for no-take zone size and species' dispersal ability below which the protection value of a no-take zone is severely compromised (Delibes *et al.* 2001; Novaro *et al.* 2005). In addition, some species may not be appropriate for protection or dispersal benefits of no-take zones because of their reproductive rates and behavior. Mobile species, including those with large home ranges (Moffitt *et al.* 2009) or seasonal changes in ecological requirements (Slough & Mowat 1996), might never be effectively protected by spatial management. In contrast, many primate species have low dispersal, slow reproduction, and complex social structures, which will limit the role of dispersal in maintaining or enhancing hunting offtake (Levi *et al.* 2009; Wiederholt *et al.* 2010).

Balancing protection and yield becomes more complex when considering multispecies harvests. Because both yield and protection are influenced by species' demographic rates, no-take zone designs are likely to be optimal for only the species considered in modeling (White *et al.* 2009). If a large no-take zone is designed to protect a mobile, far-ranging species, it will constrain the maximum harvest of other less mobile species by restricting hunter access. In order to ensure multiple species' protection within no-take zones, conservationists will have to consider trade-offs between species' characteristics, an approach that has not been considered in tropical forests. Fisheries research demonstrates that if multiple species are considered in assessing yield, designing no-take zones to optimize biomass or economic revenue might lead to an optimal level of yield but changing fish community composition, which has implications for conservation and human livelihoods (White *et al.* 2009).

Refining no-take zone design in both marine and terrestrial realms will require more knowledge of harvested species' dynamics, including dispersal and reproductive productivity within and outside no-take zones (Claudet *et al.* 2008; Botsford *et al.* 2009; Claudet *et al.* 2010; Van Vliet *et al.* 2010). The challenges of gaining this information and developing species-specific, site-specific design rules has led some marine researchers to approach no-take zone design as a risk analysis (Halpern *et al.* 2006). Researchers use interval analysis to examine best and worst case scenarios or information-gap theory to find the option that provides an acceptable outcome and is most robust to uncertainty (Halpern *et al.* 2006).

Explicitly consider no-take zone goals

Experience from the marine realm shows that results from theoretical simulations may vary widely based on how no-take zone goals are formulated (Gerber *et al.* 2003). For example, if the main goal of the no-take zone is to protect a population from overharvest, protection can be assessed in a number of ways: maximizing population abundance, minimizing the rate of population decline, or minimizing the probability that the population is extirpated or falls below some threshold (Gerber *et al.* 2003). Early fishery models focused primarily on maximizing yield, but models can also minimize variability in yield, minimize the effects of uncertainty on yield, and maintain economic revenue (Gerber *et al.* 2003; McClanahan 2010). For tropical mammals, theoretical simulations of no-take zones have examined several outcomes, including species persistence over time, the likelihood of a population falling below a threshold, and maximizing offtake while minimizing the probability of a decline (Salas & Kim 2002; Wiederholt *et al.* 2010). Design of no-take zones will be enhanced by considering different goals in simulations.

Recognize spatial variation in harvests and resources

Initial conceptions of spatial management were based on one remote no-take zone supporting a high, localized harvest. As the literature on spatial dimensions of harvesting developed, researchers realized there is often substantial spatial variation in the distribution of both resources and harvesting (Diefenbach *et al.* 2005; Ban & Vincent 2009; Van Vliet *et al.* 2010; Mockrin *et al.* in press). A more realistic treatment of the spatial dimensions of harvesting and resources leads to two important changes: examining how existing spatial variation in hunting and resources interacts with formal no-take zones and considering networks of no-take zones.

In both marine and terrestrial systems, it is unclear how no-take zone design combines with the existing, highly variable distribution of harvesters and resources. For example, in the Kabo concession, there is wide variation in hunting pressure within the area commonly hunted, or hunting catchment (Mockrin *et al.* in press). It is uncertain how this fine-grained variation in hunting pressure combines with the large no-take zone outside the hunting catchment to influence offtake and sustainability (Mockrin *et al.* in press). For species with relatively small dispersal distances, local dispersal within the catchment might be more important to hunting offtake than long-distance dispersal from a remote no-take zone. One potential method of incorporating variation in harvest from the marine realm involves starting with a high resolution map of offtake and simulating changes in harvests (Ban & Vincent 2009). Researchers left the most productive areas for harvesting open while reducing the total area exploited (Ban & Vincent 2009). More empirical evidence is needed to assess this technique, but the high resolution and focus on retaining existing harvesting areas could be effective in tropical forests.

Marine researchers also emphasize that the spatial distribution of harvesting pressure and resources will change in response to management (Botsford *et al.* 2009). Empirical work shows that effective no-take zones can lead to harvesting pressure concentrated outside the reserve ("fishing the line") (Kellner *et al.* 2007). To date, those working in tropical forests have not explored how no-take zone establishment might alter the spatial distribution of hunting and wildlife, but marine research shows that redistribution of harvesting effort after no-take zone establishment has implications for the sustainability of offtake, monitoring no-take zone effectiveness, and socioeconomic concerns of harvesters (Kellner *et al.* 2007).

Spatial variation in hunting pressure and wildlife resources over space suggests that no-take zones might be more effectively designed as networks, rather than as a lone reserve. In the marine realm, no-take zones are often designed and implemented as networks (Stewart *et al.* 2009; White *et al.* 2009). Marine no-take zone networks emerged from the realization that long-distance dispersers may be more effectively protected by a network of dispersed no-take zones (individual zones can shelter immigrants, while one central no-take zone exports all dispersers into harvested areas). Theoretical simulations show that expanding from one no-take zone into a network will alter the larger population's stability and yield by increasing edge habitat (McCullough 1996). While using a network approach would therefore be more complex, networks might also be a better fit with the spatial variation in harvesting and wildlife seen in tropical forests.

Implementation of spatial management

No-take zones are often described as less complicated to implement than quotas, requiring less investment in monitoring and enforcement (McCullough 1996; Johannes 1998; Milner-Gulland *et al.* 2003). For example, enforcing no-take zones requires protecting the area where no harvesting is allowed, as opposed to tracking a seasonal or daily limit for individual harvesters or the entire wildlife or fish population for quota enforcement. Quota management also requires intensive monitoring of harvested populations in order to revise limits. No-take zones would likely be revised less frequently, although the remaining questions about the effects of no-take zones on population persistence and yield means that monitoring after no-take zone establishment is essential (e.g., Gerber *et al.* 2007). Synthesizing past literature yields two main recommendations for future implementation in tropical forests (1) link monitoring to management through decision analysis, and (2) incorporate human dimensions monitoring and research to encourage successful implementation.

Link monitoring to management through decision analysis

In the marine realm, no-take zone monitoring can be coupled to management actions through decision analysis, a technique that has not yet been used with no-take zones in tropical forests. Decision analysis has been used in both small-scale and commercial fisheries to link biological and socioeconomic monitoring to management actions through prespecified rules (Gerber *et al.* 2007; Dowling *et al.* 2008; McGilliard *et al.* 2011; Prince 2010). Decision rules can be designed for a number of aspects of harvests: species-specific offtake for commercially important or vulnerable species, total offtake across species, changes in species composition, spatial patterns of harvesting, changing trends in catch-per-unit-effort, changes in harvests over specific areas, or combinations of these factors (Dowling *et al.* 2008). Decision rules can be used to both restrict harvesting in the case of excessive offtake, or to relax no-take regulations to allow more harvesting (e.g., Guidetti & Claudet 2010). Combining this approach with the experience gained from past work monitoring wildlife offtakes with hunters in tropical forests (e.g., Noss *et al.* 2005; Bodmer *et al.* 2009) could yield an effective way to monitor and manage no-take zones in tropical forests.

Incorporate human dimensions for successful implementation

Thus far this review has focused on the biological aspects of no-take zone design and function, but social, economic, cultural, and institutional characteristics are critical for no-take zone implementation. In the marine setting, Charles & Wilson (2009) review aspects of human dimensions that affect no-take zone implementation, including the need for meaningful participation by resource users, effective governance, understanding the costs and benefits of no-take zones, and the distribution of these costs and benefits among multiple scales and users. Although use of no-take zones in tropical forests is currently limited, understanding support and compliance from resource users is an important area of research, as there are limited resources for wildlife management in most tropical forests.

Some researchers have suggested that hunters may support no-take zones in tropical forests, with concomitant decreases in enforcement, because spatial management is similar to customary management and might enhance harvests (Fimbel *et al.* 2000; Novaro *et al.* 2000; Naranjo & Bodmer 2007). While the long history of community-based spatial management demonstrates that communities can support spatial management and self-enforce these regulations effectively under some circumstances (Ostrom 1990; Dietz *et al.* 2002; Newing & Bodmer 2003), experience from the marine realm shows that developing these systems under contemporary economic and social threats may be challenging. Self-enforced restrictions are often difficult to maintain under contemporary economic and social threats (Cinner & Aswani 2007). In addition, in some tropical forest settings there may not be past experience with customary management of wildlife hunting (Bennett *et al.* 2007). While the dispersal of animals to hunted areas may benefit hunters, marine research shows that this dispersal function would have to be well documented to obtain community support (Cinner & Aswani 2007).

Therefore, while there is experience from both marine and terrestrial realms demonstrating the importance of involving harvesters in comanagement (Newing & Bodmer 2003; Guidetti & Claudet 2010), spatial management will not necessarily be supported by resource users. Following the marine literature, changes in offtakes, income, and employment over time should all be studied to better understand relationships between no-take zones implementation, livelihoods, and support from resource users (Mascia *et al.* 2010). Building this greater understanding of human dimensions will be critical in successful implementation of no-take zones in tropical forests.

Conclusion

Although we have discussed many of the advantages of this management approach, spatial management will not be a panacea for the challenges caused by wildlife harvesting in tropical forests. In situations where habitat loss and human populations are increasing, human demand may outpace wildlife supply. In marine and terrestrial settings, spatial management is usually combined with other restrictions on gear, harvesting effort, or individual species. Depending on the goal of the no-take zone, spatial management may not be appropriate for highly mobile or sedentary species. Despite these challenges, our review of the literature on marine and terrestrial harvesting suggests that this technique holds promise for hunting management in tropical forests.

Although no-take zones offer some advantages over quotas, uncertainty about their design and the human dimensions of implementation means that they cannot be considered a simple strategy for wildlife management. Marine scientists have reached a similar conclusion: although no-take zones were envisioned for situations where funding and data were limited, studies overwhelmingly call for more monitoring and information on species demographic rates (Stewart *et al.* 2009). Given these limitations, a reasonable first goal of spatial management in tropical forests might be to protect resident wildlife in no-take zones, not attempting to maximize dispersal and hunting offtake. Protecting wildlife populations in no-take zones will require conservative placement and design to prevent hunting and dispersal from exerting a substantial drain on no-take zones. As research continues, a better understanding of the social impacts of no-take zones and wildlife demography in response to spatial variation in hunting pressure will improve management.

While spatial management is not uniquely easy to design or implement without data, the expertise developed from temperate hunting and fisheries management is directly relevant to spatial management in tropical forests. Until this point, marine fisheries and tropical forests have worked largely on parallel tracks to investigate spatial management, but the two fields are facing similar challenges, despite differences in species' productivity and mobility. A greater integration between these realms may benefit both fields.

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References

Alvard, M., Robinson J., Redford K., Kaplan H. (1997) The sustainability of subsistence hunting in the Neotropics. *Conserv Biol* **11**, 977–982.

Ban, N.C., Vincent A.C.J. (2009) Beyond marine reserves: exploring the approach of selecting areas where fishing is permitted, rather than prohibited. *PLoS One* **4**, 280–283.

Bennett, E.L., Blencowe E., Brandon K. *et al*. (2007) Hunting for consensus: reconciling bushmeat harvest, conservation, and development policy in west and central Africa. *Conserv Biol* **21**, 884–887.

Beringer, J., Seibert S.G., Reagan S., Brody J.A., Pelton M.R., VanGilder L.D. (1998) The influence of a small sanctuary on survival rates of black bears in North Carolina. *J Wildlife Manage* **62**, 727–784.

Berkes, F. (1986) Common property resources and hunting territories. *Anthropologica* **28**, 145–162.

Bodmer, R.E., Puertas P.E., Fang T. (2009) Co-managing wildlife in the Amazon and the Salvation of the Pacaya-Samiria National Reserve in Peru. Pages 104–116 in M.J. Manfredo, J.J. Vaske, P.D. Brown, E. Duke, editors. *Wildlife and society the science of human dimensions*. Island Press, Washington, DC.

Botsford, L.W., Brumbaugh D.R., Grimes C. *et al*. (2009) Connectivity, sustainability, and yield: bridging the gap between conventional fisheries management and marine protected areas. *Rev Fish Biol Fish* **19**, 69–95.

Brochet, A.L., Gauthier-Clerc M., Mathevet R., Bechet A., Mondain-Monval J.Y., Tamisier A. (2009) Marsh management, reserve creation, hunting periods and carrying capacity for wintering ducks and coots. *Biodivers Conserv* **18**, 1879–1894.

Carr, M.H., Neigel J.E., Estes J.A., Andelman S., Warner R.R., Largier J.L. (2003) Comparing marine and terrestrial ecosystems: implications for the design of coastal marine reserves. *Ecol Appl* **13**, S90–S107.

Charles, A., Wilson L. (2009) Human dimensions of marine protected areas. *ICES J Mar Sci* **66**, 6–15.

Cinner, J.E., Aswani S. (2007). Integrating customary management into marine conservation. *Biol Conserv* **140**, 201–216.

Claudet, J., Osenberg C.W., Benedetti-Cecchi L. *et al*. (2008) Marine reserves: size and age do matter. *Ecol Lett* **11**, 481–489.

Claudet, J., Osenberg C.W., Domenici P. *et al*. (2010) Marine reserves: fish life history and ecological traits matter. *Ecol Appl* **20**, 830–839.

Colding, J., Folke C. (2001) Social taboos: "invisible" systems of local resource management and biological conservation. *Ecol Appl* **11**, 584–600.

Delibes, M., Gaona P., Ferreras P. (2001) Effects of an attractive sink leading into maladaptive habitat selection. *Am Nat* **158**, 277–285.

Diefenbach, D.R., Finley J.C., Luloff A.E. *et al*. (2005) Bear and deer hunter density and distribution on public land in Pennsylvania. *Hum Dimens Wildl* **10**, 201–212.

Dietz, T., Dolsak N., Ostrom E., Stern P.C. (2002) Committee on the human dimensions of global change. Pages 3–36 in E. Ostrom, T. Dietz, N. Dolsak, P.C. Stern, S. Stonich, E.U. Weber, editors. *The drama of the commons*. Division of Behavioral and Social Sciences and Education, National Research Council, National Academy Press, Washington, DC.

Dowling, N.A., Smith D.C., Knuckey I. *et al*. (2008) Developing harvest strategies for low-value and data-poor fisheries: case studies from three Australian fisheries. *Fish Res* **94**, 380–390.

Dunlap, T.R. (1988) Sport hunting and conservation, 1880–1920. *Environ Rev* **12**, 51–60.

Fa, J.E., Brown D. (2009) Impacts of hunting on mammals in African tropical moist forests: a review and synthesis. *Mammal Rev* **39**, 231–264.

Fimbel, C., Curran B., Usongo L. (2000) Enhancing the sustainability of duiker harvesting through community participation and controlled access in the Lobéké region of southeastern Cameroon. Pages 356–374 in J.G. Robinson, E.L. Bennett, editors. *Hunting for sustainability in tropical forests*. Columbia University Press, New York.

Gadgil, M. (1987) Social restraints on exploiting nature: the Indian experience. *Dev Seeds Change* **1**, 26–30.

Gell, F.R., Roberts C.M. (2003) Benefits beyond boundaries: the fishery effects of marine reserves. *Trends Ecol Evol* **18**, 448–455.

Gerber, L.R., Botsford L.W., Hastings A. *et al*. (2003) Population models for marine reserve design: a retrospective and prospective synthesis. *Ecol Appl* **13**, 47–64.

Gerber, L.R., Wielgus J., Sala E. (2007) A decision framework for the adaptive management of an exploited species with implications for marine reserves. *Conserv Biol* **21**, 1594–1602.

Guidetti, P., Claudet J. (2010). Comanagement practices enhance fisheries in marine protected areas. *Conserv Biol* **24**, 312–318.

Halpern, B.S., Regan H.M., Possingham H.P., McCarthy M.A. (2006) Accounting for uncertainty in marine reserve design. *Ecol Lett* **9**, 2–11.

Johannes, R.E. (1978) Traditional marine conservation methods in Oceania and their demise. *Annu Rev Ecol System* **9**, 349–364.

Johannes, R.E. (1998) The case for data-less marine resource management: examples from tropical nearshore finfisheries. *Trends Ecol Evol* **13**, 243–246.

Kaltenborn, B.P., Andersen O. (2009) Habitat preferences of ptarmigan hunters in Norway. *Euro J Wildlife Res* **55**, 407–413.

Kellner, J.B., Tetreault I., Gaines S.D., Nisbet R.M. (2007) Fishing the line near marine reserves in single and multispecies fisheries. *Ecol Appl* **17**, 1039–1054.

Laudré, J., Clark T.W. (2003) Managing puma hunting in the western United States: through a metapopulation approach. *Anim Conserv* **6**, 159–170.

Le Quesne, W.J.F., Codling E.A. (2009) Managing mobile species with MPAs: the effects of mobility, larval dispersal, and fishing mortality on closure size. *ICES J Mar Sci* **66**, 122–131.

Levi, T., Shepard G.H., Ohl-Schacherer J., Peres C.A., Yu D.W. (2009) Modelling the long-term sustainability of indigenous hunting in Manu National Park, Peru: landscape-scale management implications for Amazonia. *J Appl Ecol* **46**, 804–814.

Mahoney, S.P. (2009) Recreational hunting and sustainable wildlife use in North America. Pages 266–281 in B. Dickson, J. Hutton, W.M. Adams, editors. *Recreational hunting, conservation and rural livelihoods: science and practice*. Wiley-Blackwell, Oxford, England.

McClanahan, T.R. (2010) Effects of fisheries closures and gear restrictions on fishing income in a Kenyan coral reef. *Conserv Biol* **24**, 1519–1528.

McCook, L.J., Ayling T., Cappo M. *et al*. (2010) Adaptive management of the Great Barrier Reef: a globally significant demonstration of the benefits of networks of marine reserves. *Proc Natl Acad Sci* **107**, 18278–18285.

McCullough, D. (1996) Spatially structured populations and harvest theory. *J Wildl Manage* **60**, 1–9.

McGilliard, C.R., Hilborn R., MacCall A., Punt A.E., Field J.C. (2011) Can information from marine protected areas be used to inform control-rule-based management of small-scale, data-poor stocks? *CES J Mar Sci* **68**, 201–211.

Mascia, M.B., Claus C.A., Naidoo R. (2010) Impacts of marine protected areas on fishing communities. *Conserv Biol* **24**, 1424–1429.

Milner-Gulland, E.J., Bennett E.L., SCB 2002 Annual Meeting Wild Meat Group. (2003) Wild meat: the bigger picture. *Trends Ecol Evol* **18**, 351–357.

Mockrin, M.H., Rockwell R.F., Redford K.H. (in press). Landscape features determine the distribution and sustainability of ungulate hunting in Northern Congo. *Conserv Biol*.

Moffitt, E.A., Botsford L.W., Kaplan D.M., O'Farrell M.R. (2009) Marine reserve networks for species that move within a home range. *Ecol Appl* **19**, 1835–1847.

Naranjo, E.J., Bodmer R.E. (2007). Source-sink systems and conservation of hunted ungulates in the Lacandon forest, Mexico. *Biol Conserv* **138**, 412–420.

Newing, H., Bodmer R. (2003) Collaborative wildlife management and adaptation to change: the Tamshiyacu Tahuayo communal reserve, Peru. *Nomad Peoples* **7**, 110–123.

Noss, A.J., Oetting I., Cuellar R.L. (2005) Hunter self-monitoring by the Isoseño-Guaraní in the Bolivian Chaco. *Biodivers Conserv* **14**, 2679–2693.

Novaro, A.J., Funes M.C., Walker R.S. (2005) An empirical test of source–sink dynamics induced by hunting. *J Appl Ecol* **42**, 910–920.

Novaro, A.J., Redford K.H., Bodmer R.E. (2000) Effect of hunting in source-sink systems in the neotropics. *Conserv Biol* **14**, 713–721.

Ostrom, E. (1990) *Governing the commons: the evolution of institutions for collective action*. Cambridge University Press, Cambridge, UK.

Poulsen, J.R., Clark C.J., Mavah G. (2007), Wildlife management in a logging concession in Northern Congo: can livelihoods be maintained through sustainable hunting? Pages 140–157 in G. Davies, D. Brown, editors. *Bushmeat and livelihoods: wildlife management and poverty reduction*. Blackwell Publishers, Oxford, UK.

Prince, J. (2010) Rescaling fisheries assessment and management: a generic approach, access rights, change agents, and toolboxes. *B Mar Sci* **86**, 197–219.

Roberts, C.M., Andelman S., Branch G. *et al*. (2003) Ecological criteria for evaluating candidate sites for marine reserves. *Ecol Appl* **13**, 199–214.

Robinson, J.G., Bennett E.L. (2000) *Hunting for sustainability in Tropical forests*. Columbia University Press, New York.

Salas, L.A., Kim J.B. (2002) Spatial factors and stochasticity in the evaluation of sustainable hunting of tapirs. *Conserv Biol* **16**, 86–96.

Slough, B.G., Mowat G. (1996) Lynx population dynamics in an untrapped refugium. *J Wildlife Manage* **60**, 946–961.

Stewart, G.B., Kaiser M.J., Cote I.M. *et al*. (2009) Temperate marine reserves: global ecological effects and guidelines for future networks. *Conserv Lett* **2**, 243–253.

Van Vliet, N., Milner-Gulland E.J., Bousquet F., Saqalli M., Nasi R. (2010) Effect of small-scale heterogeneity of prey and hunter distributions on the sustainability of bushmeat hunting. *Conserv Biol* **24**, 1327–1337.

White, J.W., Botsford L.W., Hastings A., Largier J.L. (2009) Population persistence in marine reserve networks: incorporating spatial heterogeneities in larval dispersal. *Mar Ecol Prog Ser* **398**, 49–67.

Wiederholt, R., Fernandez-Duque E., Diefenbach D.R., Rudran R. (2010) Modeling the impacts of hunting on the population dynamics of red howler monkeys (Alouatta seniculus). *Ecol Model* **221**, 2482–2490.

Williams, B.K., Nichols J.D., Conroy M.J. (2002) *Analysis and management of animal populations: modeling, estimation, and decision making*. Academic Press, San Diego.

Worm, B., Hilborn R., Baum J.K. *et al*. (2009) Rebuilding global fisheries. *Science* **325**, 578–585.