Predicting species interactions from edge responses: mongoose predation on hawksbill sea turtle nests in fragmented beach habitat

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Because species respond differently to habitat boundaries and spatial overlap affects encounter rates, edge responses should be strong determinants of spatial patterns of species interactions. In the Caribbean, mongooses (*Herpestes javanicus*) prey on hawksbill sea turtle (*Eretmochelys imbricata*) eggs. Turtles nest in both open sand and vegetation patches, with a peak in nest abundance near the boundary between the two microhabitats; mongooses rarely leave vegetation. Using both artificial nests and hawksbill nesting data, we examined how the edge responses of these species predict the spatial patterns of nest mortality. Predation risk was strongly related to mongoose abundance but was not affected by nest density or habitat type. The product of predator and prey edge response functions accurately described the observed pattern of total prey mortality. Hawksbill preference for vegetation edge becomes an ecological trap in the presence of mongooses. This is the first study to predict patterns of predation directly from continuous edge response functions of interacting species, establishing a link between models of edge response and species interactions.

Keywords: edge effect; habitat selection; fragmentation; generalized additive mixed model (GAMM); evolutionary trap; spillover predation

1. INTRODUCTION

Habitat fragmentation can affect communities by altering interactions among species (Fagan *et al.* 1999; Didham *et al.* 2007). In fragmented landscapes, animals often respond to habitat structure by avoiding or aggregating near edges, resulting in strong gradients of species abundance (Lidicker 1999; Ewers & Didham 2006a). Where two interacting species both occur on either side of an edge, such edge responses may simply amplify or reduce the frequency of normal interactions. However, where species occupy distinct habitats, the edge provides a unique context for their interactions and edge responses may have a strong effect on where and how often interactions take place.

Where predators and prey interact in fragmented landscapes, edge responses may influence the spatial distribution of both predation risk, the probability of predation for an individual prey in a given time interval, and total prey mortality, the total number of prey killed by predators in a given time interval. The spatial distribution of predation risk affects the relative availability of suitable 'core' habitat for prey (Robinson *et al.* 1995). Total prey mortality determines the energy flow from prey to predators, altering the dynamics of both populations (Fagan *et al.* 1999; Cantrell *et al.* 2001). The spatial

distribution of prey mortality will not necessarily match that of predation risk in fragmented landscapes. In some cases, prey may actively avoid the locations of the highest risk (e.g. Bowers & Dooley 1993). In other cases, attraction to edges may lead to convergence of predator and prey abundances, resulting in heavy mortality near the edge and creating an 'ecological trap' for prey (Gates & Gysel 1978; Ries & Fagan 2003).

If predation is proportional to contact rate between predators and prey, the principle of mass action provides a simple prediction of how edge responses will affect predation risk and total prey mortality. Mass action predicts that contact rate among species will be proportional to the product of their local densities (Cosner *et al.* 1999). It follows that (i) predation risk for individual prey across the edge will be directly proportional to the gradient of predator abundance, and (ii) the spatial distribution of total prey mortality across the edge will be directly proportional to the product of predator and prey abundances. Factors other than simple contact rate could, however, affect edge-related patterns of predation. In particular, density-dependent processes may be important. If predators actively search for prey primarily in areas of high prey density, per capita predation risk may be higher in these areas (Keyser *et al.* 1998; Lariviere & Messier 1998; Marchand & Litvaitis 2004). On the other hand, risk could be reduced through dilution effects if predators under-match prey abundance (Foster & Treherne 1981; Inman & Krebs 1987). Habitat characteristics that change across the edge, such as the structural

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complexity of vegetation, may also affect predation risk by altering the ability of predators to detect or pursue prey (Hampton 2004; Bergman *et al.* 2006).

Studies of species interactions in fragmented landscapes have found no consistent effect of edge (Paton 1994; Donovan *et al.* 1997; Lahti 2001; Batary & Baldi 2004), limiting our ability to make general predictions about how fragmentation affects communities. Despite the intuitive importance of edge responses in determining the location and frequency of species interactions in fragmented landscapes, the relationship between edge-related gradients in species abundance and observed patterns of species interactions has not been rigorously explored. Numerous studies have examined edge-related patterns of predation (reviewed by Batary & Baldi 2004), as well as the individual edge responses of predatory species (reviewed by Chalfoun *et al.* 2002) and their prey (reviewed by Ries & Sisk 2004). Surprisingly, however, no studies appear to have examined quantitatively the relative importance of predator abundance, prey abundance and edge structure in determining the pattern of predation near edges.

We investigated predation by introduced *Herpestes javanicus* (small Asian mongoose; E. Geoffroy Saint-Hilaire) on nests of *Eretmochelys imbricata* (hawksbill sea turtle; Linnaeus) in fragmented beach habitat in Barbados, West Indies. Hawksbill populations have suffered significant declines in recent decades, and the species is currently listed as critically endangered (IUCN 2007). Mongoose predation at hawksbill nesting beaches in the Caribbean can be intense, with destruction of all available nests reported for some beaches (Nellis & Small 1983). We measured gradients of abundance of mongooses and sea turtle nests across the edge between patches of vegetation and open sand. We examined predation at two temporal scales: short-term predation of artificial nests and multi-annual predation of natural hawksbill nests.

Using the mongoose–hawksbill system, we explored the ability of continuous edge response functions to predict patterns of per capita predation risk and total prey mortality across the edge. We found that the edge response of mongooses was a strong predictor of the edge effect on predation risk for hawksbill nests and that the product of mongoose and hawksbill edge responses accurately modelled the spatial pattern of total nest mortality. We suggest that this simple and general approach for linking species interactions to underlying edge responses may help to predict the consequences of landscape fragmentation for species interactions in other systems.

2. MATERIAL AND METHODS

(a) Study area and species

The study was carried out at Bath (13.187° N, 59.476° W), an important nesting beach for hawksbill sea turtles on the east coast of Barbados. Nesting at Bath occurs year-round with a peak from June to August (Beggs *et al.* 2007). The number of hawksbill nests recorded annually at Bath has varied considerably (range 15–217, mean 76.9), but showed a steady increase over the study period from 1999 to 2005.

Mongooses were introduced to the Caribbean from India in 1872 to control rodents in sugar cane plantations and are currently found on all major cane-producing islands

(Horst *et al.* 2001). Mongooses are diurnal generalist carnivores that thrive in human-altered habitats (Quinn & Whisson 2005). Individual home ranges overlap extensively, and in areas such as Bath, where anthropogenic food is abundant, local densities can exceed 10 animals ha⁻¹ (Nellis & Everard 1983; Leighton 2005). Other than crabs that sometimes burrow into nests, mongooses are the sole predators of turtle eggs at our site. Mongooses avoid contact with humans but do not have important local predators.

Female hawksbills emerge from the ocean at night to nest, and may crawl more than 100 m in search of a suitable nest site. Nesting turtles use their hind flippers to excavate a 40–60 cm deep cavity into which they deposit 100–200 soft-shelled eggs, each roughly 5 cm in diameter. They then refill the cavity, pack down the sand, conceal the location by scattering loose sand over the site and return to the ocean. Incubation lasts for approximately 60 days, and hatchlings emerge at the sand surface a few days after hatching.

Bath Beach is a 1.12 km long stretch of sand, with a cottage-lined access road parallel to the water and a local picnic area near the centre. Hawksbill nesting is confined to the area between the high water mark and barriers 10–50 m inland associated with the road and cottages. Nesting habitat is a fragmented mixture of two main microhabitat types. Approximately, 60 per cent of the potential nesting area is 'open beach': sandy areas planted with shade trees but devoid of other vegetation except sparse grass in some areas. The remaining 40 per cent is 'beach vegetation': dense patches of low shrubs (especially *Coccoloba uvifera* L. and *Thespesia populnea* L.), generally 1–3 m high. Beach vegetation forms 11 fragments ranging in area from 45 to 1650 m² (mean 600 m²). Vegetation occurs along the berm in some areas and along the inland margin of the open beach in other areas, resulting in a total of approximately 1 km of open beach-vegetation edge. The transition between vegetated and open beach microhabitats is sharp. We operationally defined 'edge' as the outer border of continuous leafy vegetation, measured to the nearest 0.1 m.

(b) Spatial patterns of abundance and nest predation

Data on hawksbill nesting at Bath were collected from 1999 to 2005 as part of the long-term monitoring programme of the Barbados Sea Turtle Project, University of the West Indies. Nests were located during the day from the disturbance left by the laying turtle, and the nest location was confirmed by excavation. We monitored the nests on daily beach surveys to determine whether they were predated by mongooses (signs of digging, mongoose tracks, at least one egg removed from the nest), hatched (signs of hatchling emergence, hatched shells at the bottom of the nest) or destroyed through other processes such as beach erosion.

We measured the edge response of nesting hawksbills by calculating the cumulative density of nests laid during each nesting season in 1 m intervals parallel to the edge (between 8 m into the vegetation and 6 m onto the open beach). To do this, we used MAPINFO v. 6.5 to separate a digital map of the beach into 1 m contour intervals relative to the edge of all vegetation fragments and divided the number of nests in each interval by the total area of the interval. We standardized densities among years by dividing densities for a given year by the total number of nests laid that year, generating proportional cumulative nest densities used for modelling edge response. To reduce bias due to stochastic effects of small sample size for densities calculated from years

Table 1. GAMMs used to model abundance and predation risk in relation to the open beach-vegetation edge on Bath Beach, Barbados. (a) Mongoose edge response, (b) hawksbill sea turtle nest abundance, (c) risk of mongoose predation on artificial nests and (d) risk of mongoose predation on hawksbill nests. Sample size, n , is the number of track pad checks in (a), the number of distance from edge intervals (15 yr^{-1} over 2 yr) in (b) and the total number of monitored nests in (c,d). Adjusted R^2 is for the final model, where only significant predictors were retained. $s(\dots)$ denotes predictors fitted as non-parametric smoothing terms; unbracketed predictors were fitted as typical parametric terms. d.f. is the estimated degrees of freedom for each term.

model	n	adj R^2	predictors	d.f.	$F(T)^a$	p
(a) mongoose activity	978	0.21	s (distance from edge)	3.78	20.40	$\ll 0.001$
(b) hawksbill nest density	30	0.87	s (distance from edge)	5.34	10.04	$\ll 0.001$
(c) artificial nest predation risk	204	0.46	s (mongoose activity)	1.00	50.81	$\ll 0.001$
			s (nest density)	1.00	0.517	0.473
			habitat	1.00	(0.543)	0.547
(d) hawksbill nest predation risk	301	0.16	s (mongoose activity)	1.00	44.48	$\ll 0.001$
			s (nest density)	1.00	1.17	0.281
			habitat	1.00	(1.356)	0.176

^aGAMMs use F -values to test the significance of non-parametric smoothing terms, while T values (in parentheses) are used for parametric terms.

where nest numbers were low, we calibrated the edge response model using data from 2004 and 2005, which had both the largest number of nests and comparable sample sizes ($n = 168$ in 2004, $n = 217$ in 2005), and used the pooled data from 1999 to 2003 for model evaluation (Guisan & Zimmermann 2000).

Data on mongoose edge response and predation of artificial nests were collected during a three-week period in October 2003, late in the main hawksbill nesting season. We measured mongoose edge response using a total of 163 'track pads', $0.5 \times 0.5 \text{ m}$ patches of natural sandy substratum smoothed to pick up the tracks of passing animals. We measured the pattern of predation using 204 artificial nests, which consisted of sixteen 15 g pieces of sausage buried 15 cm beneath the surface of the sand. This is somewhat shallower than the uppermost eggs in natural nests (approx. 30 cm), allowing artificial nests to be discovered and predated rapidly by mongooses. All track pads and artificial nests were placed along the 160 m edge of the largest vegetation fragment (1650 m^2), located near the centre of the beach. We randomly assigned each pad and nest a location along the 160 m edge and a position across the edge gradient. Positions included $-8, -7, -6, -5, -4, -3, -2, -1, 0, 1.5, 3$ and 5 m from the edge, with negative values in vegetation and positive values on the open beach. We deployed pads and nests in 10 series, with approximately 16 pads and 20 nests per series and a minimum of 2 days between series. We monitored each track pad during the daylight (05.00–19.00) portion of a 24-hour period, recording the presence/absence of mongoose tracks every 2 hours. At the end of 24 hours, we determined the fate of each artificial nest (intact or predated as indicated by digging, tracks and missing sausage) and removed all pads and nests in the series.

(c) Statistical analyses

We used generalized additive mixed models (GAMMs) to describe edge-related patterns in species abundance and to explore factors affecting the pattern of predation risk across the edge. Generalized additive models provide a flexible framework for modelling species–habitat relationships (Guisan *et al.* 2002), allowing predictors to be fitted either as parametric or non-parametric smoothing terms (Hastie & Tibshirani 1987). GAMMs extend this framework to allow variables to be modelled as random effects (Wood 2004). We used the mixed model framework of GAMMs to account

for correlation structures in the data, including year as a random variable in hawksbill nest models, series in artificial nest models and track pad identity to control for repeated measures when modelling mongoose activity. We calculated the spatial extent of the edge responses as the distance between local extrema of the second derivative of each edge response function (Ewers & Didham 2006b), using parametric polynomial terms to approximate the non-parametric smoothing terms in the original function. Models were fitted using package MGCV 1.3–19 in R v. 2.4.0 (Wood & Augustin 2002).

We tested the prediction that predation risk is driven by the patterns of predator abundance for both artificial and hawksbill nests using GAMMs to model the relationship between mongoose abundance and fate of individual nests (predated/intact). We included nest abundance (proportional cumulative density) and habitat type (vegetation/open beach) as additional predictors to test for the possible influence of density-dependent processes and habitat characteristics on predation risk. We calculated classification accuracy for each model using sensitivity–specificity plots to select the optimal probability cut-off (Hosmer & Lemeshow 2000). We used R package ROC v. 1.0–1 (Sing *et al.* 2005) to calculate the area under the curve in receiver operating characteristic (ROC) plots for each classification, providing a measure of model discrimination. ROC values range from 0 to 1, with 0.5 indicating random discrimination, values above 0.7 considered acceptable discrimination and values above 0.9 extremely rare (Hosmer & Lemeshow 2000).

To test the prediction that the product of continuous edge response functions for interacting species should predict the spatial pattern of total mortality, we multiplied mongoose and hawksbill edge response functions and used the Kolmogorov–Smirnov test to compare the resulting function with the observed distribution of predated hawksbill nests across the edge.

3. RESULTS

(a) Edge responses

Mongooses and hawksbills both showed a highly significant response to the edge of beach vegetation. The GAMMs show that the distance from the edge alone explained 21 per cent of the variance in mongoose activity (table 1a) and 87 per cent of the variance in hawksbill

Figure 1. Abundance responses of mongooses and hawksbill sea turtles to edges between open sand and patches of vegetation at Bath Beach in Barbados. (a) Mongoose abundance measured as the probability of crossing a sand pad per 2 hours interval and (b) hawksbill nest abundance measured as the proportion of total annual nests per m^2 . For mongooses, data shown are the presence/absence of mongoose tracks on sand pads for each 2 hours check period ($n=978$), with random jitter added to allow visualization of overlapping points. For hawksbill nests, open circles are proportional cumulative nest densities from 2004 and 2005 used in model calibration ($n=30$). The solid lines are the GAMM edge response function and dashed lines are ± 1 s.e. The vertical dotted lines mark the location of the edge, with positive values representing open sand and negative values representing within vegetation.

nest density (table 1b; see table S1 in the electronic supplementary material for equivalent parametric fits). The mongoose edge response extended from 3.4 m within vegetation to 1.5 m onto the open beach. Mongoose abundance dropped 96.5 per cent across the edge, with the probability of mongoose tracks during a 2-hour check period decreasing from 0.62 within vegetation to 0.02 on the open beach (figure 1a). The hawksbill edge response extended from 2.9 m within vegetation to 2.5 m onto the open beach. Proportional cumulative density of hawksbill nests increased from 0.05 on the open beach to 0.23 near the edge of vegetation (peak at 0.2 m within vegetation) and decline to 0.01 within vegetation, resulting in a 97.5 per cent change in density across the edge (figure 1b). The hawksbill edge response model, calibrated using data from 2004 to 2005, explained 68 per cent of the variation in cumulative nest density across the edge for the pooled 1999–2003 data, suggesting that the shape of the edge response function was representative of the pattern of nesting in previous years.

(b) Nest predation

Of 204 artificial nests, 120 (59.3%) were predated within 24 hours. Of 551 hawksbill nests recorded from 1999 to 2005, 149 (27.0%) were predated by mongooses during

Figure 2. GAMMs of predation risk for (a) artificial nests over a 24 hour period ($n=204$) and (b) hawksbill sea turtle nests over a 60-day incubation period ($n=301$) across the open sand-vegetation edge. Data shown are the fates of individual nests (1, predated; 0, intact), with random jitter added to allow visualization of overlapping points. The solid lines show the final GAMM for predation risk and the dashed lines are ± 1 s.e. The vertical dotted lines mark the location of the edge, with positive values representing open sand and negative values representing within vegetation.

the 60-day incubation period, with annual predation rates ranging from 17.9 to 38.9 per cent. Of the 301 nests located within the range over which edge responses were measured (between 8 m into the vegetation and 6 m onto the open beach), 144 (47.9%) were predated. Thus, only five predation events (3.4% of all mongoose predation) occurred outside this range.

(c) Predation risk

Predation risk for both real and artificial sea turtle nests showed a highly significant positive relationship with mongoose abundance (table 1c,d). However, neither nest abundance nor habitat type explained additional variation in predation risk for either real or artificial nests. The final model with mongoose activity as the sole predictor explained 46 per cent of the variance in predation risk for artificial nests and 16 per cent of the variance for hawksbill nests. The spatial pattern of predation risk for both real and artificial nests closely reflected the edge response of mongooses, being low on the open beach and increasing sharply within vegetation (figure 2). The final models correctly predicted nest fate in 82 per cent of artificial and 69 per cent of hawksbill nests. Both models showed reasonable discrimination, with area under the ROC curve being 0.88 for artificial nests and 0.74 for hawksbill nests.

Figure 3. Frequency of predated hawksbill sea turtle nests recorded from 1999 to 2005 across the open beach-vegetation edge (bars) and distribution of mortality predicted by the product of continuous edge response functions for mongooses and hawksbills (solid line).

(d) Distribution of mortality

The product of the edge response functions for mongooses and hawksbills accurately predicted the distribution of total hawksbill nest mortality across the edge, with a strong peak in mortality 1.0 m into vegetation (figure 3). There was no significant difference between predicted and observed patterns of mortality (Kolmogorov–Smirnov test: $D=0.060$, $p=0.97$).

4. DISCUSSION

(a) A simple link between edge responses and predation

The spatial pattern of predation risk for sea turtle nests across the sand-vegetation edge in beach habitat was strongly related to the gradient of mongoose abundance. This was true both for artificial nests exposed to predators for 24 hours and for natural nests of hawksbills that remained vulnerable throughout their 60-day incubation. Furthermore, the distribution of hawksbill nest mortality across the edge was accurately described by the product of mongoose and hawksbill edge responses. This first use of the edge responses of interacting species as basic predictors of the spatial pattern of interactions suggests that this approach may provide a simple framework for understanding the patterns of predation near edges.

The main assumption of this approach is that predation rate is proportional to contact frequency. Where strong gradients of density exist, density-dependent processes have the potential to alter the relationship between contact frequency and predation rate. Nest abundance did not affect predation risk, suggesting that mongooses are not specifically searching for nests near the edge where nest densities are the highest. One possibility is that actual nest densities at any particular time were simply too low to promote increased nest-searching behaviour by mongooses (Lariviere & Messier 1998) and that predation in this system is primarily incidental. If this is the case, we might expect nest density to be a more important predictor of predation at higher density nesting beaches or with continuing recovery of hawksbill populations in the future.

Differences in habitat characteristics also have the potential to alter the likelihood that contact results in predation. Bergman *et al.* (2006) examined the spatial

distribution of wolf kills in relation to wolf movements and prey abundance and found that kills occurred primarily in habitats where prey were most vulnerable. In our study, whether a nest was located in the open or in vegetation *per se* was not a significant predictor of predation risk for either natural or artificial nests beyond the effect of mongoose abundance, suggesting that those mongooses present in open habitats were as likely to detect and prey upon encountered nests as those mongooses present in vegetation. This is not particularly surprising because disturbance of the sand created by nesting turtles and researchers creating artificial nests is substantial, and these cues are likely to be equally reliable in vegetated and open habitats. Furthermore, there was no indication that predation risk was either higher or lower than that predicted by mongoose abundance right at the edge.

(b) Peaks in prey mortality: the signature of an ecological trap

The close match between predicted and observed distributions of total nest mortality suggests that measuring continuous edge responses for predators and prey at the appropriate scale for each species allows fine-grained prediction of the location and shape of the peaks in prey mortality. In our study, the peak in predation occurred 1 m inside the boundary of vegetated beach habitat, rather than being centred on the edge itself. This points to a potential source of confusion in previous studies where predation was measured only in 'edge' and 'non-edge' habitats and no edge effect was found (Lahti 2001). It is possible that in some of these cases, the edge effect occurred at some intermediate distance from the edge or at a different spatial scale than the one used in the study. Indeed, using our approach to model interactions among species with typical edge responses described in previous studies (Lidicker 1999; Ries *et al.* 2004; Ewers & Didham 2006b) suggests that peaks in species interactions should occur often and predictably at some distance from the edge itself.

In order to effectively manage populations in fragmented landscapes, it is important to know where key species interactions are taking place. Specifically, when overlap of predator and prey abundances predicts strong peaks in prey mortality associated with edges, this may signal the existence of an important ecological trap for prey species (Gates & Gysel 1978; Schlaepfer *et al.* 2002; Robertson & Hutto 2006). The high concentration of hawksbill nests in the border of beach-vegetation fragments agrees with the previous evidence that hawksbills prefer to nest in vegetated beach habitat (Ficetola 2007; Horrocks & Scott 1991; Kamel & Mrosovsky 2006). The introduction of cryptic predators such as mongooses creates an ecological trap for hawksbills that continue to prefer to nest in vegetation, despite much higher predation risk in vegetated habitat than in the adjacent non-vegetated portions of the beach (Schlaepfer *et al.* 2005; Robertson & Hutto 2006). In such cases, accurately predicting the location and width of peaks in predation would allow spatially explicit management approaches for protecting prey species such as localized predator control or the designation of appropriate buffer zones around reserves.

(c) Artificial nests and predator tracking as new tools for sea turtle conservation

Data on predation can be difficult and labour intensive to obtain, especially where the species of interest are rare (Engeman *et al.* 2006). We show that two relatively simple and inexpensive techniques, artificial nest experiments and passive tracking of predator abundance, applied over a three-week period, successfully predicted multi-annual spatial patterns of nest predation for hawksbills. Engeman *et al.* (2003, 2005) recently developed the first passive tracking methods for sea turtle nest predators to improve control of raccoons and armadillos on nesting beaches in Florida. Our study confirms the applicability of passive tracking for introduced mongooses in the Caribbean and establishes a practical method for using tracking data to predict the spatial patterns of predation. Artificial nests have been widely used to document the edge effects on avian nest predation (Batary & Baldi 2004) but their use for studies of reptile nests is a new development and has thus far been limited to freshwater turtles (Marchand *et al.* 2002). There is a risk in using short-term experiments to predict long-term patterns, and the use of artificial nests has been specifically criticized (Wilson *et al.* 1998; Moore & Robinson 2004). The availability of a long-term dataset on hawksbill nest predation allowed us to directly compare the patterns of predation from short-term artificial nest experiments to those for hawksbill nests over several years. While absolute predation risk was much higher for artificial nests than for natural nests, the pattern of predation risk across the edge was strikingly similar. The strong relationship between measured mongoose abundance and predation risk, and similarity of GAMMs for both real and artificial nests, suggests that passive tracking and artificial nests provide reliable information on predation in this system. These methods may be particularly useful in the cases where management decisions require a rapid assessment of relative predation risk in the areas where long-term monitoring data are unavailable.

While introduced mongooses have been suggested as an important threat to sea turtle eggs in the Caribbean (Small 1982; Nellis & Small 1983; Coblentz & Coblentz 1985), this is the first study of the factors affecting predation in this system. We confirm that mongoose predation can result in significant egg mortality and show that predation risk is directly related to the patterns of mongoose abundance. Mongooses moving in the open respond to humans by seeking refuge in vegetation, and the spatial pattern of mongoose abundance relative to vegetative cover is consistent with avoidance of beachgoers. This suggests that in more isolated areas, mongooses may venture further onto the open beach, resulting in higher predation rates such as 100 per cent predation as reported by Nellis & Small (1983) for certain beaches in the US Virgin Islands. These findings are broadly relevant to hawksbill sea turtle conservation in the Caribbean where the introduced mongooses are abundant, and point to the general importance of habitat structure in modulating the impact of invasive species on native species decline (Didham *et al.* 2007).

In this study, we show that the edge response functions for predators and prey can be used to predict the shape and spatial extent of the edge effects on predation. Our approach allows quantification of the influence of

density-dependent processes and habitat-specific effects, allowing these to be taken into account when modelling predation. However, even where such effects occur, their impact may be small relative to the effect of predator abundance, and we suggest that the product of predator and prey edge response functions may provide a robust approximation of the pattern of prey mortality in many systems. By establishing a heuristic link between the existing models of species edge responses (e.g. Ries & Sisk 2004; Ewers & Didham 2006b) and the observed patterns of species interactions in fragmented habitat (e.g. Gates & Gysel 1978; Brand & George 2000), the approach developed here may help resolve the ongoing controversy over the general importance of fragmentation for predator–prey interactions.

This research adhered to the Association for the Study of Animal Behaviour/Animal Behaviour Society Guidelines for the Use of Animals in Research (published on the Animal Behaviour website), the legal requirements of the country in which the work was carried out and all institutional guidelines.

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