

Ecology, 87(5), 2006, pp. 1086–1093
 © 2006 by the Ecological Society of America

RESPONSE OF PREDATORS TO LOSS AND FRAGMENTATION OF PREY HABITAT: A REVIEW OF THEORY

KRISTA L. RYALL¹ AND LENORE FAHRIG

Department of Biology, Carleton University, Ottawa, Ontario K1S 5B6 Canada

Abstract. Despite extensive empirical research and previous reviews, no clear patterns regarding the effects of habitat loss and fragmentation on predator–prey interactions have emerged. We suggest that this is because empirical researchers do not design their studies to test specific hypotheses arising from the theoretical literature. In fact, theoretical work is almost completely ignored by empirical researchers, perhaps because it may be inaccessible to them. The purpose of this paper is to review theoretical work on the effects of habitat loss and fragmentation on predator–prey interactions. We provide a summary of clear, testable theoretical predictions for empirical researchers. To test one or more of these predictions, an empiricist will need certain information on the predator and prey species of interest. This includes: (1) whether the predator is a specialist on one prey species or feeds on many kinds of prey (omnivore and generalist); (2) whether the predator is restricted to the same habitat type as the focal prey (specialist), can use a variety of habitats but has higher survival in the prey habitat (omnivore), or lives primarily outside of the focal prey's habitat (generalist); (3) whether prey-only patches have lower prey extinction rates than predator–prey patches; and (4) whether the prey emigrate at higher rates from predator–prey patches than from prey-only patches. Empiricists also need to be clear on whether they are testing a prediction about habitat loss or habitat fragmentation and need to conduct empirical studies at spatial scales appropriate for testing the theoretical prediction(s). We suggest that appropriate use of the theoretical predictions in future empirical research will resolve the apparent inconsistencies in the empirical literature on this topic.

Key words: fragmentation; habitat loss; predator–prey interaction; spatial scale; theoretical models.

INTRODUCTION

Increasing intensity of land use by humans has led to the loss and fragmentation of natural habitats. The impact of these changes on the abundance and persistence of single species, and also on species diversity, has received considerable attention (reviewed in Fahrig 2003). Single-species models typically predict negative effects of habitat loss and fragmentation on the abundance or persistence of populations. However, habitat loss and fragmentation also may alter interactions among species (Didham et al. 1996), such as among predators and their prey, resulting in effects that are not predicted from single-species models.

Manuscript received 18 July 2005; revised 17 November 2005; accepted 22 November 2005. Corresponding Editor: O. J. Schmitz.

¹ Present address: Natural Resources Canada, Canadian Forest Service, P.O. Box 960, University Drive, Corner Brook, Newfoundland A2H 6J3 Canada.
 E-mail: kryall@nrcan.gc.ca

Based on a search of *Biological Abstracts* up to May 2005, using key words such as predator, prey, landscape, and habitat, as well as loss, destruction, fragmentation, or isolation, we found >1300 empirical papers with results on some aspect of how predator–prey interactions are affected by habitat loss. However, reviews of this empirical research reveal no clear patterns or conclusions. For example, Chalfoun et al. (2002) report that while most studies (57%) find no effect of patch size on predator abundance, 26% find increased abundance in smaller patches and 17% report the opposite. In addition, while one review reports strong edge effects on predation levels (Paton 1994), two others find that more than half of the studies report no significant edge effect on levels of nest predation (Lahti 2001, Chalfoun et al. 2002). To date, it would appear that no clear conclusions are possible.

Despite the interest and the volume of papers published on this research topic, it does not seem to be advancing. We suggest that an examination of the

TABLE 1. Summary of assumptions regarding biology of predators in theoretical papers.

Predator type	No. studies	Feeding strategy	Habitat use/restrictions	Effect of prey on predator populations	Effect of predators on prey populations
Specialist	7	one prey species	restricted to same habitat as prey species	predator abundance strongly related to prey abundance	can increase <i>or</i> decrease prey extinction risk
Omnivorous	3	many prey species	“matrix-tolerant”: can persist in non-prey habitat (matrix), but with higher mortality rates than in prey habitat	predator abundance partially related to prey abundance	increase prey extinction risk
Generalist	7	many prey species	“matrix-based”: live primarily in matrix but can also occur in prey habitat	predator abundance not limited or regulated by prey abundance	increase prey extinction risk

Note: Some studies included separate models examining different predator types; thus the total number of studies listed is greater than the 12 papers reported in the review.

relevant theory on predator–prey interactions might provide needed clarity. There are several theoretical models that explicitly examine predator–prey interactions following habitat loss and fragmentation (e.g., Nee et al. 1997, Bascompte and Solé 1998, Rushton et al. 2000, Nakagiri et al. 2001, Schneider 2001, Swihart et al. 2001, Prakash and de Roos 2002, Kondoh 2003, Nakagiri and Tainaka 2004). Unfortunately, this theoretical work is not being incorporated into the empirical research. Either empirical researchers are not aware that these models and their predictions exist, or the theoretical work is presented in a way that makes it seem irrelevant or inaccessible. Consideration of the predictions of these predator–prey models in empirical research could greatly clarify the often-conflicting body of empirical research on this topic.

Our purpose is to review the theoretical literature on how predator–prey interactions are influenced by habitat loss and fragmentation. We first review theoretical models of the effects of prey habitat loss on predator–prey interactions, followed by models of the effects of prey habitat fragmentation per se (the breaking apart of a constant amount of habitat; i.e., fragmentation without loss of habitat). Our intention is to organize and clarify theoretical assumptions and their predictions, making them more accessible to empirical researchers. We hope that this will facilitate empirical researchers directly testing theoretical predictions, which should lead to the emergence of more conclusive patterns.

Assumptions regarding predator biology

Theoretical studies differ in their assumptions regarding the predator’s feeding strategy and use of habitat, and the impact of predators on prey populations. First, predators may be either specialists or generalists in regard to the number of prey species that they use (Table 1). Whereas specialist predators are assumed to feed only on one prey species (Bascompte and Solé 1998, Nakagiri et al. 2001, Swihart et al. 2001, Prakash and de Roos 2002, Kondoh 2003, Nakagiri and Tainaka 2004), omnivorous or generalist predators are assumed

to feed and persist on a variety of prey species (Swihart et al. 2001, Melian and Bascompte 2002). Survival rates of omnivores in the face of loss or fragmentation of the preferred prey’s habitat are assumed to depend on the degree of polyphagy and on the quality of the alternate prey (Swihart et al. 2001). Generalist predators, in contrast, are assumed to obtain most of their required resources from sources other than the focal prey species (Laurance and Yensen 1991, Cantrell et al. 2001, 2002, Swihart et al. 2001), feeding only opportunistically on the focal prey species that is experiencing habitat loss and/or fragmentation.

Use of habitat also differs significantly among the different modeled predator types (Table 1). Specialist predators are assumed to be restricted to the same habitat as are their prey; loss of prey habitat is, therefore, also loss of predator habitat (Bascompte and Solé 1998, Swihart et al. 2001, Prakash and de Roos 2002). In some models, specialist predators are assumed to be able to temporarily survive in patches without prey, but ultimately go extinct without an influx of prey (Nakagiri et al. 2001, Kondoh 2003, Nakagiri and Tainaka 2004). Omnivorous predators are assumed to be capable of persisting in habitats not used by the focal prey species (the matrix), but with elevated mortality rates in the matrix; omnivorous predators are therefore “matrix tolerant” (Swihart et al. 2001). Generalist predators, in contrast, are assumed to live primarily in the matrix, but readily intrude into the habitat of the prey species in question; generalist predators are therefore “matrix based” (Laurance and Yensen 1991, Cantrell et al. 2001, 2002, Schneider 2001, Swihart et al. 2001).

The simulated predators differ in their impacts on prey population dynamics. Depending on the model, specialist predators are assumed either to increase the rate of extinction in predator–prey patches (Bascompte and Solé 1998, Nakagiri et al. 2001, Swihart et al. 2001, Melian and Bascompte 2002, Kondoh 2003, Nakagiri and Tainaka 2004) or, alternatively, to reduce the extinction rate of prey by slowing the rate of exploitation of patch resources by prey (Prakash and de Roos

TABLE 2. Summary of predictions and assumptions of theoretical research into effects of prey habitat loss and fragmentation on predator–prey interactions.

No. studies	Predictions	Important assumptions leading to the predictions
Habitat loss		
6	Abundance of specialist predators is more negatively affected by habitat loss than is abundance of their prey.	Specialist predators have strong top-down influence on prey populations and are limited to the same habitat as the prey.
5	Prey populations can increase with habitat loss due to reduction in specialist predator populations.	Cost of predation exceeds cost of habitat loss on prey populations; prey have higher dispersal rates out of predator–prey patches than prey-only patches; resource exploitation by prey is slower in predator–prey patches than in prey-only patches.
3	Omnivorous (matrix-tolerant) predators are less negatively affected by habitat loss than are specialist predators.	Omnivores can survive in patches without the focal prey species, although with elevated mortality rates.
3	Incursions by generalist (matrix-based) predators reduce core area and increase critical patch size for prey.	Generalist predators are not limited by prey populations; generalist predators thrive in the matrix.
1	Generalist predators have a higher negative impact on prey population with increasing prey habitat loss.	Generalist predators are not limited by prey populations.
Habitat fragmentation		
5	Prey habitat fragmentation has negative effects on specialist predator populations, which increases persistence of both predator and prey populations.	Predator and prey disperse to nearest neighbors; prey have higher dispersal rates out of predator–prey patches than prey-only patches; extinction rates of both predators and prey in predator–prey patches are lower than that in prey-only patches.
2	Prey habitat fragmentation has negative effects on specialist predator populations, which decreases persistence of both predator and prey populations.	Prey have lower dispersal capabilities than predators; extinction rates of both predators and prey in predator–prey patches are higher than in prey-only patches.
6	Prey habitat fragmentation results in increased predation by generalist predators, leading to increased prey extinction rates.	Generalist predators invade prey patches from matrix habitat through edges; predators cause significant mortality on prey populations.

Note: Some studies included separate models examining loss and fragmentation; thus the total number of studies listed is greater than the 12 papers reported in the review.

2002). Specialists are themselves assumed to be limited or regulated by the abundance of their prey populations (Bascompte and Solé 1998, Nakagiri et al. 2001, Swihart et al. 2001, Prakash and de Roos 2002). Matrix-tolerant omnivorous predators are assumed to increase the rate of prey extinction in predator–prey patches (Swihart et al. 2001, Melian and Bascompte 2002). Finally, matrix-based generalist predator populations are assumed to be completely independent of the prey species experiencing habitat loss, but they cause considerable mortality on those prey populations, and thereby increase their extinction rate (Laurance and Yensen 1991, Cantrell et al. 2001, 2002, Schneider 2001, Swihart et al. 2001). These assumptions regarding habitat and prey requirements and local predator–prey dynamics are critical in determining the theoretical predictions.

Effects of predator biology on predicted effects of habitat loss on predator–prey interactions

The predicted impact of habitat loss on predator–prey interactions differs depending on the type of simulated predator (Table 2). Models predict that specialist predators are negatively affected by habitat loss to a greater degree than their prey (Fig. 1a) (Bascompte and Solé 1998, Nakagiri et al. 2001, Swihart et al. 2001, Melian and Bascompte 2002, Kondoh 2003, Nakagiri and Tainaka 2004). This results in lower predicted

specialist predator abundance or patch occupancy with loss of prey habitat (which is also predator habitat for specialist predators). Omnivores are predicted to be less vulnerable to prey habitat loss than are specialist predators, but are still more vulnerable to habitat loss than their prey (Swihart et al. 2001, Melian and Bascompte 2002) (Fig. 1b: omnivore). In contrast, generalist predators, living primarily in the matrix, are predicted to benefit from prey habitat loss if the habitat that replaces it provides the generalist predators with additional resources (Fig. 1b: generalist) (Swihart et al. 2001). Therefore, the different feeding strategies completely alter the impact of loss of prey habitat on predator–prey interactions.

Models also predict that the impact of prey habitat loss on prey populations can be mitigated by reductions in their associated specialist predator populations. Specifically, some specialist predator–prey models predict that prey populations actually increase in abundance, occupancy of patches, or persistence following low-to-moderate levels of habitat loss (Table 2, Fig. 1a: prey2) (see Bascompte and Solé 1998, Nakagiri et al. 2001, Swihart et al. 2001, Prakash and de Roos 2002, Nakagiri and Tainaka 2004). In these five studies, prey abundance or density of sites occupied are reported as a fraction of the total original number of habitat patches available (with the exception of Bascompte and Solé

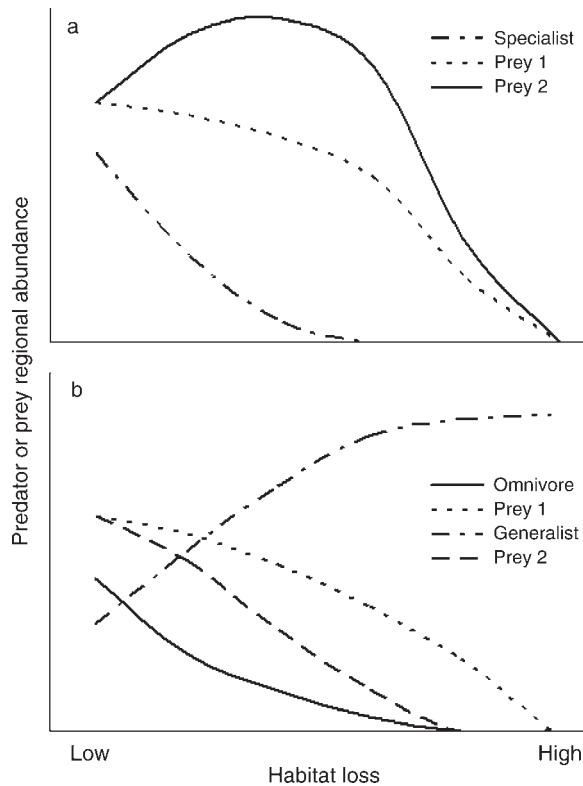


FIG. 1. (a) Predicted effect of increasing prey habitat loss on predator or prey populations for specialist predators and two alternative outcomes for prey populations: simple decline with habitat loss for prey 1 (Bascompte and Solé 1998, Melian and Bascompte 2002, Kondoh 2003, Nakagiri and Tainaka 2004), or initial increase in prey abundance due to declining predator populations for prey 2 (Bascompte and Solé 1998, Nakagiri et al. 2001, Swihart et al. 2001, Prakash and de Roos 2002, Nakagiri and Tainaka 2004). (b) Predicted effect of increasing prey habitat loss on predator or prey populations for omnivore predators able to use alternate prey but with elevated mortality rates (Swihart et al. 2001, Melian and Bascompte 2002) or those generalist predators preferring the matrix, with populations independent of the focal prey population (Rushton et al. 2000, Schneider 2001, Swihart et al. 2001). In (b), prey 1 illustrates the effect of an omnivore on prey populations, whereas prey 2 illustrates the greater decline in prey populations associated with generalist predators.

[1998: Fig. 7b], which depicts the fraction occupied with respect to the number available, i.e., non-destroyed). The theoretical models suggest that the cost of habitat loss to the prey can be compensated for by the reduction in predation (Bascompte and Solé 1998). This can occur if: (1) the dispersal rate of prey out of predator-prey patches is higher than from prey-only patches, increasing the rate at which prey-only patches are created; or (2) the extinction rate of prey in predator-prey patches is lower than in prey-only patches (Prakash and de Roos 2002). This represents a situation in which prey resource use is slower when predators are present, thus reducing overexploitation of resources by prey that could subsequently lead to prey patch extinction. Therefore, although predators cause prey mortality, this cost can be

offset by the beneficial side effects of predators on prey populations that are experiencing habitat loss. However, once the predators become extinct due to prey habitat loss, the prey populations are predicted to rapidly decline with further habitat loss (Bascompte and Solé 1998, Nakagiri et al. 2001, Swihart et al. 2001, Prakash and de Roos 2002, Nakagiri and Tainaka 2004). The potential increase in prey populations with low-to-moderate habitat loss is completely overlooked in a single-species model of the prey species, and has not been considered in empirical research. Interestingly, this prediction also suggests a threshold beyond which prey populations are predicted to decline rapidly after previously being abundant.

The importance of species interactions is highlighted in another model with three trophic levels (prey, predator, and a top predator). In this model, the top predator always declines with loss of prey habitat (Nakagiri and Tainaka 2004). Initially this can lead to an increase in the intermediate predator, resulting in a subsequent decline in prey populations. However, once the top predator goes extinct, the model shifts to the two-species interaction state, with a decline in the remaining predator population. At this point, the prey species is predicted to again possibly increase with loss of habitat before ultimately declining at high levels of habitat destruction (Nakagiri and Tainaka 2004). Results of this model again suggest that when extinction of one species occurs (i.e., the top predator), the effect of subsequent habitat loss on surviving species can change completely.

Mortality caused by generalist predators, in contrast, is always predicted to exacerbate the negative effects of prey habitat loss on prey populations. Incursion by matrix-based generalist predators into prey patches is predicted to increase the critical patch size below which prey cannot persist (Laurance and Yensen 1991, Cantrell et al. 2001, 2002). Models also predict that generalist predators will cause prey to occupy a lower percentage of patches or to have a higher risk of extinction than in the absence of predation (Fig. 1b: generalist and prey) (Rushton et al. 2000, Schneider 2001, Swihart et al. 2001). Therefore, the predicted effects of prey habitat loss on the prey vary markedly, depending on which type of predator they are interacting with and on the degree of habitat loss.

Effects of predator biology on predicted effects of habitat fragmentation per se on predator-prey interactions

Effects of fragmentation per se of prey habitat are modeled by comparing predictions from a nonspatial mean field model to those from an equivalent spatially explicit model with the same amount of prey habitat available (Bascompte and Solé 1998, Schneider 2001, Swihart et al. 2001, Prakash and de Roos 2002, Kondoh 2003, Nakagiri and Tainaka 2004). Mean field models provide no spatial context for habitat or predator or prey populations and assume that complete mixing of

dispersing individuals occurs at each time step. In contrast, spatially explicit models use a grid system of cells, provide a spatial context for habitat patches, and limit dispersal to neighboring cells. In these spatially explicit models, when habitat is removed it is broken into smaller, more isolated patches; therefore, both habitat loss and fragmentation occur simultaneously.

Models of effects of fragmentation per se of prey habitat generate predictions paralleling those of the habitat loss models. Habitat fragmentation per se is predicted to have a negative effect on specialist predator populations (Table 2), and a reduction in specialist predators typically leads to increased equilibrium densities or persistence of prey (Bascompte and Solé 1998, Schneider 2001, Swihart et al. 2001, Prakash and de Roos 2002, Nakagiri and Tainaka 2004). In some studies, specialist predator-prey systems are predicted to persist down to lower amounts of habitat, in the spatially explicit model simulating fragmentation per se (Swihart et al. 2001, Prakash and de Roos 2002), than in the corresponding mean field model simulating habitat loss only. However, other models predict decreased persistence of specialist predator-prey systems (Nakagiri et al. 2001) or decreased persistence of specialist predators (Nakagiri and Tainaka 2004) when simulating fragmentation per se vs. habitat loss. In a tritrophic model, fragmentation per se generally decreased the food chain length, and persistence of the system depended on relative colonization rates of the predator and prey (Kondoh 2003). Thus, models predict varying effects of fragmentation per se on specialist predator-prey interactions, depending on their specific assumptions.

Certain assumptions affect the predicted effect of fragmentation per se on specialist predator-prey systems. Increased persistence with fragmentation is predicted when: (1) prey are assumed to be more mobile than their specialist predators (Schneider 2001); (2) local dispersal creates aggregations of patches of predators and prey; (3) prey have higher emigration rates from predator-prey patches due to the presence of the specialist predators, which results in increased rates of colonization of new patches by prey; and (4) prey in specialist predator-prey patches are assumed to have lower extinction rates than prey in prey-only patches (Swihart et al. 2001, Prakash and de Roos 2002). The last would be expected if predation were to reduce the rate of exploitation of prey resources by keeping the prey population lower. In another model, however, increased persistence with habitat fragmentation is predicted when prey have lower colonization rates than their predators; this occurs because prey are assumed to otherwise cause complete extinction of their plant resources in predator-free patches (Kondoh 2003). Decreased persistence of specialist predator-prey systems with habitat fragmentation is predicted if: (1) prey are assumed to be more restricted in their movement than their predators (Nakagiri et al. 2001, Nakagiri and Tainaka 2004); and (2) specialist

predators increase extinction rates of prey in predator-prey patches (Nakagiri et al. 2001, Nakagiri and Tainaka 2004). Alternatively, decreased persistence of a tritrophic system, particularly at low levels of fragmentation, is predicted if prey have higher colonization rates than their predators (Kondoh 2003), again because prey are assumed to cause the extinction of their plant resources, thus exacerbating the effects of habitat loss and fragmentation. Therefore, assumptions regarding dispersal tendencies and abilities, the impact of prey on their resources, and the impact of predation on prey populations strongly affect predictions regarding the effect of habitat fragmentation per se on predator-prey systems.

For generalist predators living in the matrix, fragmentation per se of prey habitat is predicted to have a positive effect on the generalist predator populations and a negative effect on prey populations because of the increased predation pressure (Table 2). This occurs because there is an increasing amount of edge habitat per unit area of prey habitat and, subsequently, an increased incursion of generalist predators into prey habitat (Schneider 2001). Therefore, models predict different effects of prey habitat fragmentation on specialist vs. generalist predator populations, paralleling the predictions for habitat loss.

DISCUSSION

Our review demonstrates that the theoretical predictions regarding predator-prey interactions and habitat loss and fragmentation are actually quite clear and straightforward. However, this body of theoretical work is almost completely ignored by empirical researchers. Of the more than 1300 empirical papers on this topic, only 4.4% are listed in *CrossRef*, *ScienceDirect* as citing just three of the theoretical models: Laurance and Yensen (1991), Rushton et al. (2000), and Schneider (2001). However, closer examination of the abstracts of these 58 papers determined that only seven (0.5%) were actually relevant to predator-prey interactions and habitat loss or fragmentation. As well, these papers referred only to generalist predators and their interactions with prey. Otherwise, citations of these theoretical papers are restricted to other theoretical work. This topic could be greatly advanced if these theoretical predictions and their assumptions were considered and incorporated into empirical research.

Our review of the theoretical models evaluating the effects of habitat loss and fragmentation on predator-prey interactions highlights the importance of (1) the feeding habit of the predator in question (i.e., whether specialist, omnivore, or generalist) and (2) whether the matrix supports or does not support predator populations. We conclude that the biggest factor that prevents clear patterns from emerging from empirical research is the typically inadequate information provided on feeding and habitat requirements of the focal predator species. Separating predators by key features of their biology, particularly feeding strategy and habitat use, would

prove more useful than categorizing them by size or taxon (i.e., Crooks and Soulé 1999, Chalfoun et al. 2002, Crooks 2002) and would enable researchers to more clearly test the predictions of the theoretical models.

In addition to the ideas reviewed here, there are several other concepts in the predator-prey literature that could interact with the effects of habitat loss and fragmentation on predator-prey relationships. For example, the relative importance of top-down vs. bottom-up regulation (Hunter and Price 1992, Hunter et al. 1997, Leibold et al. 1997) and the occurrence and stability of predator-prey cycles (Hilborn 1975, Hastings 1977, 1978, Kareiva 1987, Hassell 2000, Bonsall et al. 2002) might be influenced by habitat loss or fragmentation. Habitat loss and/or fragmentation could also influence the occurrence of apparent competition (Holt 1977, 1984, Comins and Hassell 1996, Abrams et al. 1998, Namba et al. 1999, Bonsall and Hassell 2000, King and Hastings 2003) or the persistence or influence of keystone predators (Mills et al. 1993, Menge et al. 1994, Leibold 1996). Although some of this research examines the effects of spatial heterogeneity or metapopulation structure on predator-prey interactions, none explicitly models the issue of habitat loss and fragmentation *per se*. Such studies are therefore beyond the scope of this review, but are areas for future theoretical investigation.

It was not our intention to review the empirical research. However, we must mention we encountered a widespread problem in the literature: the preponderance of empirical studies conducted at the patch scale. This is in contrast with the majority of theoretical models that are conducted at the landscape scale, appropriate to the processes of habitat loss and fragmentation. This overemphasis on the smaller spatial scale in empirical work may obscure important effects. For example, documentation of “edge effects” on predator-prey systems is common in the empirical literature (reviewed by Paton 1994, Lahti 2001, Chalfoun et al. 2002). However, when viewed in the context of the theoretical literature examined here, it seems likely that species interactions are altered not due to the edge *per se*, but rather to changes in the amount and type of habitat at the landscape scale. This is supported by reviews suggesting that edge effects often occur only when high amounts of habitat are lost (Lahti 2001) or when loss of prey habitat is associated with increases in generalist-predator habitat, e.g., open or agricultural habitat (Andrén 1995). Both of these situations allow matrix-based generalist-predator populations to build up to high levels and cause increased rates of predation on prey species restricted to habitat patches (e.g., forest remnants). Only empirical research conducted at the appropriate landscape scale will accurately characterize the response of predators to habitat loss and fragmentation.

Of particular importance is the prediction that the impact of habitat loss on prey populations can depend on the level of habitat loss that has already occurred. Theoretical models predict that prey could increase with

initial reductions in habitat due to a reduction in associated specialist-predator populations. If the prey species in question is a potential pest, then increases in its populations could lead to outbreaks, possibly with important management implications. However, the models also predict that, once predators become extinct, prey populations decline precipitously with habitat loss. If the focal prey species is an endangered or threatened species, then conservation research must not ignore this prediction. Although field surveys may suggest that populations of a given species are thriving despite some loss of habitat, further loss may be beyond the threshold for persistence of both the predator and prey species. This could lead to sudden and drastic declines in populations of the endangered species. This nonlinear response of prey populations to habitat loss due to altered predator-prey interactions is a key theoretical prediction that needs to be tested empirically.

Theoretical models suggest that local predator-prey dynamics within prey patches can affect the landscape-scale effects of prey habitat loss and fragmentation on predator-prey systems. Two local conditions are particularly important: (1) when the prey extinction rate is lower in predator-prey patches than in prey-only patches, and (2) when the prey dispersal rate is higher from predator-prey patches than from prey-only patches. These conditions can lead to the somewhat counterintuitive prediction that prey habitat loss can lead to an increase in prey population abundance and persistence. These predictions do not occur in simple single-species models or in multispecies models where predators have no effect on prey population dynamics (e.g., one set of model conditions in Bascompte and Solé [1998], Nee et al. [1997]). On occasion, these two conditions have been demonstrated empirically, i.e., delayed overexploitation of prey resource patches in the presence of predators rather than in their absence (Pels and Sabelis 1999, van der Meijden and van der Veen-van Wijk 1997), and higher emigration from predator-prey patches than from prey-only patches (Bernstein 1984), but never in the context of changes in predator and prey populations following prey habitat loss and/or fragmentation.

Finally, examination of some empirical studies reveals effects that have not been incorporated in the theoretical models. For example, Cronin (2003a) reports that densities of specialist parasitoids actually increase with patch isolation (a measure of habitat loss at the landscape scale) because parasitoids are thought to be reluctant to leave such patches. In other studies, parasitoids have significantly increased oviposition rates (Cronin and Strong 1999, Cronin 2003b) or higher parasitism rates (Doak 2000) in isolated habitat patches. Such enhanced reproductive output may mitigate the effects of reduced colonization of patches by predators following habitat loss. Therefore, even though these parasitoids would be classified as “specialists,” and are predicted to decline with habitat loss, their altered reproductive patterns would not fit this prediction. Such

behavioral or physiological responses are not currently features of theoretical models, and should be incorporated into further theoretical work.

To summarize, the following questions should be addressed by empirical researchers attempting to determine what theoretical predictions are appropriate for their system: (1) What is the feeding strategy of the focal predator? Is the predator most likely a specialist on one prey species, or does it feed on many kinds of prey? (2) What habitats are used by the predator? Is it restricted to one habitat type along with its prey (specialist)? Can it use a variety of different habitats, but with higher survival in the habitat of the focal prey species (omnivore)? Does the predator live primarily outside of the focal prey's habitat (generalist)? (3) Is habitat loss or habitat fragmentation per se being examined? (4) What is the appropriate spatial scale of examination? Effects of habitat loss and fragmentation per se are modeled, and should be tested, at the landscape scale. What area of habitat would influence the focal predator (and prey) species during their life cycle? (5) Do prey exploit their resources more slowly in predator-prey patches than in prey-only patches? (6) Do prey emigrate at higher rates from predator-prey patches than from prey-only patches?

We have provided a summary of clear, testable theoretical predictions for empirical researchers on the effects of habitat loss and fragmentation on predator-prey interactions. Use of these predictions in future empirical research will greatly increase the coherence of empirical results. We encourage empirical researchers to strengthen the theoretical basis of the research that they conduct. Of equal importance, to bridge the gap between theoretical and empirical work, theoretical modeling papers need to provide summaries of clear predictions that can readily be incorporated and tested by empirical researchers.

ACKNOWLEDGMENTS

We thank the members of the Landscape Ecology Laboratory at the Ottawa-Carleton Institute of Biology for discussions that greatly improved the manuscript. This work was supported by grants from the Government of Ontario and the Natural Sciences and Engineering Research Council of Canada (NSERC) to L. Fahrig.

LITERATURE CITED

- Abrams, P. A., R. D. Holt, and J. D. Roth. 1998. Apparent competition or apparent mutualism? Shared predation when populations cycle. *Ecology* **79**:201–211.
- Andr n, H. 1995. Effects of landscape composition on predation rates at habitat edges. Pages 225–255 in L. Hansson, L. Fahrig, and G. Merriam, editors. Mosaic landscapes and ecological processes. Chapman and Hall, London, UK.
- Bascompte, J., and R. V. Sol . 1998. Effects of habitat destruction in a prey-predator metapopulation model. *Journal of Theoretical Biology* **195**:383–393.
- Bernstein, C. 1984. Prey and predator emigration responses in the acarine system *Tetranychus urticae*–*Phytoseiulus persimilis*. *Oecologia* **61**:134–142.
- Bonsall, M. B., D. R. French, and M. P. Hassell. 2002. Metapopulation structures affect persistence of predator-prey interactions. *Journal of Animal Ecology* **71**:1075–1084.
- Bonsall, M. B., and M. P. Hassell. 2000. The effects of metapopulation structure on indirect interactions in host-parasitoid assemblages. *Proceedings of the Royal Society of London, Biology* **267**:2207–2212.
- Cantrell, R. S., C. Cosner, and W. F. Fagan. 2001. How predator incursions affect critical patch size: the role of the functional response. *American Naturalist* **158**:368–375.
- Cantrell, R. S., C. Cosner, and W. F. Fagan. 2002. Habitat edges and predator-prey interactions: effects on critical patch size. *Mathematical Biosciences* **175**:31–55.
- Chalfoun, A. D., F. R. Thompson, and M. J. Ratnaswamy. 2002. Nest predators and fragmentation: a review and meta-analysis. *Conservation Biology* **16**:306–318.
- Comins, H. N., and M. P. Hassell. 1996. Persistence of multispecies host-parasitoid interactions in spatially distributed models with local dispersal. *Journal of Theoretical Biology* **186**:19–28.
- Cronin, J. T. 2003a. Matrix heterogeneity and host-parasitoid interactions in space. *Ecology* **84**:1506–1516.
- Cronin, J. T. 2003b. Patch structure, oviposition behavior, and the distribution of parasitism risk. *Ecological Monographs* **73**:283–300.
- Cronin, J. T., and D. R. Strong. 1999. Dispersal-dependent oviposition and the aggregation of parasitism. *American Naturalist* **154**:23–36.
- Crooks, K. R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation Biology* **16**:488–502.
- Crooks, K. R., and M. E. Soul . 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* **400**:563–566.
- Didham, R. K., J. Ghazoul, N. E. Stork, and A. J. Davis. 1996. Insects in fragmented forests: a functional approach. *Trends in Ecology and Evolution* **11**:255–260.
- Doak, P. 2000. The effects of plant dispersion and prey density on parasitism rates in a naturally patchy habitat. *Oecologia* **122**:556–567.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* **34**:487–515.
- Hassell, M. P. 2000. The spatial and temporal dynamics of host-parasitoid interactions. Oxford University Press, Oxford, UK.
- Hastings, A. 1977. Spatial heterogeneity and the stability of predator-prey systems. *Theoretical Population Biology* **12**:37–48.
- Hastings, A. 1978. Spatial heterogeneity and the stability of predator-prey systems: predator-mediated coexistence. *Theoretical Population Biology* **14**:380–395.
- Hilborn, R. 1975. The effect of spatial heterogeneity on the persistence of predator-prey interactions. *Theoretical Population Biology* **8**:346–355.
- Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* **12**:197–229.
- Holt, R. D. 1984. Spatial heterogeneity, indirect interactions, and coexistence of prey species. *American Naturalist* **124**:377–406.
- Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: Heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* **73**:724–732.
- Hunter, M. D., G. C. Varley, and G. R. Gradwell. 1997. Estimating the relative roles of top-down and bottom-up forces on insect herbivore populations: a classic study revisited. *Proceedings of the National Academy of Sciences (USA)* **94**:9176–9181.

- Kareiva, P. 1987. Habitat fragmentation and the stability of predator–prey interactions. *Nature* **328**:388–390.
- King, A. A., and A. Hastings. 2003. Spatial mechanisms for coexistence of species sharing a common natural enemy. *Theoretical Population Biology* **64**:431–438.
- Kondoh, M. 2003. Habitat fragmentation resulting in overgrazing by herbivores. *Journal of Theoretical Biology* **225**:453–460.
- Lahti, D. C. 2001. The “edge effect on nest predation” hypothesis after twenty years. *Biological Conservation* **99**:365–374.
- Laurance, W. F., and E. Yensen. 1991. Predicting the impacts of edge effects in fragmented habitats. *Biological Conservation* **55**:77–92.
- Leibold, M. A. 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. *American Naturalist* **147**:784–812.
- Leibold, M. A., J. M. Chase, J. B. Shurin, and A. L. Downing. 1997. Species turnover and the regulation of trophic structure. *Annual Review of Ecology and Systematics* **28**:467–494.
- Melian, C. J., and J. Bascompte. 2002. Food web structure and habitat loss. *Ecology Letters* **5**:37–46.
- Menge, B. A., E. L. Berlow, C. A. Blanchette, S. A. Navarrete, and S. B. Yamada. 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecological Monographs* **64**:249–286.
- Mills, C. S., M. E. Soulé, and D. F. Doak. 1993. The keystone species concept in ecology and conservation. *BioScience* **43**:219–224.
- Nakagiri, N., and K. Tainaka. 2004. Indirect effects of habitat destruction in model ecosystems. *Ecological Modelling* **174**:103–114.
- Nakagiri, N., K. I. Tainaka, and T. Tao. 2001. Indirect relation between species extinction and habitat destruction. *Ecological Modelling* **137**:109–118.
- Namba, T., A. Umemoto, and E. Minami. 1999. The effects of habitat fragmentation on persistence of source–sink metapopulations in systems with predators and prey or apparent competitors. *Theoretical Population Biology* **56**:123–137.
- Nee, S., R. M. May, and M. P. Hassell. 1997. Two-species metapopulation models. Pages 123–147 in I. Hanski and M. Gilpin, editors. *Metapopulation biology, ecology, genetics and evolution*. Academic Press, San Diego, California, USA.
- Paton, P. W. C. 1994. The effect of edge on avian nest success: How strong is the evidence? *Conservation Biology* **8**:17–26.
- Pels, B., and M. W. Sabelis. 1999. Local dynamics, over-exploitation and predator dispersal in an acarine predator–prey system. *Oikos* **86**:573–583.
- Prakash, S., and A. M. De Roos. 2002. Habitat destruction in a simple predator–prey patch model: How predators enhance prey persistence and abundance. *Theoretical Population Biology* **62**:231–249.
- Rushton, S. P., G. W. Barreto, R. M. Cormack, D. W. Macdonald, and R. Fuller. 2000. Modelling the effects of mink and habitat fragmentation on the water vole. *Journal of Applied Ecology* **37**:475–490.
- Schneider, M. F. 2001. Habitat loss, fragmentation and predator impact: spatial implications for prey conservation. *Journal of Applied Ecology* **38**:720–735.
- Swihart, R. K., Z. Feng, N. A. Slade, D. M. Mason, and T. M. Gehring. 2001. Effects of habitat destruction and resource supplementation in a predator–prey metapopulation model. *Journal of Theoretical Biology* **210**:287–303.
- van der Meijden, E., and C. A. M. van der Veen-van Wijk. 1997. Tritrophic metapopulation dynamics: A case study of ragwort, the cinnabar moth and the parasitoid *Cotesia popularis*. Pages 387–405 in I. Hanski and M. Gilpin, editors. *Metapopulation biology, ecology, genetics and evolution*. Academic Press, San Diego, California, USA.