

Spatial and temporal dynamics of turtle nest predation: edge effects

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We determined the effect of distance from ecological edges, both wooded and water edges, on nest predation for 862 painted turtle, *Chrysemys picta*, nests from 1995 to 1999 at an ~ 1.5 ha study site. In three of five years and overall, nests closer to the water edge had a higher probability of predation; and in one year nests closer to the wooded edge had a higher probability of predation. Although more turtles nested closer to the water edge as the nesting season progressed in some years and overall, this behavior does not explain the observed patterns of nest predation. We present a novel application of the cubic spline analysis to address the dynamics of predation across continuous distances from an edge and identify threshold values where the predation rate levels off. Threshold values of ~ 25–40 m were detected in 1995, 1998, and with all five years combined. However, even though a significant edge effect was detected in 1997, a threshold was not clear. While an edge effect on predation was not detected in each year, this study provides evidence for a strong effect of distance from the water edge on nest predation over significant ecological time. Focusing on turtle nest predation and smaller spatial scales addresses previous taxonomic and spatial bias in edge effects research, and provides further support for the ecological importance of edge effects.

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Many important ecological and evolutionary processes vary over time and space (reviewed in Turner 1989). Some population processes, such as predation, are negatively influenced by spatial proximity to ecological edges (Gates and Gysel 1978, Yahner 1988, Murcia 1995). To better understand the influence of edges on ecological processes such as nest predation, studies are needed that capture variation in nest success over various spatial and temporal scales. Delimiting the spatial extent and temporal continuity of edge effects is important to understanding its ecological and evolutionary impact on a particular population. Additionally, the complexity of variables involved in nest predation warrants thorough spatial and temporal investigation.

Many studies address the effects of distance from an ecological edge on nest predation (e.g. birds: Gates and

Gysel 1978, Johnson and Temple 1990, Niemuth and Boyce 1997; turtles: Temple 1987). Nest success declines near edges for some species, most evidence coming from avian studies (reviewed in Paton 1994). Variation exists, however, in the response of different species to edges and in the response of a given species to different edge types (Pasitschniak-Arts et al. 1998, Luck et al. 1999). Many factors influence the effect of edges on nest predation including plot size (Wilcove 1985, Johnson and Temple 1990), nest type (Møller 1989), plot age (Yahner and Wright 1985), predator densities (Angelstam 1986, Andrén 1992), and landscape context (Andrén 1992, Donovan et al. 1997). Though many of these aspects have been addressed in previous edge effects studies, several crucial avenues of research remain unexplored.

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Paton (1994) identified several short-comings in edge effects studies and suggested that future research focus on 1) examining smaller spatial scales because nest edge effects usually occur within 50 m of an edge, 2) quantifying threshold values of predation rates as a function of distance from an edge, 3) assessing the influence of the landscape, and 4) determining the influence of predator densities and search patterns. Several studies have addressed landscape and predator issues in relation to edge effects (Angelstam 1986, Andrén 1992, Donovan et al. 1997), however, studies focusing on smaller spatial scales or determining threshold distances of predation rates (i.e. points 1 and 2) are lacking. Furthermore, to strengthen the general implications of this important ecological phenomenon, we suggest that future research should also incorporate taxonomic groups other than birds (e.g. reptiles, amphibians, insects) and be conducted over multiple years. Previous research in this area has focused almost exclusively on birds (but see Temple 1987) and on short-term projects, and is therefore limited in its general ecological and evolutionary insight. Multi-year studies in particular are essential for understanding variation in, and annual consequences of, nest predation due to edge effects. Focusing on these issues helps to evaluate the generality and long-term ecological impact of nest edge effects in natural populations.

In this paper, we use data from a long-term study of nesting ecology of the painted turtle, *Chrysemys picta*, to evaluate the effect of proximity to two different edge types, both wooded and water, on nest predation. We incorporate two of Paton's (1994) suggestions for future research on edge effects by considering a smaller spatial scale and presenting an approach to quantifying threshold values of predation rates for years with significant edge effects. Additionally, we evaluate the dynamics of nest predation over continuous distances, examine a non-avian species to counteract previous taxonomic bias, and consider five years of data to determine the temporal consistency of predation patterns. Addressing these important aspects of nest edge effects complements other work on the importance of the landscape and predators (Angelstam 1986, Andrén 1992, Donovan et al. 1997), and contributes to understanding the generality of this ecological phenomenon.

Methods

Study site

We conducted this research at the Thomson Causeway Recreation Area near Thomson, Illinois, USA (41°57'N, 90°7'W) from 1995 to 1999. This work represents a portion of a larger study of painted turtle nesting ecology started in 1989 (Janzen 1994, Weisrock and Janzen 1999). The Thomson Causeway is an

~450 × 900 m island near the eastern bank of the Mississippi River. The nesting area is on the east side of the island facing Illinois and separated from the mainland by a 200 m wide marsh. Turtles nest in an approximately 75 × 250 m (~1.5 ha) area characterized by short grass, loamy soil, heterogeneous overstory vegetation, and no slope except for a short incline up from the water. The south and west sides of the nesting area are bordered by wooded areas and the east side by the marsh, referred to as the wooded and water edges, respectively. The north side is similar to the entire grassy nesting area, but is bisected by a short road (Janzen 1994). Most turtles enter the study area from the water along the east side and nest throughout the site.

Data collection

During each year of the study, we monitored the nesting area for female painted turtles and previously laid nests from late May to early July. After locating a nest, we mapped it to local landmarks for future identification. We excavated most nests immediately after oviposition to determine clutch size and weigh eggs and then returned eggs to the nest to incubate naturally. In 1998 and 1999, approximately 20% of the nests were left undisturbed to determine if human excavation of nests influenced the probability of predation. Predation dates for nests were recorded until field work concluded in early July. Nests were then left undisturbed until late September when hatchlings were present. We recorded any additional predation events at this time, and nests were then excavated and hatchlings transported to the laboratory for overwintering. Hatchlings in this population naturally overwinter in the nest and emerge in the spring (Weisrock and Janzen 1999). In each year, hatchlings from a subset of nests remained in the ground until March to overwinter naturally (1995 N = 11; 1996 N = 30; 1997 N = 29; 1998 N = 10; 1999 N = 12; Weisrock and Janzen 1999). None of these naturally overwintering nests were destroyed by predators after September. Thus, it is unlikely that excavating nests in September precluded any further predation events.

The only predation events observed at this site were nocturnal; we never observed nest predation during the day. Raccoons (*Procyon lotor*) and striped skunks (*Mephitis mephitis*) were observed destroying painted turtle nests at this site (F. Janzen, pers. obs.). Other potential predators include woodchucks (*Marmota monax*), muskrats (*Ondatra zibethica*), squirrels (*Sciurus carolinensis*), red fox (*Vulpes vulpes*), opossum (*Didelphis virginiana*), fox snakes (*Elaphe vulpina*), and feral cats.

We established Cartesian coordinates for each nest using the INTERPNT program (Boose et al. 1998), which established x, y-coordinates for each nest by

triangulation. The distance from each nest to three other previously mapped nests was measured and then used to calculate coordinates. We mapped 862 nests from 1995 to 1999 with little mapping error (i.e. error per measurement ranged from 0 to 15 cm with an average error of < 1 cm). We created Geographic Information Systems (GIS) coverages from these coordinates for all five years in ArcView (ESRI Inc. 1998).

In 1997 and 1998, we measured the shortest distance from each nest to the wooded edge and the water edge with a hand-held measuring tape. Using these data, we reconstructed the study site boundary in a GIS coverage. We then measured the distance from the wooded and water edges for the 1995, 1996, and 1999 nests using ArcView. The boundary between the wooded or water edges and the nesting area has remained constant over the last 12 years (F. Janzen, pers. obs.).

Data analysis

We used a likelihood-ratio G-test to determine if excavating nests influenced predation rates in 1998 and 1999 and multiple logistic regression to test for effects of distance from the wooded and water edges on the probability of nest predation. A potentially confounding factor in this study was within-season temporal pattern of nesting, that is, the date each nest was laid. Therefore, for years with both a significant edge effect on predation and a significant linear relationship between date laid and distance from the edge, we included the date laid as well as distance from the water and wooded edges in the final multiple logistic regression analysis. Initial multiple logistic regression models contained distance from the water and distance from the woods as the independent variables and the dependent variable was predation status, a binominal response. We used a residual analysis for distance from the wooded edge and date laid in the final multiple logistic regression model because the independent variables were correlated. We removed the effect of distance from the water from the distance from the woods and date laid (when applicable) through a residual analysis. Thus, residual distances from linear regressions of distance from the water on distance from the woods and date laid (when applicable) were independent variables along with the original distance from the water in the final analysis. Tests were conducted for each of the five years separately and with all five years combined.

To supplement this inferential statistical analysis and to identify threshold distances from the edge, we used a cubic spline algorithm to visualize the dynamics of predation across continuous distances from each edge (Schluter 1988). For the purposes of this study, we defined a threshold as the distance from the edge or range of distances where the survival probabilities began to level off or reach an asymptote. Cubic splines

are a nonparametric alternative to traditional regression methods previously suggested for estimating the form of natural selection (Schluter 1988). The only assumption is smoothness of the fitted curve. Here, cubic splines were used to estimate the change in the probability of nest survival over continuous distances from the edge without forcing the data to fit a particular regression model. For this application, cubic splines are better than traditional regression methods, which force a predetermined curve to the data. Standard errors for the splines were calculated by bootstrapping the original data 100 times. Analyses were performed for each year and all years combined. Statistical tests were conducted using JMP version 3.2 (SAS Inc. 1997) and cubic splines were conducted using Schluter's (1988) program.

Results

Predation rates varied considerably among the five years of this study ranging from a low of 19.7% in 1997 to a high of 76.2% in 1999 (Table 1). The number of nests laid in a year was not correlated with predation rate ($P = 0.78$). Significant edge effects were detected in years with low (1997: 19.7%), moderate (1998: 35.4%), and high (1995: 64.6%) predation (Table 1). No difference in predation rates occurred between excavated and unexcavated nests in 1998 ($G = 0.100$, $df = 1$, $P = 0.752$), a moderate predation year (35.4%), or 1999 ($G = 0.101$, $df = 1$, $P = 0.750$), a high predation year (76.2%). Therefore, excavating nests to count and weigh eggs is unlikely to have influenced predation in this study.

No effect of distance to the wooded or water edge on the probability of nest predation was detected in 1996 or 1999. Nests in 1995, 1997, and 1998 had a higher probability of predation as distance from the water edge decreased, and nests in 1998 had a higher probability of predation as the relative distance from the wooded edge decreased (Table 1). The combined analysis with all five years showed a strong effect with the probability of predation decreasing with distance from the water edge (Table 1). Both a significant edge effect and a significant relationship between the distance from the edge and date laid occurred in 1995, 1997, and overall (Table 2). Thus, date laid was included in the final multiple logistic regression model for 1995, 1997, and overall. Date laid did not have a significant effect on the probability of predation 1995 or 1997 (Table 1). Overall, nests had a higher probability of predation earlier in the nesting season, which, in conjunction with the increase in nests closer to the water edge as the nesting season progressed, is not consistent with within-season temporal nesting patterns causing the observed edge effects on predation.

Cubic spline analyses were used to visualize the dynamics of predation across increasing distances from water edge and to detect threshold values for survival. Multiple logistic regression and cubic spline results were generally consistent with higher probabilities of survival farther from the water edge in 1995, 1997, 1998, and overall, but not in 1996 and 1999 (Table 1 and Fig. 1). The probability of survival approached a threshold at ~40 m from the water edge in 1995 and the rate of increase in the survival probability began to level off at ~25 m in 1998. In 1997, the probability of survival fluctuated markedly with probabilities of nearly 0.6 at 3 m and 26 m and a probability above 0.8 from 6 to 21 m and >30 m (Fig. 1). Delimiting a threshold for 1997 was not appropriate due to these fluctuations. With all years combined, the probability of survival increased from 0.35 to 0.6 across the first 30–40 m from the water edge and then reached an asymptote. This pattern represents a substantial increase in the probability of survival for nests farther from the water edge.

Discussion

Habitat edges can cause a variety of biotic and abiotic changes that affect organisms; and many interacting factors may lead to spatial and temporal variation in the presence or intensity of edge effects (Murcia 1995). This five-year analysis of nest predation patterns at a small spatial scale detected a higher probability of predation closer to the water edge in most years and with all years combined and closer to the wooded edge in one year (Table 1 and Fig. 1). We were able to visualize the dynamics of predation at increasing distances from the edges by uniquely applying cubic spline

analysis, and to determine an approximate threshold for most years with significant effects of distance from an edge on predation. Overall, this study supports the generality of the negative impact of ecological edges on nest predation across temporal and spatial scales and taxonomic groups. However, among-year variation in detecting edge effects may bias the conclusions of short-term studies.

Spatial dynamics of edge effects

In the only other non-avian edge effect study, Temple (1987) found significantly higher nest predation within 50 m of marsh or wooded edge habitat for 22 nests of three turtle species monitored over a five-year period. In years with a significant edge effect in our study (i.e. 1995, 1997, and 1998), there was a higher probability of nest survival as distance from the water or wooded edge increased (Table 1 and Fig. 1). Changes in the probability of survival occurred over the first ~40 m in 1995, ~25 m in 1998, and ~35 m in 1997, though the changes fluctuated in 1997 (Fig. 1). The average of these threshold values, ~30 m, was observed in the spline for the five years combined (Fig. 1). Though no statistical rule exists for extracting threshold values from cubic splines, trends in the probability of predation and approximate threshold values are apparent and standard errors from bootstrapping provide confidence levels.

The importance of identifying threshold values of predation is twofold. First, distances where survival probabilities quickly change or level off are important for understanding the scale at which edges influence predation. Predation rates may reach an asymptote after certain distances. Such data are important for

Table 1. Effects of distance from the edge and date laid on the probability of predation for painted turtle nests. Results from multiple logistic regression analyses with the distance from the water edge, residuals of distance from the wooded edge and residuals of date laid (when applicable) as independent variables and nest fate as the dependent variable. An * indicates a higher probability of predation as distance from the water edge decreased or as residual distance from the wooded edge decreased and an ** indicates a higher probability of predation relatively earlier in the nesting season. The predation rate and number of nests laid for each year and overall are also given.

Year	Independent variables	χ^2	<i>P</i>	% Predation	Number of nests laid
1995	Water edge	11.96	0.0005*	64.6	130
	Woods edge	0.01	0.93		
	Date laid	0.10	0.75		
1996	Water edge	0.59	0.44	46.0	150
	Woods edge	1.67	0.20		
1997	Water edge	7.92	0.005*	19.7	198
	Woods edge	0.19	0.66		
	Date laid	1.06	0.30		
1998	Water edge	20.48	<0.0001*	35.4	178
	Woods edge	6.51	0.01*		
1999	Water edge	1.24	0.27	76.2	206
	Woods edge	1.84	0.18		
Overall	Water edge	18.83	<0.0001*	47.8	862
	Woods edge	1.64	0.20		
	Date laid	6.66	0.01**		

Table 2. Linear regression results for the relationship between distance from the edge, either wooded or water, and the date each nest was laid. Nesting dates indicate the dates for the first and last nest of each year. The number of nests used in these analyses was less than the number of nests laid because the date laid was not known for every nest. Linear regressions were corrected for multiple comparisons ($K = 2$) with the Dunn-Sidak method giving a P value for significance of $P = 0.025$ (Sokal and Rohlf 1995).

Year	Edge type	r	P	Nesting dates	Number of nests
1995	Water	-0.23	0.008	1 Jun-	130
	Woods	0.10	0.26	25 Jun	
1996	Water	-0.21	0.03	12 Jun-	115
	Woods	0.10	0.31	2 Jul	
1997	Water	-0.38	<0.0001	8 Jun-	171
	Woods	0.23	0.003	31 Jun	
1998	Water	-0.07	0.40	26 May-	145
	Woods	0.11	0.20	2 Jul	
1999	Water	-0.05	0.53	26 May-	182
	Woods	0.04	0.58	1 Jul	
Overall	Water	-0.14	0.0002		743
	Woods	0.09	0.01		

integrating information about the ecological mechanisms responsible for these predation patterns, such as predator search behavior. Second, knowledge of a general pattern for threshold values is valuable for conservation and management workers (Paton 1994). Consistent threshold distances across different plot sizes would suggest that ecological mechanisms responsible for edge effects operate at similar spatial scales. Though generalization of threshold values detected in this study should be made cautiously, the approximately 30–40 m threshold identified here corresponds to edge effects found in other studies with larger study sites ranging from 31 to 1084 ha (Winter et al. 2000). Moreover, Andrén and Angelstam (1988) found a decrease in predation from 35 to 10% as distance from an edge in a forest went from approximately 30 to 100 m. Finally, Paton (1994) suggested that predation rates are often significantly greater within 50 m of an edge. Thus, a threshold of ~30–50 m may be relevant for a wide range of spatial scales, but this hypothesis needs further testing.

Temporal dynamics of edge effects

We evaluated edge effects at two temporal scales in this study, both within- and among-years. Water edge effects on predation were not detected in every year of this study, but when significant effects were detected in 1995, 1997, and 1998, they showed a similar pattern of increasing probability of survival with distance. Such year-to-year differences in detecting an edge effect, however, emphasize the importance of multi-year studies. Indeed, nest survival rates vary between years and seasons within a year in other studies (Pasitschniak-Arts and Messier 1995). A hypothetical two-year study at our site including only 1997 and 1998 would have incorrectly concluded that nest predation always increases near the water edge and that the predation rate

is relatively low (Table 1). Despite strong edge effects in some years, the multi-year dimension of this study provided important insight into among-year temporal variation.

Focusing on within-year temporal dynamics, a significant negative relationship between distance from the water edge and date laid corresponded with significant edge effects in two years (1995 and 1997) and overall (Table 1 and 2). Thus, a possible mechanism for edge effects on predation at this site is temporal change in

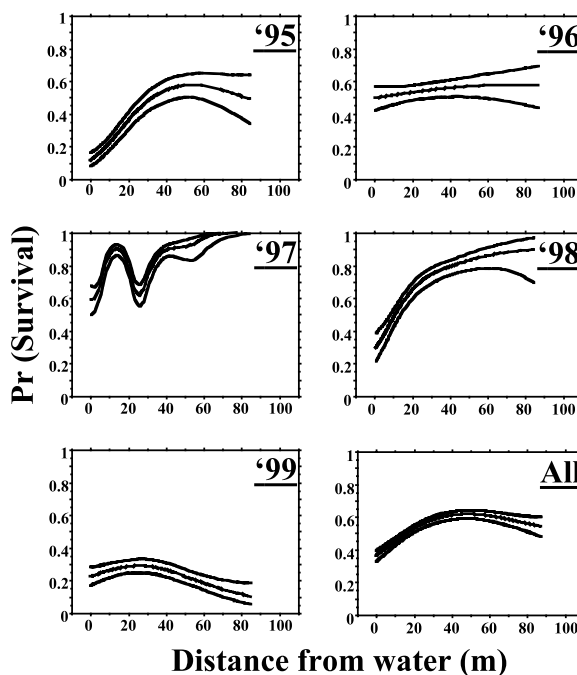


Fig. 1. Cubic splines for the probability of survival as distance from the water edge increases. Analyses for each of the five years (1995–1999) separately and all five years combined are shown. Lines bracketing the splines are the standard errors calculated by bootstrapping the original data 100 times.

nesting behavior: increasing nest numbers closer to the water edge as the nesting season progresses may lead to greater risk of predation. However, date had no effect on the probability of predation in 1995 and 1997. Overall, there was a higher probability of predation relatively earlier in the nesting season (Table 1), which is inconsistent with differential nesting behavior causing an edge effect. We can also rule out within-season temporal and spatial effects of female body size as possible causative factors because linear regressions between plastron length (a measure of female size) with distance from the water and date laid were not significant ($P > 0.05$ for all years).

Implications for ecological processes and population dynamics

The water edge in this study represents an abrupt ecological edge. For terrestrial predators, the water edge demarcates where resources transition from completely unavailable to available to some degree. According to a model by Angelstam (1986), as productivity in the habitat island increases compared to the surrounding matrix, predation rates in the island should increase. Our results are largely consistent with this model. Similarly, Indigo Bunting nest predation rates were twice as high along abrupt edges compared to more gradual edges where plant succession was occurring (Suarez et al. 1997). Ratti and Reese (1988) also found higher nest predation in abrupt-edge subplots compared to feathered-edge subplots using artificial nests. Thus, predators may benefit from foraging in areas with higher productivity and mediate the potential risks in this environment by not penetrating too far into the habitat island. The wooded edge in our study is also abrupt, but foraging opportunities likely exist on both sides of this edge in contrast to the water edge. Thus supporting the result of stronger edge effects due to water edge compared to the wooded edge. The abruptness of the water edge may be an important factor in the predator-prey interaction leading to predation edge effects in this study.

For turtles, the biological importance of the water edge is clear. Females must venture onto land to lay their eggs and a trade-off between nesting close to the edge, risking future fitness, and nesting farther from the edge, risking predation or desiccation themselves, may ensue. Given the few adult turtles found dead at this site and the overall nest predation rate of nearly 50%, nest predation seems to be a stronger relative selection pressure at this site. Nest predation may also be influenced by other spatial patterns such as the density of nests in a given area. Several avian studies have detected density-dependent predation (Martin 1988, Page et al. 1983), but in the one turtle nest study to assess the effect of density, predation was independent of density (Burke et al. 1998).

Considering the abiotic effects of edges is also warranted, particularly in oviparous reptiles in which nest microenvironments influence critical offspring traits such as sex and body size (Cagle et al. 1993, Packard et al. 1999, Weisrock and Janzen 1999). Painted turtles exhibit temperature-dependent sex determination such that females are produced at relatively warmer temperatures and males at cooler temperatures (Janzen and Paukstis 1991). Overstory vegetation is a strong predictor of nest temperatures and nest sex ratios at this site (i.e. more overstory vegetation leads to cooler nest temperatures and male biased sex ratios) (Janzen 1994, Weisrock and Janzen 1999). Edges often mark transitions of environmental variables including temperature (Murcia 1995, Báldi 1999). At our site, ground temperatures near the water edge may be relatively warmer because of the lack of trees to the east, and near the wooded edge ground temperatures may tend to be cooler because of the continuous stand of trees to the west. These differences in ground temperatures coupled with the effect of edges on predation at this site may result in biased cohort sex ratios. For example, there was a higher probability of predation closer to the water edge in 1995, 1997, and 1998, thus more relatively warmer, female-producing nests were likely lost to predation. Further studies are needed to determine the magnitude of temperature differences between nest sites along the water and wooded edges, and whether biased predation due to edges might influence the overall sex ratio of the population. If edge effects truly influence sex ratios, then sex-specific recruitment and long-term population dynamics may be influenced dramatically. The consequences of edge effects may extend beyond the direct demographic impact of predation; indirect effects on cohort sex ratios and offspring phenotypes are also possible.

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References

Andrén, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. – *Ecology* 73: 794–804.

- Andrén, H. and Angelstam, P. 1988. Elevated predation rates as an edge effect in habitat islands: experimental evidence. – *Ecology* 69: 544–547.
- Angelstam, P. 1986. Predation on ground-nesting birds' nests in relation to predator densities and habitat edge. – *Oikos* 47: 365–373.
- Báldi, A. 1999. Microclimate and vegetation edge effects in a reedbed in Hungary. – *Biodiversity Conserv.* 8: 1697–1706.
- Boose, E. R., Boose, E. F. and Lezberg, A. L. 1998. A practical method for mapping trees using distance measurements. – *Ecology* 79: 819–827.
- Burke, V. J., Rathburn, S. L., Bodie, J. R. and Gibbons, J. W. 1998. Effect of density on predation rate for turtle nests in a complex landscape. – *Oikos* 83: 3–11.
- Cagle, K. D., Packard, G. C., Miller, K. and Packard, M. J. 1993. Effects of the microclimate in natural nests on development of embryonic painted turtles, *Chrysemys picta*. – *Funct. Ecol.* 7: 653–660.
- Donovan, T. M., Jones, P. W., Annand, E. M. and Thompson, F. R. 1997. Variation in local-scale edge effects: mechanisms and landscape context. – *Ecology* 78: 2064–2075.
- ESRI Inc. 1998. ArcView GIS Version 3.1. – Redlands, CA.
- Gates, J. E. and Gysel, L. W. 1978. Avian nest dispersion and fledging success in field-forest ecotones. – *Ecology* 59: 871–883.
- Janzen, F. J. 1994. Vegetational cover predicts the sex ratio of hatchling turtles in natural nests. – *Ecology* 75: 1593–1599.
- Janzen, F. J. and Paukstis, G. L. 1991. Environmental sex determination in reptiles: ecology, evolution, and experimental design. – *Quart. Rev. Biol.* 66: 149–179.
- Johnson, R. G. and Temple, S. A. 1990. Nest predation and brood parasitism of tallgrass prairie birds. – *J. Wildlife Man.* 54: 106–111.
- Luck, G. W., Possingham, H. P. and Paton, D. C. 1999. Bird responses at inherent and induced edges in the Murray Mallee, South Australia. 2. Nest predation as an edge effect. – *Emu* 99: 170–175.
- Martin, T. E. 1988. On the advantage of being different: nest predation and the coexistence of species. – *PNAS* 85: 2196–2199.
- Møller, A. P. 1989. Nest site selection across field-woodland ecotones: the effect of nest predation. – *Oikos* 56: 240–246.
- Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. – *Trends Ecol. Evol.* 10: 58–62.
- Niemuth, N. D. and Boyce, M. S. 1997. Edge-related nest losses in Wisconsin pine barrens. – *J. Wildlife Man.* 61: 1234–1239.
- Packard, G. C., Miller, K., Packard, M. J. and Birchard, G. F. 1999. Environmentally induced variation in body size and condition in hatchling snapping turtles (*Chelydra serpentina*). – *Can. J. Zool.* 77: 278–289.
- Page, G. W., Stenzel, L. E., Winkler, D. W. and Swarth, G. W. 1983. Spacing out at Mono Lake: breeding success, nest density and predation in the snowy plover. – *Auk* 100: 13–24.
- Pasitschniak-Arts, M. and Messier, F. 1995. Risk of predation on waterfowl nests in the Canadian prairies: effects of habitat edges and agricultural practices. – *Oikos* 73: 347–355.
- Pasitschniak-Arts, M., Clark, R. G. and Messier, F. 1998. Duck nesting success in a fragmented prairie landscape: is edge effect important? – *Biol. Conserv.* 85: 55–62.
- Paton, P. W. C. 1994. The effect of edge on avian nest success: how strong is the evidence? – *Conserv. Biol.* 8: 17–26.
- Ratti, J. T. and Reese, K. P. 1988. Preliminary test of the ecological trap hypothesis. – *J. Wildlife Man.* 52: 484–491.
- SAS Institute Inc. 1997. JMP user's guide, Version 3.2. – SAS Institute, Cary, NC.
- Schluter, D. 1988. Estimating the form of natural selection on a quantitative trait. – *Evolution* 42: 849–861.
- Sokal, R. R. and Rohlf, F. J. 1995. *Biometry*. – W. H. Freeman.
- Suarez, A. V., Pfennig, K. S. and Robinson, S. K. 1997. Nesting success of a disturbance-dependent songbird on different kinds of edges. – *Conserv. Biol.* 11: 928–935.
- Temple, S. A. 1987. Predation on turtle nests increases near ecological edges. – *Copeia* 1987: 250–252.
- Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. – *Annu. Rev. Ecol. Syst.* 20: 171–197.
- Weisrock, D. W. and Janzen, F. J. 1999. Thermal and fitness-related consequences of nest location in painted turtles (*Chrysemys picta*). – *Funct. Ecol.* 13: 94–101.
- Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. – *Ecology* 66: 1211–1214.
- Winter, M., Johnson, D. H. and Faaborg, J. 2000. Evidence for edge effects on multiple levels in tallgrass prairie. – *Condor* 102: 256–266.
- Yahner, R. H. 1988. Changes in wildlife communities near edges. – *Conserv. Biol.* 2: 333–399.
- Yahner, R. H. and Wright, A. L. 1985. Depredation on artificial ground nests: effects of edge and plot age. – *J. Wildlife Man.* 49: 508–513.