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Landowners and cat predation across rural-to-urban landscapes

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Abstract

Fluctuations of bird abundances have been attributed to such factors as supplemental feeding, landscape change, and habitat fragmentation. Notably absent from consideration, however, is the role of private landowners and their actions, such as owning free-ranging domestic cats (*Felis catus*; cats allowed free access to the outdoors). To understand the impacts of cat predation on birds, we surveyed all 1694 private landowners living on three breeding bird survey (BBS) routes (~120 km) that represent a continuum of rural-to-urban landscapes in Southeastern Michigan, where the majority (>90%) of land is privately owned. Our data indicate that among the 58.5% of landowners that responded, one quarter of them owned outdoor cats. On average a cat depredated between 0.7 and 1.4 birds per week. A total of 23+ species (12.5% of breeding species) were on the list of being killed, including two species of conservation concern (Eastern Bluebirds and Ruby-throated Hummingbirds). Across the three landscapes there were ~800 to ~3100 cats, which kill between ~16,000 and ~47,000 birds during the breeding season, resulting in a minimum of ~1 bird killed/km/day. While the number and density (no./ha) of free-ranging cats per landowner differed across the rural to urban landscapes, depredation rates were similar. Landowner participation in bird feeding showed no relationship with the number of free-ranging cats owned. Similarly, selected demographic characteristics of landowners were not significantly related to the number of free-ranging cats owned. Our results, even taken conservatively, indicate that cat predation most likely plays an important role in fluctuations of bird populations and should receive more attention in wildlife conservation and landscape studies.

Keywords: Domestic cat (*Felis catus*); Landowner; Human impacts; Breeding bird survey; Rural to urban; Bird feeding; Private land; Human-dominated landscape

1. Introduction

Since the mid 1960s, long-term data on breeding birds have indicated that many species are declining or fluctuating throughout the Midwest and Eastern United States (Robbins et al., 1989; Terborgh, 1989). These declines and fluctuations have been attributed to factors such as habitat fragmentation and destruction (Robbins et al., 1989; Donovan and Flather, 2002), landscape change (Flather and Sauer, 1996), and direct mortality due to events (e.g. culling by farmers) on the wintering-grounds of the neotropics (Rappole and McDonald, 1994; Basili and Temple, 1999). Largely absent from consideration in the potential mechanisms responsible for influencing breeding bird abundances are the landowners that live in the landscapes being investigated. Because private landowners are the ultimate controllers of their land, they may be carrying out a wide variety of actions that could influence bird abundances and distributions. Their cumulative and collective effects across large areas and over time may be even more drastic. Furthermore, landowners living in rural landscapes may carry out activities at different levels than those in urban landscapes. Such differences may in part explain the substantial variations in bird abundances and diversity often noted along urban to rural gradients or in urban contexts (e.g. Emlen, 1974; Hohtola, 1978; Cam et al., 2000).

Because of the potential for significant landowner effects on birds, there has been increased attention directed towards the integration of social and economic components into questions of avian distributions (Hostetler,

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1999). However, until recently ecologists have largely ignored the human components in ecological research (Lubchenco et al., 1991; Gallagher and Carpenter, 1997; Vitousek et al., 1997; Liu, 2001). As a result, ecologists' understanding of how humans interact with and influence different ecosystems, and the species they contain, is still in its early stage (Redman, 1999). To move beyond this basic level, ecologists are increasingly incorporating socioeconomics, human demography, and social science techniques, such as social surveys, to understand the interrelationship between humans and the ecosystems within which they live (Turner et al., 1996; Liu et al., 1999, 2001). As human behaviors are the direct force affecting ecosystems, it is essential to incorporate human behaviors into the understanding of ecological patterns such as abundance and diversity of bird species.

One specific behavior that could negatively impact breeding birds is allowing domestic cats (*Felis catus*) free access to the outdoors. Although free-ranging domestic cats (i.e. house cats that have free access to the outdoors; a.k.a. outdoor cats) predominantly depredate small mammals (Fitzgerald and Turner, 2000), birds constitute a large secondary source of prey (Coman and Brunner, 1972; Pearre and Maass, 1998). While the fact that cats prey upon birds is unquestioned, the degree to which they negatively impact bird populations (or any prey species) has been a point of contention in the literature (Barratt, 1998). Because domestic cats have coexisted with humans for centuries, Fitzgerald and Turner (2000) argue that any continental population of birds that could not withstand predation by cats would have been extirpated long ago. Another perspective holds that cats are simply occupying the role of a natural predator. That is, cats are assumed to fill a role similar to that of species such as raccoons (*Procyon lotor*), skunks (*Mephitis mephitis*), and raptors. A final point that has been made is that people simply observe avian depredation by cats more than other natural phenomena because it takes place during the day time and often close to the house, which results in the assumption that cats are reducing bird populations (see Patronek, 1998 for details).

Countering the previous points is the fact that domestic cats are subsidized predators and are thus likely to have a larger total effect on bird species. Specifically, humans provide domestic cats a level of maintenance that other predators do not receive (Coleman and Temple, 1993). As a result they may exist in higher densities and exert a greater predatory effect than natural predators. Second, cats are opportunistic predators (Coman and Brunner, 1972), both in terms of time and habitat location (Barratt, 1997), meaning they will depredate a prey item if they encounter it. Third, in many human-dominated landscapes where top-level predators are absent, domestic cats may be extolling an even larger predatory effect due to a mesopredator release effect (Crooks and Soulé, 1999; Risbey et al., 2000). The mesopredator release effect is simply the situation in which top level predators have either been greatly reduced or extirpated, resulting in an increase of second-tier predators, such as skunks, raccoons, and domestic cats. Fourth, cats often depredate birds more during the breeding months when nestlings and fledglings are bountiful (Eberhard, 1954; Dunn and Tessaglia, 1994). Fifth, cats may be directly competing with avian predators, such as American Kestrels (*Falco sparverius*), Northern Harriers (*Circus cyaneus*) and Red-tailed Hawks (*Buteo jamaicensis*; George, 1974). Finally, even very low cat depredation could negatively impact the breeding success and viability of a species (Crooks and Soulé, 1999).

As part of a larger effort to understand and integrate the social and ecological factors influencing breeding bird abundances among different rural to urban landscapes (Lepczyk et al., 2002), we sought to address the roles of free-ranging cats and the landowners that own them. Specifically, we were interested in ascertaining: (1) the proportion of landowners that allow their cats outside; (2) the number and density (cats/ha) of cats each household owned that were allowed access to the outside; (3) how many dead or injured birds a week the cats brought in during the breeding season (i.e. April through August); (4) what cat predation rates were at the landscape level; (5) what bird species were brought home by the cats; and, (6) if differences existed across a rural to urban gradient.

Aside from understanding the six aforementioned issues, we also tested three a priori hypotheses. Our first hypothesis was that because bird feeders may act to magnify local bird densities, a relationship would exist between both the number and density of bird feeders and cat depredation rates. We predicted that as the number and/or density of bird feeders increased there would be a related increase in the number of birds depredated per cat. In addition, because the role of domestic cats as predators has received widespread attention among academic and professional organizations (e.g., Cooper Ornithological Society's resolution on Public Policies Regarding Feral and Free-ranging Cats; American Bird Conservancy Resolution on Free-roaming Cats), non-academic venues (e.g. National Audubon Society Resolution on Cats; Wisconsin Natural Resources Magazine), veterinarians, and non-profit educational programs (e.g. American Bird Conservancy's *Cats Indoors!*), we also sought to integrate our results with demographic parameters of the landowners to test two other hypotheses. Specifically, we hypothesized that the number of free-ranging cats would be a function of a landowner's age and educational level. In the case of a landowner's age we predicted a positive relationship between age and number

of free-ranging cats they would own, since the impetus to keep cats indoors has been a relatively recent phenomenon that likely influences younger landowners more than older landowners. Likewise, we predicted a negative relationship between education and free-ranging cats, such that the more education a landowner had the fewer free-ranging cats they would own. We based this prediction on the grounds that many public and private organizations as well as veterinarians have strongly advocated keeping cats indoors and that the more education a landowner has the greater the chance that they have been exposed to such a message.

2. Methods

To address the research questions, test our hypotheses, and match the scale of study areas with locations where long-term data on bird abundance and distribution have been collected (Vogt et al., 2002), we used three breeding bird survey (BBS) routes (route numbers 53, 167, and 168) in Southeastern Michigan, United States (Fig. 1), where >90% of the land is privately owned. We chose these three routes because they represent a continuum from rural to urban landscapes, based on their geographic locations, average land parcel sizes, and socio-demographic compositions. Specifically, route 53 (hereafter termed Rural) is very rural, has a low population density, large land parcels, and is removed from any large city center or urban location. Route 168 (hereafter termed Urban) ranges from being very suburban to being urban, has a high population density, small land parcels, and transects or parallels residential locations and city centers. Finally, route 167 (hereafter termed Suburban) straddles the demographic differences between routes 53 and 168 by being suburban, has intermediate population density and land parcel sizes, and runs parallel to (but never intersects) large residential and city center locations. In addition, all three routes occur in a heterogeneous and human dominated region that is undergoing rapid urbanization (Rutledge and Lepczyk, 2002), which is representative of many other regions in North America. The last reason for selecting these three routes is that they remain active BBS routes, monitored annually by the United States Fish and Wildlife Service, which allows for future evaluations to be conducted, and hence, comparisons made over time.

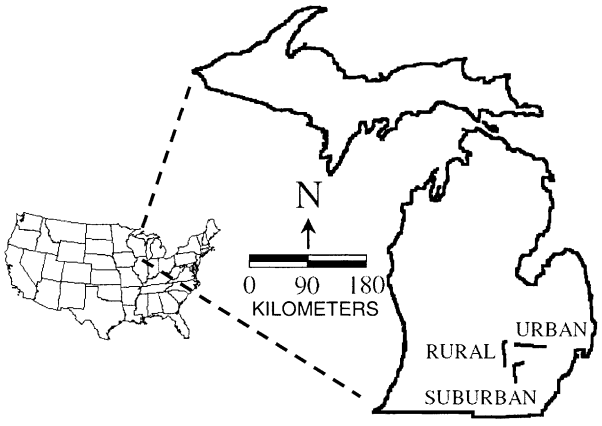

Fig. 1. Location of the three BBS routes/study landscapes in Southeastern Michigan. Route 53 is Rural, route 167 is Suburban, and route 168 is Urban. Each BBS route is 39.4 km in length.

To integrate information about human behaviors into the understanding of landowner impacts on bird abundance, we conducted a social survey of landowners. For our study, we chose all private landowners who owned property immediately adjacent to the road along which each of the three BBS routes is run. We identified the landowners through a combination of driving each route and using county tax records and plat maps. Utilizing this combined approach we identified a total of 1694 private landowners (331 on Rural, 390 on Suburban, and 973 on Urban).

We administered a mail survey instrument between October and December of 2000 following the Total Design Method (Dillman, 1978, 2000). The survey instrument and procedures were fully evaluated for ethical appropriateness by the Michigan State University Committee on Research Involving Human Subjects prior to mailing. To encourage responses we established a toll-free telephone line for landowners to contact us with any questions and offered prize drawings as an incentive. Briefly, an initial survey was mailed during the first week of October 2000. A reminder/thank you postcard was sent out 2 weeks later. Finally, a second survey was sent out 2 weeks after the postcard to those who had not responded to the prior mailings.

Our sampling framework was designed to capture only private landowners, hence, any survey returned from a church, business or public land owner that might have accidentally been included in the initial sample was removed from the study. Similarly, surveys that were returned as undeliverable by the United States Postal Service (USPS), where the recipient was deceased, or where different landowners had the same address as another landowner and were returned as undeliverable by the USPS, were removed from the sample. Surveys received after 31 December 2000 were not included in any analyses. If landowners owned multiple parcels that were not connected to one another, then they were asked to complete the survey in relation to only one of the parcels. However, if the landowner owned multiple parcels that were all contiguous with one another, then they were asked to fill out the survey in relation to the entire block of land. Surveys that were returned blank (i.e. not filled out) or contained notes indicating no interest in participating in the survey were considered a non-response. Similarly, landowners that called to indicate they were unable or had no desire to participate in

the survey were considered non-respondents. Non-respondents were included in the final corrected sample size.

To ascertain the impact of free-ranging cats on bird abundance we asked the following questions in our survey: (1) How many cats does your household own that are allowed access to the outside? (2) If you or members of your household own cats that are allowed access to the outside, approximately how many dead or injured birds a week do all the cats bring in during the spring and summer months (April through August) (0, 1, 2–3, 4–5, 6–7, 8–9, 10–15, 16–20, more than 20)? (3) Can you or anyone in your household identify any of the bird species brought home by your cat(s) (yes, no, unsure)? (4) Please list the names of the bird species that your cat(s) has brought home during the spring and summer months on the lines below. With regard to the number and density of bird feeders the following questions were asked: (5) Does anyone in your household feed birds on your property (yes, no)? (6) How many bird feeders do you have on your property? (7) Approximately how large is your parcel of land? Finally, to ascertain basic demographic statistics of the landowners we asked the following questions: (8) In what year were you born? (9) Are you: Male, Female? (10) How many people currently live in your household? (11) What is the highest level of school completed or degree you have received (Some school completed, but no high school diploma; High school graduate or general equivalency diploma; some college, but no degree; Associates degree in college; Bachelor's degree; Master's, professional, or doctoral degree)? The six educational choices offered were a condensation of the nine categories used in the United States Census form that pooled post-baccalaureate degrees together.

In cases where the respondents did not explicitly follow the survey instructions, we edited the data as follows. For fill-in-the-blank questions that asked for a single numeric response, we took the arithmetic mean if a respondent put a range. In a single case a respondent put a question mark for the number of cats allowed access to the outdoors. Because all subsequent questions that were contingent upon the number of cats were answered as owning an outdoor cat, we conservatively assumed that the landowner had at least one cat. However, in cases where landowners had no cats allowed access to the outdoors, but answered questions contingent on the fact that they did own them, we converted the values to blank (i.e. no data) entries. In the cases where respondents were asked for only a single response to a categorical question but filled in two blanks, we used a coin toss to decide the answer. For the bird species brought home by the cats we corrected all spelling/grammatical mistakes and made the following assumptions based on colloquial terminology and bird descriptions compared to known species in the surrounding landscape. Redbirds and red birds were assumed to be Northern Cardinals (*Cardinalis cardinalis*). Turtle doves and doves were assumed to be Mourning Doves (*Zenaida macroura*). Honey-sucking birds and hummers were assumed to be Ruby-throated Hummingbirds (*Archilochus coubris*), as no other hummingbirds inhabit Michigan. Canary, yellow canary, wild canary, yellow finch, and golden finch were assumed to be American Goldfinches (*Carduelis tristis*). Crackles or crackens were assumed to be Common Grackles (*Quiscalus quiscula*). Red finches and red-breasted finches were assumed to be Purple Finches (*Carpodacus purpureus*). Finally, barn sparrow was changed to Sparrow, even though it is most likely a House Sparrow, because of the potential for misidentification.

Because of the potential for under-reporting cat depredation (see Section 4), we initially calculated a predation rate based on all landowners that had outdoor cats, even if they indicated predation rates of zero (Predation Rate 1, hereafter termed PR1). However, we also calculated a second predation rate (Predation Rate 2, hereafter termed PR2) based only on landowners that had outdoor cats for which they reported one or more birds killed or injured per week. Given the uncertainty related to the number of cats and their associated predation rates with regard to the non-respondents, we used several different estimates of non-respondent outdoor cat ownership to provide a plausible range when scaling-up the results to the landscape level. To estimate the total number of birds depredated over the breeding season in each landscape we considered non-respondents from three perspectives: (1) non-respondents have the same number of outdoor cats as respondents, (2) non-respondents have 50% the number of outdoor cats as respondents, and (3) non-respondents have 150% the number of outdoor cats as respondents. Under each assumption we applied both rates of predation, such that under Predation Rate 1 the total number of birds killed over the breeding season = (number of non-respondents) × (mean number of cats/landowner) × (weekly predation rate) × (22 weeks) + (number of birds killed over 22 weeks from respondents). In the case of Predation Rate 2 we calculated the total number of birds killed over the breeding season = (number of non-respondents) × (proportion of landowners that had cats that killed or injured one or more bird a week) × (mean number of cats/landowner) × (weekly predation rate) × (22 weeks) + (number of birds killed over 22 weeks from respondents). We estimated the potential proportion of landowners involved in allowing their cats outdoors across each landscape by assuming that all non-respondents did not have cats allowed outdoors (minimum estimate) and then assuming that they all did have cats allowed outdoors (maximum).

Statistical analyses were performed using the multivariate general linear hypothesis module in SYSTAT

5.03 (Wilkinson, 1992). All density measures were calculated using the parcel sizes reported by the landowners. Response rate and the proportion of landowners owning outdoor cats across each landscape were compared using a two-way contingency table with a Pearson Chi-square test statistic. Comparisons between cat and non cat owners were carried out using t-tests, while comparisons across landscapes were carried out with ANOVA. Landscape differences were compared using Tukey's HSD procedure (Zar, 1996). Data are reported as means±SE (as 100% of the population was sampled, but only ~59% responded), unless otherwise noted, with a P-value of 0.05 considered significant.

Of the 1694 landowners initially identified, 40 were removed from consideration because they were a business or church, had property outside the sampling region, already responded based on another parcel of land within the study landscapes, or their address information was incorrect, thus reducing the corrected population size to 1654. Among these 1654 we received 968 completed surveys, yielding a 58.5% response rate. Response rates in different landscapes were 64.8% for Rural (212 of 327), 61.5% for Suburban (233 of 379), and 55.2% for Urban (523 of 948), which were significantly different ($\chi^2=11.11$; df = 2; $P=0.0039$).

3. Results

A total of 253 (26.1%) landowners had cats that were allowed access to the outside. Of these 253 landowners, 71 (33.5%) were in the Rural landscape, 75 (32.2%) were in the Suburban landscape, and 107 (20.5%) were in the Urban landscape, indicating a significantly different proportion of respondents due to the lower frequency in the Urban landscape ($\chi^2=19.09$; df = 2; $P=0.00007$). The total number of free-ranging cats across all landscapes was 656 (Table 1), ranging from 1 to 30 per landowner with a mean of 2.59±0.20 per landowner (Fig. 2). Overall, the mean number of free-ranging cats per landowner was significantly different by landscapes ($F=6.175$; df = 2, 250; $P=0.0024$; Table 1), but specific landscape differences were only significant between the Rural and Urban landscapes ($P=0.0013$). Similarly, the density of cats (no./ha) was significantly different by landscape ($F=9.74$; df = 2, 239; $P=0.000086$), with the Urban landscape being different from both the Rural ($P=0.00045$) and the Suburban landscapes ($P=0.00086$; Table 1).

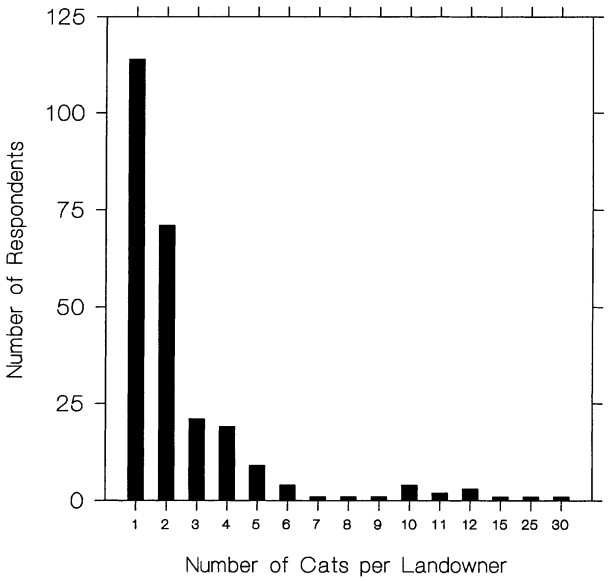

Fig. 2. Frequency distribution of the number of cats reported to be allowed outdoors per landowner.

Of the 253 landowners owning outdoor cats, the mean number of birds depredated per cat per week (PR1) across all landscapes was 0.683±0.12 ($n=245$) and was similar among all landscapes ($F=0.213$; df = 2, 242; $P=0.808$; Table 2). Recalculating predation rates based only on landowners that had outdoor cats (PR2) for which they reported one or more birds killed or injured per week reduced the sample size to 118 (Table 2). Of these 118 landowners, the mean number of birds depredated per cat per week (PR2) across all landscapes was 1.42±0.22 (Table 2). As with PR1, PR2 was similar among all three landscapes ($F=0.567$; df = 2, 115; $P=0.57$; Table 2). Based upon PR1 the overall average total number of birds killed per cat during the breeding season was 15 compared with an overall overage of 31 using PR2 (Table 2). Summing each individual cat's

Table 1
Summary information for free-ranging cat owners by landscape

	Landscape			Average
	Rural	Suburban	Urban	
Free-ranging cats (no./landowner)[b]	3.62±0.37 (71)	2.56±0.36 (75)	1.94±0.30 (107)	2.59±0.20 (253)
Total no. of free-ranging cats	257	192	207	656*
Cat density (no./ha)[a,b]	1.19±0.22 (66)	1.37±0.24 (75)	3.43±0.53 (101)	2.18±0.25 (242)

Values are means±SE, with values in parentheses indicating the sample size. Superscript letters represent significant differences between landscapes: [a]Suburban and Urban, and [b]Rural and Urban.

* The number is a total, not an average.

Table 2
Predation rates for free-ranging cat owners by landscape

	Landscape			Average
	Rural	Suburban	Urban	
Predation rate 1 (no. birds killed/cat/week)	0.77±0.32 (67)	0.58±0.13 (72)	0.70±0.15 (106)	0.68±0.12 (245)
Predation rate 2 (no. birds killed/cat/week)	1.48±0.59 (35)	1.09±0.22 (38)	1.65±0.31 (45)	1.42±0.22 (118)
Total birds killed (no./cat) under predation 1	16.99	12.64	15.40	15.02
Total birds killed (no./cat) under predation 2	32.52	23.95	36.27	31.19
Total birds killed by cats during breeding season	1138	910	1632	3680*

Values are means±SE, with values in parentheses indicating the sample size.
* The number is a total, not an average.

predation rate over the breeding season indicated that the total number of birds killed across the three landscapes was 3680 (Table 2). Depredation rates were not correlated with the number of bird feeders located on each landowner's property ($r^2=0.015$; $P=0.10$; Fig. 3), and were not influenced by landscape type (landscape×number of bird feeders; $F=0.281$, df=2, 180; $P=0.756$). Similarly, depredation rates were not correlated with the density (no./ha) of bird feeders ($r^2<0.001$; $P=0.631$). Scaling the proportion of landowners that have outdoor cats to the landscape level (by incorporating assumptions about non-respondents) indicates that between 15 and 56% of landowners potentially have outdoor cats (Table 3). At the landscape level the total number of predatory outdoor cats ranged from ~800 to ~3100, which killed between ~16,000 and ~47,000 birds (Table 3).

Of the 118 landowners that reported their cats killing or injuring one or more birds a week, 75 (63.6%) were able to identify specific species of birds brought home by their cats. Twenty-three unique species of birds or groups of birds were identified by the landowners (Appendix), which is undoubtedly a conservative estimate (see Section 4). The species identified in greatest numbers were Sparrows and Blue Jays (*Cyanocitta cristata*), while the least common were Dark-eyed (Slate-colored var.) Junco (*Junco hyemalis*) and the Tufted Titmouse (*Baeolophus bicolor*; Appendix).

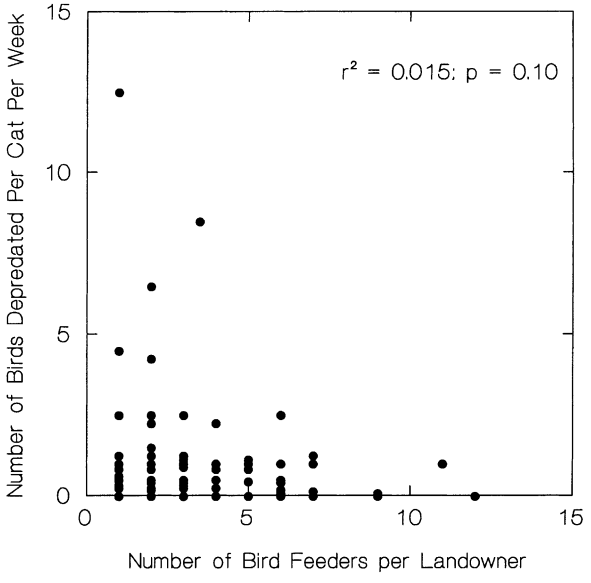

Fig. 3. Number of bird feeders per landowner versus number of birds depredated per week per cat.

In terms of landowner demography, the average age ($n=241$) of the respondents owning outdoor cats was 51.3±0.86 years compared with 50.4±0.51 years for respondents not owning outdoor cats ($n=690$), indicating no significant difference in age ($t=0.905$; df=929; $P=0.366$). Similarly, there were no differences in age among free-ranging cat owners across the three landscapes ($F=0.633$; df=2, 238; $P=0.532$; Table 4). In addition there was no relationship between respondent's age and the number of cats allowed access to the outdoors ($r^2<0.0005$; $P=0.925$). With regard to educational level there was a significant difference among free-ranging cat owners across the landscapes ($F=26.897$; df=2, 238; $P<0.000005$; Table 4), but not between free-ranging cat owners and non free-ranging cat owners ($F=1.650$; df=1, 926; $P=0.199$) nor was there an interaction between free-ranging cat ownership and landscape type ($F=0.083$; df=2, 926; $P=0.921$). The significant difference in educational level among owners of free-ranging cats was found to be between Rural and Suburban, and Suburban and Urban landscapes, but not between the Rural and Urban landscapes. Similarly, there was no relationship between respondent's educational level and the number of cats allowed access to the outdoors ($r^2<0.002$; $P=0.461$).

4. Discussion

Overall, our results indicate that free-ranging domestic cats depredated a minimum of 12.5% of the known breeding bird species (based on 23 of ~184), including two species of conservation concern (Eastern Bluebird and Ruby-throated Hummingbird). In the case of the Eastern Bluebird, the location of the three landscapes represents an area of Michigan where the species is rarest

Table 3
Landscape level results of the proportional range of landowners allowing cats outdoors, the number of possible cats that are predatory, the density per linear kilometer of predatory cats, and the total number of birds killed under differing estimation procedures

	Route classification			Total
	Rural	Suburban	Urban	
Potential range (%) of landowners having cats	21.7–56.9	19.8–58.3	11.3–56.1	15.3–56.8*
Total number of cats (no./ln km)				
(assumption 1 & predation 1)	465 (11.8)	379 (9.6)	619 (15.7)	1463 (12.4)
(assumption 1 & predation 2)	290 (7.3)	205 (5.2)	325 (8.3)	820 (6.9)
(assumption 2 & predation 1)	673 (17.1)	566 (14.4)	1032 (26.2)	2271 (19.2)
(assumption 2 & predation 2)	419 (10.6)	307 (7.8)	542 (13.7)	1267 (10.7)
(assumption 3 & predation 1)	881 (22.4)	753 (19.1)	1444 (36.6)	3078 (26.0)
(assumption 3 & predation 2)	549 (13.9)	408 (10.4)	758 (19.2)	1714 (14.5)
Total birds killed				
(assumption 1 & predation 1)	4664	3295	7981	15,939
(assumption 1 & predation 2)	5356	3340	9483	18,179
(assumption 2 & predation 1)	8190	5679	14,329	30,260
(assumption 2 & predation 2)	9573	5770	17,333	32,677
(assumption 3 & predation 1)	11,716	8064	20,678	40,458
(assumption 3 & predation 2)	13,791	8201	25,184	47,176

The three assumptions are that (1) non-respondents have 50% the number of cats as respondents, (2) non-respondents have the same number of cats as respondents, and (3) non-respondents have 150% the number of cats as respondents. Each assumption was estimated with two predation rates, the first of which (predation rate 1) includes all cats, even if they have predation rates of zero, whereas the second (predation rate 2) includes only cats that killed or injured one or more birds per week.

* The number is an average, not a total.

Table 4
Age and education of free-ranging cat owners by landscape

	Landscape			Average
	Rural	Suburban	Urban	
Respondent age	51.4±1.67 (68)	52.6±1.47 (72)	50.3±1.35 (101)	51.3±0.86 (241)
Respondent educational level[a,b,*]	3.09±0.17 (67)	4.22±0.17 (72)	3.58±0.14 (102)	3.64±0.10 (241)

Values are means±SE, with values in parentheses indicating the sample size. Superscript letters represent significant differences between landscapes: [a]Rural and Suburban, [b]Suburban and Urban.

* Educational level was a categorical response from 1 to 6 (see Section 2) with a higher number indicating more education.

and not always identified on bird atlas survey routes (Brewer et al., 1991). Ruby-throated Hummingbirds are the only species of hummingbirds that breed in Michigan and are not typically associated with cat predation given their small body size. Aside from the Eastern Bluebird and Ruby-throated Hummingbird, the species depredated in our study are concordant with other studies that most of the birds being taken by cats were ground or low brush feeders (Appendix) and typically associated with bird feeders and suburban landscapes (Mead, 1982; Dunn and Tessaglia, 1994; Carss, 1995; Barratt, 1997). Although the species group of Sparrows could not be broken down into species, it is very likely that the dominant species observed was the House Sparrow (*Passer domesitcus*). Sparrows were also the most commonly observed depredated species found in England and Australia (Churcher and Lawton, 1987; Barratt, 1997).

Although no extremely rare species or species of state or national concern were identified by landowners, that does not mean that cats were not preying upon them. In fact several factors would lend support to the fact that other species are likely being depredated. First, because only two-thirds of landowners were able to identify the birds brought home by their cats, it is very probable that other species were taken in the properties of the remaining one-third of landowners that acknowledged cat depredation. Second, the ability of respondents to identify birds correctly is unknown. People are most familiar with common and brightly colored species. Furthermore, most people tend to use general colloquial terms, such as Sparrows. Because the ability to discern specific Sparrow species can be very difficult (Sibley, 2000) and other sparrows such as the Chipping Sparrow (*Spizella passerina*) often occur in residential areas, it is very likely that the group "Sparrows" in the Appendix

consisted of at least two to three separate sparrow species. Thus, there is most certainly a detection bias among the respondents. Third, respondents only identified birds that were brought home by their cats. Thus, no measure of what species may have been consumed in the field were recorded. Fourth, cats often depredate nestlings (Churcher and Lawton, 1987; Dunn and Tessaglia, 1994), which can be very difficult to identify, especially if very young or recently hatched. Fifth, cats are opportunistic predators, suggesting that they are likely to prey upon any species that is present in their territory. Finally, our survey made no attempt to establish predation rates by feral cats, which also have an effect on birds and wildlife. As a result of these factors, the observed species and species groups being depredated are almost certainly an underestimate of the true number of species. Keeping these points in mind, our estimate of the number of species depredated should be considered quite conservative.

At the landscape scale the total number of outdoor cats and the number of birds killed over the breeding season is quite wide ranging, depending upon the assumptions regarding non-respondents. Under the assumption that only respondents had outdoor cats, there were only 656 cats reported (Table 1) and 3680 birds killed over the breeding season. However, as discussed later, it is unrealistic to assume that non-respondents had no outdoor cats. Using three different estimates of non-respondent cat numbers (Table 3), along with the two predation rates, yielded an estimate of between ~16,000 and ~47,000 birds killed during the breeding season across the three landscapes. Considering that the three landscape routes cover ~120 km (each BBS route is 39.4 km long), even the low estimate of birds killed represents nearly one bird killed per day per kilometer (16,000 birds/120 km/22 weeks/7 days = 0.87 birds killed per km per day). There were several notable differences observed across the three landscapes selected in this investigation. Specifically, landowners in the Urban landscape were significantly less likely to own free-ranging cats than were landowners in either the Rural or Suburban landscape. However, in terms of the number of free-ranging cats per landowner a steady decline existed from the Rural landscape to the Urban landscape (Table 1), even though only the Rural and Urban landscape were significantly different from one another. Landowners in the Urban landscape, however, had significantly higher densities of free-ranging cats (i.e. they had more cats per hectare) than did landowners in either the Rural or Suburban landscapes (Table 1). This increase in cat densities from Rural-to-Urban landscapes is similar to what was recently found by Haskell et al. (2001), where greater cat densities were associated with greater housing densities in Urban landscapes. Ultimately, while predation rates displayed no difference across the landscapes (Table 2), the greater number of landowners in the Urban landscape, coupled with greater cat densities, is one of the main reasons for a greater total predatory effect in the Urban landscape (Tables 1 and 3).

Because cat predation is often witnessed at bird feeders (Dunn and Tessaglia, 1994) and bird feeders can act to magnify bird densities we had predicted that there would be a positive correlation between bird feeder number or density and depredation rates. However, we found no support for this hypothesis. The lack of a relationship may be due to the fact that there are relatively few landowners that both allow their cats outdoors and feed birds or that place bird feeders in accessible places for cats. Regardless of the specific reason(s) why we found no support for our hypothesis, the lack of correlation is important in that it suggests that bird feeding is not exasperating predation rates by cats.

Similar to our first hypothesis, we found no relationships between age or education of the respondents and the number of free-ranging cats owned, indicating that our last two hypotheses should also be rejected. The fact that age and educational level show no relationship with the number of cats allowed access to the outdoors is somewhat troubling. Given the amount of attention being directed toward keeping domestic cats indoors by private interest groups, veterinarians, public school systems, and professional scientific organizations, we had predicted a positive effect of age and a negative effect of education on the number of cats allowed access to the outdoors. Instead we found no relationship, suggesting that either the information is not reaching the targeted audience, or that there is a general indifference to the role of cats as predators. One additional reason may be that people may know not to let cats outdoors, but not act accordingly (i.e. action does not follow knowledge). The only factor that showed any relationship with the number of free-ranging cats was household size (i.e. number of people living in a residence). Although not explicitly tested as an a priori hypothesis, we investigated the effect of household size simply as a possible demographic factor. The positive relationship between the number of people living at a residence and the number of cats is not totally surprising as larger residences are more likely to have children who own pets.

One caveat of our study is that landowners may have underestimated the number of cats they allow access to the outside. Such a result was found in a similar study of landowners in Wisconsin (Coleman and Temple, 1993). This underestimate may be due to incomplete knowledge or a desire to positively bias answers that the respondent felt were associated with negative connotations (Dillman, 1978). In addition, we found that a very common volunteered response among landowners that had no outdoor cats was that either their neighbors owned outdoor cats or that feral cats were present in the vicinity of their land. Given the frequency of these

responses relative to the number of landowners that reported owning outdoor cats suggests that at least some landowners under reported or chose not to report the number of outdoor cats they owned. Thus, just as our estimate of bird diversity is likely to be conservative, so is our estimate of free-ranging cat density. As a result, the actual number of free-ranging cats is in all likelihood larger than our estimate.

Besides the potential underestimate of outdoor cats, our study almost certainly underestimated the predation rate. This underestimate can be attributed to the following points. First, only 47% of outdoor cat owners indicated that their cat(s) brought home dead or injured birds. It is improbable that the remaining 53% of landowners' cats simply did not prey upon birds. Second, respondents based their cat's predation rate only on the birds actually brought home or visible to them, thus missing birds killed and/or consumed in the field. Third, just as with outdoor cat ownership, respondents may have underestimated the predation rate as they associate it with negative connotations. As a result, the actual predation rate and hence total number of birds killed are most certainly underestimates. Even in the face of such underestimates our study demonstrates the significant impact of outdoor cats on birds.

While we cannot specifically conclude that cats are depredating rare or threatened species in the three landscapes, there is a strong likelihood that they are impacting some species of concern. The fact that both Eastern Bluebirds and Ruby-throated Hummingbirds were listed indicates that some species of concern are being captured. Furthermore, given the opportunistic predatory nature of cats coupled with one third of respondents' inability to discern bird species suggests that our finding of 23 species or groups of birds being depredated by free-ranging cats is a conservative estimate. Similarly, by incorporating the potential for undercount of cats by respondents and the lack of any evaluation of feral cats, the number of cats per landowner is also likely to be a conservative estimate. Given these factors it is noteworthy to point out that a number of additional bird species that merit special concern occur along the three BBS routes and/or in the surrounding landscape. These species include three listed as special concern in Michigan [Western Meadowlark (*Sturnellla neglecta*), Hooded Warbler (*Wilsonia citrina*), and Prothonotary Warbler (*Protonotaria citrea*)], one species that is listed as threatened by the State of Michigan [Yellow-throated Warbler (*Dendroica dominica*)], three that the US Fish and Wildlife Service designated as being of management concern [Henslow's Sparrow (*Ammodramus henslowii*), Cerulean Warbler (*Dendroica cerulea*), Golden-winged Warbler (*Vermivora chrysoptera*)], and species that are at the edge of their range, such as the Dickcissel (*Spiza americana*) (Adams et al. 1988; Brewer et al. 1991). A number of other special concern, threatened, and endangered bird species occur within the vicinity of the study areas, but can be considered at lower potential for free-ranging cat depredation due to either their large body sizes or nesting locations [e.g. Red-shouldered Hawk (*Buteo lineatus*)].

Although our research highlights a number of important findings regarding outdoor cats, there remains many aspects that are in need of further research. First, there is a general paucity of research related to predation and behavior of feral cats, and how they compare with outdoor cats. Given the increase in feral cat colonies throughout the United States and their controversial management, an understanding of specific differences, if any, between outdoor cats and feral cats is urgently needed (Clarke and Pacin, 2002). Second, conservation biologists lack data on how specific levels of cat predation depress wildlife populations and if there are thresholds at which cat densities become a biologically significant source of mortality. Third, a similarly related unknown is how cat predation affects wildlife populations at different spatial scales. Fourth, no information exists on how declawing or neutering and spaying may affect cat behavior and predation rates. Fifth, aside from the present study, no information exists on the human dimensions of allowing cats outdoors and what factors underlie this human behavior. Lastly, conservation education efforts need to be assessed, specifically in regards to outdoor and feral cats, and this assessment needs to be repeated over time to investigate if peoples' attitudes and behaviors change. These six points represent specific next steps for conservation research on the domestic cat, but by no means are an exhaustive list.

In terms of management and conservation implications, our results, even taken conservatively, indicate that free-ranging cats are killing a large number and wide range of bird species. Our results also highlight the fact that there is still an urgent need to educate landowners and policy makers regarding the negative impacts of free-ranging cats. Furthermore, our study illustrates how important private landowners are in influencing the ecosystem around them. Only by incorporating their knowledge, decisions, and actions into ecological research can ecologists fully understand the complex nature of populations and ecosystems on the landscape.

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Appendix. Bird species reported to be depredated by outdoor cats and the number of different respondents identifying each species

Bird species	No. of observations
American Goldfinch (*Carduelis tristis*)	6
American Robin (*Turdus migratorius*)	12
Barn Swallow (*Hirundo rustica*)	4
Blackbird[a]	2
Black-capped Chickadee (*Poecile atricapilla*)	8
Blue Jay (*Cyanocitta cristata*)	14
Common Grackle (*Quiscalus quiscula*)	1
Eastern Bluebird (*Siala sialis*)[b]	6
European Starling (*Sturnus vulgaris*)	5
Finch[a]	3
House Finch (*Carpodacus mexicanus*)	1
House Sparrow (*Passer domesticus*)	1
Mourning Dove (*Zenaida macroura*)	6
Northern Cardinal (*Cardinalis cardinalis*)	2
Nuthatch[a]	2
Purple Finch (*Carpodacus purpureus*)	2
Ruby-throated Hummingbird (*Archilochus coubris*)[b]	3
Dark-eyed (Slate colored var.) Junco (*Junco hyemalis*)	1
Song Sparrow (*Melospiza melodia*)	1
Sparrow[a]	51
Swallow[a]	3
Tufted Titmouse (*Baeolophus bicolor*)	1
Wren[a]	2

[a] Two or more possible species could be interpreted, thus species level information is not presented.

[b] Denotes species of conservation concern.

References

Adams Jr., R.J., McPeek, G.A., Evers, D.C., 1988. Bird population changes in Michigan, 1966–1985. Jack-Pine Warbler 66, 71–86.

American Bird Conservancy. Cats Indoors! Available from http://www.abcbirds.org/cats/catsindoors.htm.

American Bird Conservancy Resolution on Free-roaming Cats. Available from http://www.abcbirds.org/cats/Resolution.pdf.

Barratt, D.G., 1997. Predation by house cats, *Felis catus* (L.), in Canberra, Australia. I. Prey composition and preference. Wildlife Research 24, 263–277.

Barratt, D.G., 1998. Predation by house cats, *Felis catus* (L.), in Canberra, Australia. II. Factors affecting the amount of prey caught and estimates of the impact on wildlife. Wildlife Research 25, 475–487.

Basili, G.D., Temple, S.A., 1999. Dickcissels and crop damage in Venezuela: Defining the problem with ecological models. Ecological Applications 9, 732–739.

Brewer, R., McPeek, G.A., Adams, R.J., 1991. The Atlas of Breeding Birds of Michigan. Michigan State University Press, East Lansing, MI.

Cam, E., Nichols, J.D., Sauer, J.R., Hines, J.E., Flather, C.H., 2000. Relative species richness and community completeness: birds and urbanization in the Mid-Atlantic states. Ecological Applications 10, 1196–1210.

Carss, D.N., 1995. Prey brought home by two domestic cats (*Felis catus*) in northern Scotland. Journal of Zoology, London 237, 678–686.

Churcher, P.B., Lawton, J.H., 1987. Predation by domestic cats in an English village. Journal of Zoology 212, 439–455.

Clarke, A.L., Pacin, T., 2002. Domestic cat "colonies" in natural areas: a growing exotic species threat. Natural Areas Journal 22, 154–159.

Coleman, J.S., Temple, S.A., 1993. Rural residents' free-ranging domestic cats: a survey. Wildlife Society Bulletin 21, 381–390.

Coman, B.J., Brunner, H., 1972. Food habits of the feral house cat in Victoria. Journal of Wildlife Management 36, 848–853.

Cooper Ornithological Society's resolution on Public Policies Regarding Feral and Free-ranging Cats. Available from http://cooper.org/cos/67thResolutions.htm#POP.

Crooks, K.R., Soulé, M.E., 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400, 563–566.

Dillman, D.A., 1978. Mail and Telephone Surveys: The Total Design Method. Wiley-Interscience, New York.

Dillman, D.A., 2000. Mail and Internet Surveys: The Tailored Design Method, second ed. John Wiley and Sons, Inc, New York, NY.

Donovan, T.M., Flather, C.H., 2002. Relationships among North American songbird trends, habitat fragmentation, and landscape occupancy. Ecological Applications 12, 364–374.

Dunn, E.H., Tessaglia, D.L., 1994. Predation of birds at feeders in winter. Journal of Field Ornithology 65, 8–16.

Eberhard, T., 1954. Food habits of Pennsylvania house cats. Journal of Wildlife Management 18, 284–286.

Emlen, J.T., 1974. An urban bird community in Tuscon, Arizona: derivation, structure, regulation. Condor 76, 184–197.

Fitzgerald, B.M., Turner, D.C., 2000. Hunting behaviour of domestic cats and their impact on prey populations. In: Turner, D.C., Bateson, P. (Eds.), The Domestic Cat: The Biology of its Behavior. second ed. Cambridge University Press, Cambridge, pp. 151–175.

Flather, C.H., Sauer, J.R., 1996. Using landscape ecology to test hypotheses about large-scale abundance patterns in migratory birds. Ecology 77, 28–35.

Gallagher, R., Carpenter, B., 1997. Human-dominated ecosystems. Science 277, 485.

George, W.G., 1974. Domestic cats as predators and factors in winter shortages of raptor prey. Wilson Bulletin 86, 384–396.

Haskell, D.G., Knupp, A.M., Schneider, M.C., 2001. Nest predator abundance and urbanization. In: Marzluff, J.M., Bowman, R.,

Donnelly, R. (Eds.), Avian Ecology and Conservation in an Urbanizing World. Kluwer Academic Publishers, Boston, pp. 243–258.
Hohtola, E., 1978. Differential changes in bird community structure with urbanisation: a study in Central Finland. Ornis Scandinavica 9, 94–100.
Hostetler, M., 1999. Scale, birds, and human decisions: a potential for integrative research in urban ecosystems. Landscape and Urban Planning 45, 15–19.
Lepczyk, C.A., Mertig, A.G., Liu, J., 2002. Landowner perceptions and activities related to birds across rural-to-urban landscapes. In: Chamberlain, D., Wilson, E. (Eds.), Avian Landscape Ecology. Proceedings of the 2002 Annual UK-IALE Conference, pp. 251–259.
Liu, J., 2001. Integrating ecology with human demography, behavior, and socioeconomics: needs and approaches. Ecological Modeling 140, 1–8.
Liu, J., Ouyang, Z., Tan, Z., Taylor, W., Groop, R., Tan, Y., Zhang, H., 1999. A framework for evaluating effects of human factors on wildlife habitat: the case of the giant pandas. Conservation Biology 13, 1360–1370.
Liu, J., Linderman, M., Ouyang, Z., An, L., Yang, J., Zhang, H., 2001. Ecological degradation in protected areas: the case of Wolong Nature Reserve for giant pandas. Science 292, 98–101.
Lubchenco, J., Olson, A.M., Brubaker, L.B., Carpenter, S.R., Holland, M.M., Hubbell, S.P., Levin, S.A., MacMahon, J.A., Matson, P.A., Melillo, J.M., Mooney, H.A., Peterson, C.H., Pulliam, H.R., Real, L.A., Regal, P.J., Risser, P.G., 1991. The Sustainable Biosphere Initiative: an ecological research agenda. Ecology 72, 371–412.
Mead, C.J., 1982. Ringed birds killed by cats. Mammal Review 12, 183–186.
National Audubon Society Resolution on Cats. Available from http://www.audubon.org/local/cn/98march/cats.html.
Patronek, G.J., 1998. Free-roaming and feral cats—their impact on wildlife and human beings. Journal of the American Veterinary Medical Association 212, 218–226.
Pearre Jr., S., Maass, R., 1998. Trends in the prey size-based trophic niches of feral and House Cats *Felis catus* L. Mammal Review 28, 125–139.
Rappole, J.H., McDonald, M.V., 1994. Cause and effect in population declines of migratory birds. Auk 111, 652–660.
Redman, C.L., 1999. Human dimensions of ecosystem studies. Ecosystems 2, 296–298.
Risbey, D.A., Calver, M.C., Short, J., Bradley, J.S., Wright, I.W., 2000. The impact of cat and foxes on small vertebrate fauna of Heirisson Prong, Western Australia. II. A field experiment. Wildlife Research 27, 223–235.
Robbins, C.S., Sauer, J.R., Greenberg, R.S., Droege, S., 1989. Population declines in North American birds that migrate to the neotropics. Proceedings of the National Academy of Sciences of the United States of America 86, 7658–7662.
Rutledge, D.T., Lepczyk, C.A., 2002. Landscape change: Patterns, effects, and implications for adaptive management of wildlife resources. In: Liu, J., Taylor, W.W. (Eds.), Integrating Landscape Ecology into Natural Resources Management. Cambridge University Press, Cambridge, pp. 312–333.
Sibley, D.A., 2000. The Sibley Guide to Birds. Knopf, New York.
Terborgh, J., 1989. Where Have All The Birds Gone? Princeton University Press, Princeton.
Turner, M.G., Wear, D.N., Flamm, R.O., 1996. Land ownership and land-cover change in the southern Appalachian highlands and the Olympic peninsula. Ecological Applications 6, 1150–1172.
Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 1997. Human domination of Earth's Ecosystems. Science 277, 494–499.
Vogt, K.A., Grove, M., Asbjornsen, H., Maxwell, K.B., Vogt, D.J., Sigurðardóttir, R., Larson, B.C., Schibli, L., Dove, M., 2002. Linking ecological and social scales for natural resource management. In: Liu, J., Taylor, W.W. (Eds.), Integrating Landscape Ecology into Natural Resources Management. Cambridge University Press, Cambridge, pp. 143–175.
Wilkinson, L., 1992. SYSTAT for Windows, version 5. SYSTAT, Evanston, IL.
Wisconsin Natural Resources Magazine. Available from http://www.wnrmag.com/stories/1996/dec96/cats.htm.
Zar, J.H., 1996. Biostatistical Analysis, third ed.. Prentice Hall, Upper Saddle River.