The Journal of Wildlife Management 75(5):1177–1185; 2011; DOI: 10.1002/jwmg.145

Research Article

Home Range, Habitat Use, and Activity Patterns of Free-Roaming Domestic Cats

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ABSTRACT We used radio-telemetry and collar-mounted activity sensors to compare home range size, habitat use, and activity patterns of owned and unowned free-roaming cats on the outskirts of Champaign-Urbana, Illinois, USA. Owned cats (3 M, 8 F) had smaller home ranges than unowned cats (6 M, 10 F), but we failed to detect consistent differences in home range size between the sexes or among seasons. Home ranges of unowned cats included more grassland and urban area than predicted based on availability in all seasons, and farmsteads were selected in fall and winter. Within home ranges, unowned cats shifted their use of habitats among seasons in ways that likely reflected prey availability, predation risk, and environmental stress, whereas habitat use within home ranges by owned cats did not differ from random. Unowned cats were more nocturnal and showed higher overall levels of activity than owned cats. Space use and behavioral differences between owned and unowned cats supported the hypothesis that the care a cat owner provides influences the impact a cat has on its environment, information that is important for making decisions on controlling cat populations.

KEY WORDS activity patterns, *Felis catus*, feral cats, free-roaming cats, habitat use, home range, radio-telemetry, survival.

Wildlife conservation and health issues associated with free-roaming domestic cats have received increasing attention (Patronek 1998, Slater 2004). For example, domestic cats (hereafter, cats) depredate a variety of wildlife, particularly small mammals and birds (e.g., Jones and Coman 1981, Liberg 1984, Mitchell and Beck 1992, Woods et al. 2003). Negative effects of introduced cats on wildlife populations, including causing extinctions, have been documented on oceanic islands (Nogales et al. 2004). Population-level impacts of introduced cats on prey species have also been reported in Australia (reviewed by Dickman 2009). Population and community-level effects of free-roaming cats on prey species have only recently been evaluated (Kays and DeWan 2004, Baker et al. 2005, Beckerman et al. 2007, Sims et al. 2008).

Free-roaming cats can also transmit a variety of diseases to wildlife (Aramini et al. 1998, Kauhala and Holmala 2006), livestock (Mateus-Pinilla et al. 2002), pets (Meireles et al. 2004, Nutter et al. 2004), and humans (Hill and Dubey 2002). Some diseases, such as rabies and feline immunodeficiency virus (FIV), are transmitted through direct contact, whereas others, such as toxoplasmosis (*Toxoplasma gondii*), can be spread through shed oocysts in feces (Dubey and Frenkel 1973). *T. gondii* is a protozoan parasite contracted through ingesting oocytes present in the environment or from eating infected meat or prey. Cats are the only species known to shed oocysts of *T. gondii* in their feces, and this disease can pose serious health risks to wildlife (Conrad et al. 2005), livestock (Dubey et al. 1995), and humans (Hill and Dubey 2002).

Controversies about management of cats are social and political as much as ecological (Slater 2004, Lord 2008). An unresolved question is whether owned free-roaming cats (i.e., pets that are allowed to roam freely) have similar ecological impacts as unowned free-roaming cats (i.e., feral cats; Kays and DeWan 2004). Although several studies have examined home range size of cats (e.g., Liberg 1980, Warner 1985, Hall et al. 2000, Molsher et al. 2005), few have directly compared space use by owned and unowned cats simultaneously (e.g., Schmidt et al. 2007). If space use of owned cats is more limited in area and restricted to the vicinity of their owners' homes (Kays and DeWan 2004, Schmidt et al. 2007), they could have less impact than unowned cats on wildlife populations in natural areas such as nature preserves, parks, and habitat restoration sites. Habitats where cats are most active can also indicate where risk of exposure to *Toxoplasma* oocytes is greatest, and cats that range over greater areas may be more implicated in dispersal of oocytes. Activity patterns of owned and unowned cats could also indicate if different prey species (e.g., nocturnal versus diurnal) are at risk of depredation. Activity patterns also indicate the likelihood of direct interactions between owned and

Received: 22 March 2010; Accepted: 16 November 2010;
Published: 21 April 2011

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unowned cats that could result in conflict or direct transmission of disease. Additionally, Schmidt et al. (2007) reported that ownership status was positively related to survival of free-roaming cats. Survival rates of free-roaming cats reflect risk of exposure to a variety of mortality factors, including predation, vehicle collisions, nuisance animal control, and disease, as well as the general health of the animal and its susceptibility to environmental stresses.

Our goal was to compare spatial ecology, behavior, and survival of owned and unowned free-roaming cats. We predicted that: 1) owned cats would have smaller home ranges than unowned cats; 2) home ranges of owned cats would be closely associated with the homes of their owners and habitat use of owned cats would reflect habitat availability near their owners' homes, whereas unowned cats would show a greater degree of habitat selection reflecting their foraging and denning needs; 3) activity patterns of owned cats would differ from the typical nocturnal pattern shown by other wild, native cats, whereas activity patterns of unowned cats would more closely correspond to native cat activity; and 4) owned cats would have greater short-term survival than unowned cats.

STUDY AREA

We conducted a radio-telemetry study of free-roaming cats in southeastern Champaign-Urbana, Illinois, USA (40°04′ N, 88°13′ S) during January 2007–May 2008. Champaign-Urbana had a human population of 112,611 and an area of 114 km^2 and was located within one of the most intense agricultural regions of the United States. Row crops dominated surrounding land cover, with annual crop harvest occurring from September to November. Vegetation cover previously provided by corn and soybeans was removed during harvest. Average annual precipitation was 104.3 cm and average annual temperature was 10.8° C (Illinois State Water Survey 2009). The study area was comprised of rural farmland, the University of Illinois South Farms agricultural research complex, medium-use public recreation areas (including restored prairie habitat), and urban residential and industrial areas.

METHODS

We defined our 2,544-ha study area as the area needed to encompass the home ranges of all radio-marked cats in the study (Fig. 1). We digitized land use types in the study area from 1999 to 2000 digital ortho quadrangles (1:24,000) using ArcMap 9.2 (Environmental Systems Research Institute, Redlands, CA) and classified land use types into 6 categories: grassland, forest, low-density urban, high-density urban, farmsteads, and row crops (Table 1). We updated and verified accuracy of our land use maps by driving all roads and modifying any observable boundaries or land use designations that did not correspond to our photo-based interpretation.

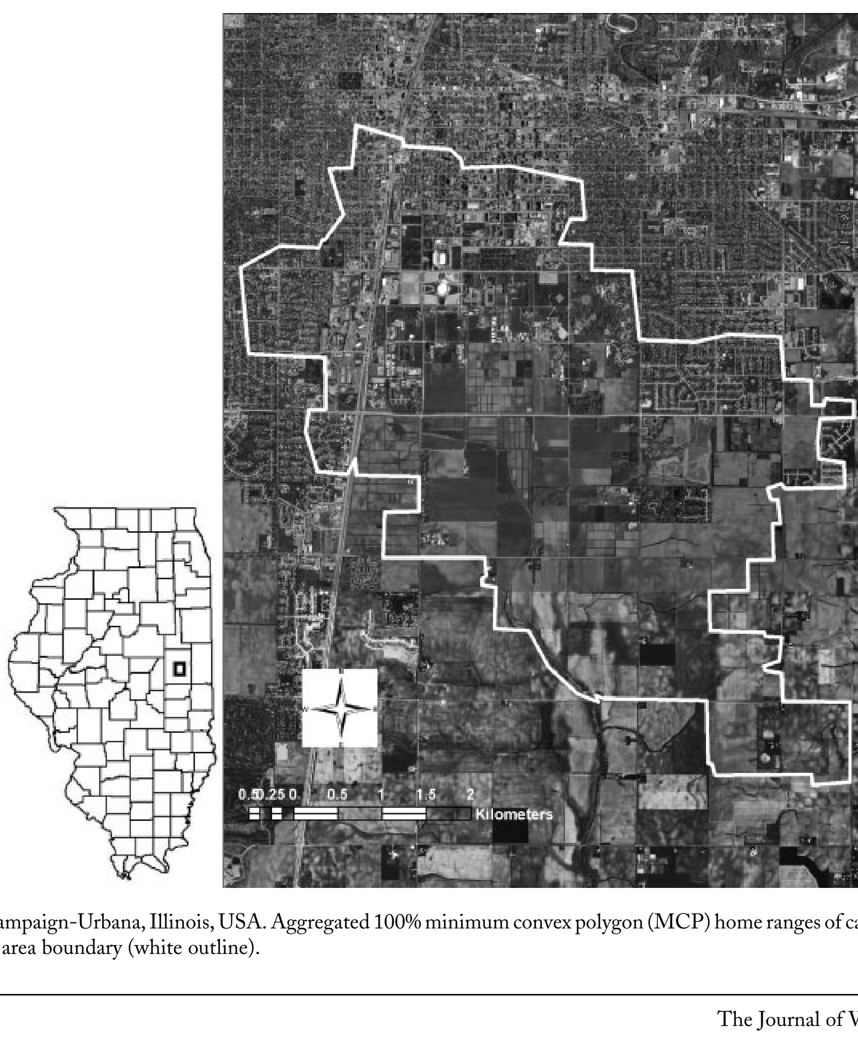

Figure 1. Study area in Champaign-Urbana, Illinois, USA. Aggregated 100% minimum convex polygon (MCP) home ranges of cats radiotracked during 2007–2008 determined the study area boundary (white outline).

Table 1. Land use classes delineated from digital orthoquadrangles (1999–2000) for the domestic cat study area in Champaign-Urbana, Illinois, USA.

Habitat classification	% Study area
Grassland (parks, cemeteries, pastures, wheat)	19.4
Forest (orchards, wooded corridors, woodlots)	2.8
Low-density urban (urban residential)	7.6
High-density urban (industrial, roads, parking lots)	31.0
Farmsteads (livestock buildings, farm houses)	3.7
Row crops (corn, soybeans)	35.5

Classification of Cats and Radio-telemetry

We distinguished 2 groups of cats: 1) owned cats that were fed and cared for by humans, typically living in human dwellings during part of the diurnal cycle, and 2) unowned cats that were not observed being fed or cared for by humans. We contacted cat owners in the study area beginning in January 2007 and asked them to participate in the study. After acquiring written permission from their owners, we fitted cats with a 2-stage pulsing transmitter (Sparrow Systems, Fisher, IL) attached to an adjustable break-away collar. Radiocollars and transmitters were <3% of the body mass of the cats on which they were fitted. We did not solicit a priori information on how long cats were left outdoors on any given day, but we confirmed that their owners left them outside unattended. We obtained all telemetry locations we used for analyses of home range size and habitat use while owned cats were outside their owner's dwellings.

We obtained our sample of unowned cats by overnight live trapping on the University of Illinois South Farms on the southern edge of Champaign-Urbana. Trapping occurred 4 nights per week from May to November 2007, then, opportunistically through January 2008, using Tomahawk live traps (Model 108, 81.3 cm × 25.4 cm × 30.5 cm; Tomahawk Live Trap Company, Tomahawk, WI) baited with sardines. We sedated all captured cats with an intramuscular injection of 0.08 mg/kg of medetomidine hydrochloride (Domitor; Orion Corporation, Espoo, Finland; Granholm et al. 2006, Plumb 2008) or 1–2.2 mg/kg xylazine hydrochloride (Anased; Akorn Inc., Decatur, IL; Plumb 2008). We reversed the effects of sedation with an intramuscular administration of the alpha$_2$-adrenergic antagonist atipamezole (Antisedan; Orion Corporation) at 0.2 mg/kg (Nielson 1999, Granholm et al. 2006). In some cases, when unowned cats appeared especially aggressive, slightly larger doses of up to 0.10 mg/kg sedative were required. We classified cats as unowned if they did not have a collar, rabies tags, or microchip, and by their general condition and aggressive behavior; no cats so classified were ever located in human dwellings or behaved as if associated with dwellings. We determined the sex of captured cats, and examined them for intact testes (males) or neuter scars. We then fitted sedated cats with a radiocollar and released them at the capture site. All animal handling techniques were approved by the University of Illinois Institutional Animal Care and Use Committee (protocol no. 06193).

We located radiocollared cats via triangulation (White and Garrott 1990) using a vehicle-mounted, 3-element Yagi directional antenna and compass or via ground-based homing using a hand-held, 3-element Yagi antenna. We obtained 3–5 bearings within 10 min for each location to reduce telemetry error. We obtained both diurnal (2 times/week) and nocturnal (2 times/week) locations from January 2007 to May 2008. We used data from the activity transmitters (described below) to maximize tracking efforts during periods when cats were most likely to be active, and we attempted to locate every radiocollared cat during each tracking session. We entered data into a Geographic Information System in ArcMap 9.2 for analyses of home ranges and habitat use.

Home Range Analyses

We used bootstrap functionality (100 replicates per individual) in the Home Range Extension (Carr and Rodgers 1998) for ArcView 3.3 (Environmental Systems Research Institute) to estimate the number of locations needed reliably portray 100% minimum convex polygons (MCP). We then used Home Range Tools (HRT) in ArcMap 9.2 (Rodgers et al. 2007) to calculate the 95% MCP for each cat for which we had sufficient locations. We also used HRT to calculate home range areas (95% probability area) using a fixed kernal estimator (KDE) for comparison to previous studies, as both MCP and KDE are commonly reported. We calculated total (i.e., annual) home range area for each cat based on all locations and home ranges for 3 seasons: summer (22 Jun–23 Sep 2007), fall (24 Sep–22 Dec 2007), and winter (23 Dec 2007–20 Mar 2008). Data collected in spring (22 Mar–21 Jun 2008) were too limited for estimating home ranges. We used a 2-way analysis of variance (ANOVA) to determine effects of sex, ownership status, and their interaction on annual home range size (SAS Version 9.2; SAS Institute, Inc., Cary, NC). We report seasonal home range size, but sample sizes in some sex and ownership categories were too small for statistical analyses. We used a Shapiro–Wilks test to evaluate normal distribution of the residuals, then log-transformed estimates of home range size before running ANOVAs to meet assumptions of normality.

Habitat Use

We used compositional analysis (Aebischer et al. 1993) to examine habitat use of unowned cats at 2 spatial scales: use of land cover categories within the home range (95% MCP) compared to that available in the study area (second-order selection, Johnson 1980) and use of land cover categories within buffered location points compared to available land cover within the home range (third-order selection, Johnson 1980). We examined only third-order habitat selection for owned cats because their owners determined general locations of home ranges. The South Farms, where trapping for unowned cats occurred, was on the University of Illinois campus and portions bordered or were classified as urban areas. The sample of owned cats was distributed in both southern Champaign and rural areas near the South Farms. Cats in both categories potentially had access to the full variety of habitats we examined.

We used the maximum likelihood estimation (MLE) algorithm in Locate III (Nams 2006) to calculate mean telemetry error for points with >2 bearings. Mean telemetry error (0.5 ha) was equivalent to a circular buffer with a 40-m radius around each location; we used the amount of each land cover type within this buffer as our measure of habitat use in analyses of third-order selection. We used the Hawth's Tools Extension (Beyer 2004) in ArcMap 9.2 to calculate habitat used and available.

Activity Patterns

To quantify cat activity patterns, 23 of the radiotransmitters had an SQ-SEN-200 series tilt and vibration sensor (SignalQuest, Inc., Lebanon, NH) to function as an omnidirectional movement detector. These sensors recorded the amount and duration of activity as positional shifts (1 or 0), measured 256 times per second and recorded as totals per 3-min blocks. Transmitters were programmed to transmit the activity data over an amplitude-modulated (AM) signal at a specified time each day. We then loaded these data onto a computer and converted them to a useable format using specialized software (Sparrow Systems).

To establish activity level thresholds for our analyses, we collected 29.2 hr of observational data from 3 owned cats and 1 unowned cat fitted with activity sensors. An observer classified the behavior of the cat as 0, 1, or 2 for each 3-min block of time. We classified denning or sleeping behaviors as 0, low-activity behaviors such as walking, grooming, and feeding as 1, and high-activity behaviors such as playing, capturing prey, and running as 2. Observers classified 972 intervals as denning or sleeping, 261 intervals as low activity, and 66 intervals as high activity. We used the numbers of shifts per 3-min interval recorded by the activity sensors collected for the same cats during the same time periods to set 3 thresholds for the activity sensor data: we classified <2,500 shifts per 3-min interval as sleeping or denning, 2,501–10,499 shifts per 3-min interval as low activity, and >10,500 shifts per 3-min interval as high activity.

Due to the large size of the data files obtained from activity transmitters, we loaded raw data into a database at the National Center for Supercomputing Applications at the University of Illinois. We used a mixed model approach with repeated measures (PROC MIXED; SAS version 9.2) to determine the effects of sex, season, and ownership status on number of intervals classified as denning or sleeping, low activity, and high activity. We tested distribution of the residuals for normality using a Shapiro–Wilks test, then log-transformed the data on activity to meet assumptions of normality before running the mixed model ANOVAs. We used least squares means to compare each level of activity across seasons.

Survival

We estimated survival time in days for all adult cats we radiotracked. We recorded missing animals as censored observations. We estimated the cumulative probability of survival times for all cats using the LIFETEST procedure (SAS version 9.2) and tested the difference in mean survival times of owned and unowned cats from January 2007 to May 2008 with a log-rank test.

RESULTS

Home Range Analyses

We radiotracked 24 unowned cats (11 M, 13 F) and 18 owned cats (8 M, 10 F), for a total of 2,237 locations. Bootstrap analysis determined that estimates of home range size reached an asymptote after 27 locations for unowned cats and 10 locations for owned cats. Of our radiotracked cats, 27 met those criteria (mean no. of locations = 82.9 ± 10.0 [SE], range 27–231); 16 were unowned (6 M, 10 F) and 11 were owned (3 M, 8 F). All owned cats were neutered. Two of the unowned cats were also neutered (1 M, 1 F). Analyses of home ranges based on 95% MCP and 95% KDE yielded similar results (i.e., the same effects were statistically significant), so we report statistical analyses only for 95% MCP home ranges.

Annual home range size (95% MCP) differed by ownership status ($F_{1,18} = 6.63$, $P = 0.02$). Owned cats had smaller home ranges than unowned cats (Table 2). Effects of sex ($F_{1,18} = 2.57$, $P = 0.13$) and the interaction between sex and ownership status ($F_{1,18} = 2.53$, $P = 0.13$) were not significant. Three of the 6 male unowned cats had home ranges considerably larger (86.7 ha, 284.4 ha, and 547.1 ha) than all but one unowned female cat (241.1 ha; home ranges of the other 9 unowned females ranged from 14.1 ha to 64.8 ha). However, the other 3 unowned males, including the neutered individual, had annual home ranges <10 ha. When we parsed data by season, differences in home range size (95% MCP) among seasons were not apparent (Table 3). Other patterns, such as owned cats having smaller home ranges than unowned cats, and 3 of the 6 male unowned cats having larger home ranges than female unowned cats, remained. Annual home ranges of unowned cats were larger than seasonal home ranges because individuals shifted space use depending on season, a pattern we did not observe for owned cats.

Table 2. Home range estimates (ha; 95% minimum convex polygon [MCP] and 95% kernal density estimator [KDE]) for owned and unowned free-ranging cats in Champaign-Urbana, Illinois, USA, 2007–2008. Data are means, standard error (SE), and sample size (*n*).

	95% MCP			95% KDE		
Ownership status and sex	**Mean**	**SE**	***n***	**Mean**	**SE**	***n***
Owned						
Male	1.83	1.42	3	5.16	4.89	3
Female	1.92	1.09	8	1.95	0.87	8
Unowned						
Male	157.01	89.44	6	103.17	73.52	6
Female	56.59	21.34	10	57.92	33.61	10

Table 3. Home range estimates (ha; 95% minimum convex polygon [MCP]) for owned and unowned free-ranging domestic cats in Champaign-Urbana, Illinois, USA across seasons. Summer: 22 June 2007–23 September 2007, Fall: 24 September 2007–22 December 2007, Winter: 23 December 2007–20 March 2008. Data are means, standard error (SE), and sample size (n).

	Summer			Fall			Winter		
Ownership status and sex	**Mean**	**SE**	***n***	**Mean**	**SE**	***n***	**Mean**	**SE**	***n***
Owned									
Male	0.04	NA	1	0.06	NA	1	0.09	NA	1
Female	0.6	0.3	5	2.1	1.4	6	0.3	0.1	4
Unowned									
Male	87.7	54.6	6	73.8	38.6	6	76.4	64.6	4
Female	32.5	7.8	9	27.7	9.1	10	31.9	19.6	10

Habitat Use

Land cover within 95% MCP home ranges differed from that of the study area for unowned cats in summer ($\chi^2_5 = 17.8$, $P < 0.01$), fall ($\chi^2_5 = 20.4$, $P < 0.01$), and winter ($\chi^2_5 = 34.9$, $P < 0.001$). Row crops were included in home ranges less than expected throughout the year, forest was included less than expected in summer and fall, and residential areas were included less than expected in fall and winter (Fig. 2). Grasslands were included more than expected based on availability in all seasons, urban areas were included more than expected in summer and winter (a similar trend noted in fall was not quite significant), and farms were included more than expected in fall and winter (Fig. 2). Within home ranges, habitat use by unowned cats also differed from random in summer ($\chi^2_5 = 12.3$, $P = 0.04$), fall ($\chi^2_5 = 15.3$, $P = 0.01$), and winter ($\chi^2_5 = 27.6$, $P < 0.001$). Unowned cats shifted their use of habitats among seasons. Row crops were used less than expected in fall and winter but not during summer. Urban areas were used more than expected in winter but not in summer or fall. Forests were used less than expected in summer but more than expected in fall and winter (Fig. 2). In contrast, habitat use within home ranges by owned cats did not differ from random ($\chi^2_5 = 7.5$, $P = 0.20$).

Activity Patterns

Activity sensors recorded >15,060 hr of data from 23 cats (15 unowned, 8 owned). Data from 3 owned cats were not collected consistently (e.g., cats were indoors at times the sensors were programmed to transmit their data and signal transmission was blocked), therefore, we based analyses on 15 unowned (9 F, 6 M) and 5 owned (3 F, 2 M) cats. On average, owned cats spent 80% of the time denning or sleeping, 17% in low activity, and 3% in high activity (Fig. 3). Unowned cats spent 62% of the time denning or sleeping, 23% in low activity, and 14% in high activity (Fig. 3). Time spent denning or sleeping was lower for unowned cats than owned cats ($F_{1,16} = 12.1$, $P < 0.01$). Time spent in low activity did not differ between owned and unowned cats ($F_{1,16} = 4.2$, $P = 0.06$), but unowned cats spent more time than owned cats in high activity ($F_{1,16} = 16.8$, $P < 0.01$). Males and females did not differ in mean time spent denning or sleeping ($F_{1,16} = 0.4$, $P = 0.5$), in low activity ($F_{1,16} = 2.4$, $P = 0.14$), or in high activity ($F_{1,16} = 2.0$, $P = 0.17$). Time spent denning or sleeping differed across seasons ($F_{3,43} = 10.42$, $P < 0.001$), as did time spent in low activity ($F_{3,43} = 17.5$, $P < 0.001$) and in high activity ($F_{3,43} = 8.31$, $P < 0.001$). Denning or sleeping was done less in fall than in other seasons, and time spent in

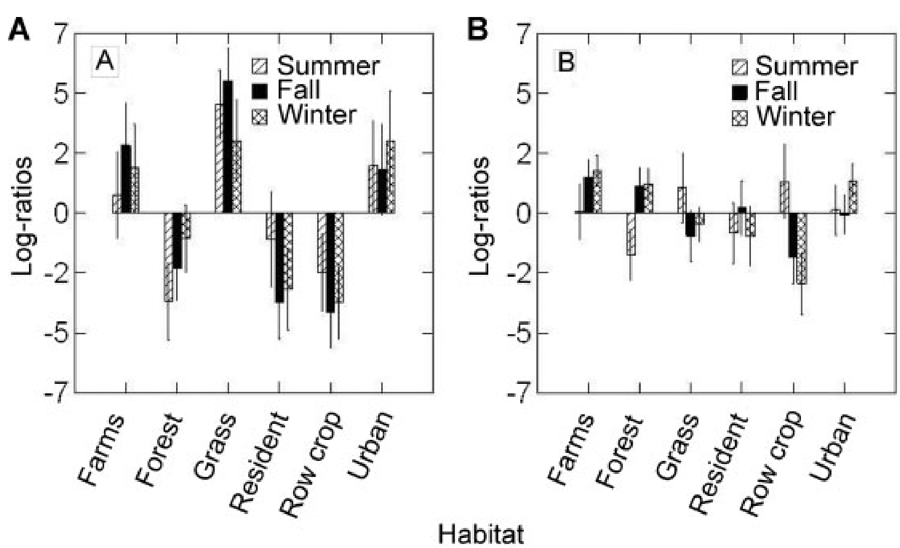

Figure 2. Seasonal habitat use of unowned free-roaming cats in Champaign-Urbana, Illinois, USA, 2007–2008. Log-ratio means from the compositional analysis (selection for [+], selection against [−]) are shown for (A) land cover in the 95% minimum convex polygon (MCP) home range compared to land cover in the study area (second-order selection, Johnson 1980), and (B) land cover in 40-m radius buffers around telemetry locations compared to land cover in the 95% MCP home range (third-order selection). Error bars represent ± 1 standard error.

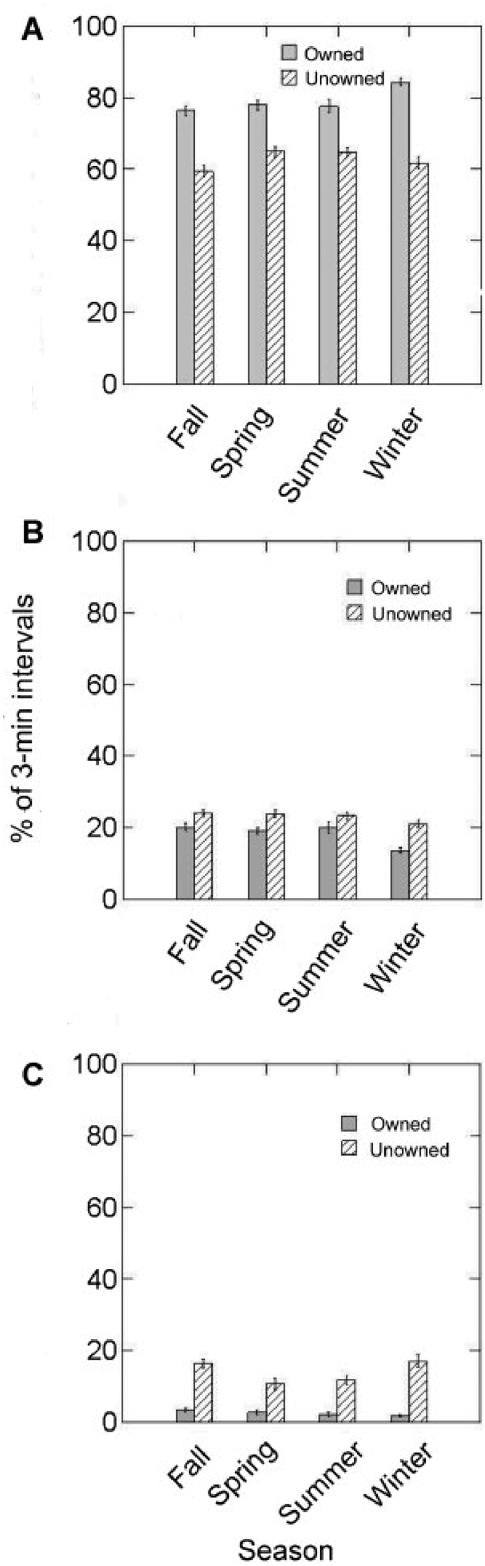

Figure 3. Mean percent time (% of total 3-min intervals) spent (A) denning or sleeping, (B) in low-activity behaviors, and (C) in high-activity behaviors by owned and unowned free-roaming cats in Champaign-Urbana, Illinois, USA, 2007–2008, by season. Error bars represent ± 1 standard error.

high activity was greater in fall than in other seasons (pairwise least square means, all $P < 0.05$). Time spent in low activity was less in winter than in the other 3 seasons (pairwise least square means, all $P < 0.05$).

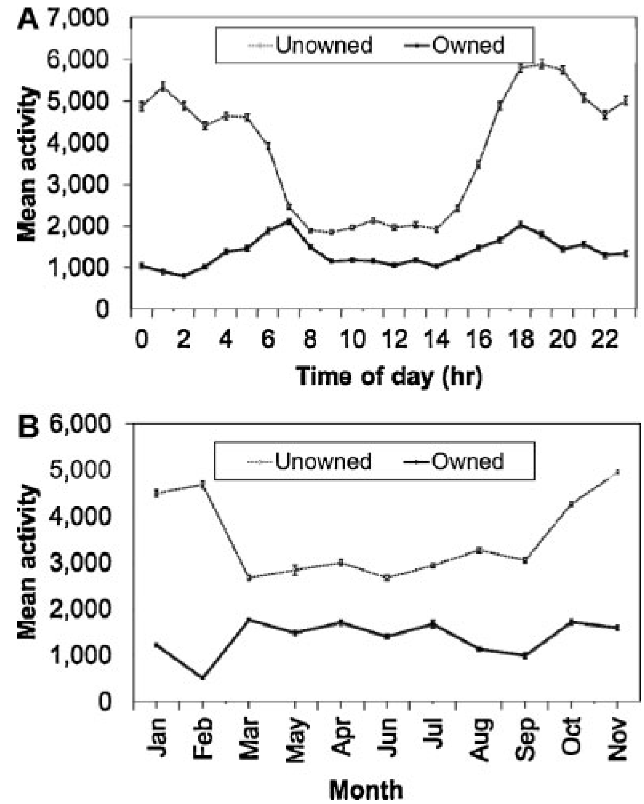

Figure 4. (A) Diel and (B) annual patterns patterns of activity by free-roaming owned ($n = 8$) and unowned ($n = 15$) cats in Champaign-Urbana, Illinois, USA, 2007–2008. Activity is represented as mean number ± standard error of positional shifts recorded by activity sensors (256 per second possible) per 3-min interval (i.e., 20 intervals per hour) per cat, by hour of the day for diel patterns and by month for annual patterns.

We plotted diel and seasonal activity patterns of owned and unowned cats. Owned cats were most active between 0430–0800 hr and 1600–2100 hr (Fig. 4A). Unowned cats showed more activity throughout the 24-hr period and had both higher levels and more prolonged periods of nocturnal activity, with their greatest activity between 1700 and 0600 hours (Fig. 4A). Owned cats showed lower levels of activity than unowned cats throughout the year, with slightly depressed activity in January–February and August–September (Fig. 4B). In contrast, unowned cats showed greatest activities in October–February.

Survival

We calculated survival estimates from data on 39 adult cats (27 unowned, 12 owned) monitored over a span of 16 months. One of the 12 (8.3%) owned cats was killed by a car during the study period. Six of the 27 (22.2%) unowned cats in the sample died during the study period: 2 were killed by coyotes (*Canis latrans*), we found 1 in a dumpster with no external indications of cause of death, and 3 disappeared but we considered them likely mortalities. We tracked 2 of the latter for <2 weeks, but they had been easy to locate and occupied small home ranges before their disappearance. The disappearances occurred during summer, when all transmitters appeared to be working, and we searched the surrounding area extensively for the next several weeks without relocating them. The third was a neutered male that occupied a small home range around a farm building for over a year and had been regularly observed by the farm workers, then disappeared the day an unneutered male we were tracking entered that building. We censored 5 other unowned cats (4 M, 1 F) that disappeared during our study. Cumulative survival analysis indicated that 50% of unowned cats would be expected to die within 392 days; we could not calculate a mean survival estimate for owned cats during the study period because so few mortalities occurred. However, 92% of owned cats remained alive after 596 days of observation. The difference between survival distributions of owned and unowned cats was nearly significant (log-rank $\chi^2 = 2.7$, $P = 0.051$), but sample sizes of mortalities were small.

DISCUSSION

We found that owned and unowned free-roaming cats differed in home range size, habitat use, and activity patterns. Unowned cats had larger home ranges than owned cats. Schmidt et al. (2007) also reported that home range size decreased with ownership in the only other radiotracking study to date that simultaneously monitored owned and unowned free-roaming cats. Supplemental feeding generally decreases home range size of mammals (Boutin 1990, Koganezawa and Imaki 1999). Unowned cats must search to acquire food, whereas owned cats are fed, suggesting supplemental feeding decreases home range size in domestic cats as well (Tennent and Downs 2008). Some studies reported high population densities of unowned cats in places where they receive supplemental feeding, especially urban and suburban areas (Turner and Bateson 2000). However, Calhoon and Haspel (1989) reported that supplemental feeding did not affect population density of cats in their study area and that the distribution of cats was affected by the availability of shelter rather than food. Thus, factors other than supplemental feeding may also influence the spatial distribution and home range sizes of cats.

The neutered male in our study had the smallest 95% MCP home range (5.8 ha) among the unowned male cats, but the neutered female had a home range size (36.1 ha) about average for our sample of female unowned cats; both had home ranges larger than any of the owned cats. Gutilla and Stapp (2010) also report that neutered unowned cats did not have significantly smaller ranges than unneutered cats. Therefore, we do not consider neutered or unneutered status to be the primary determinant of differences in home range size between owned and unowned free-roaming cats in our study. Regardless of why home ranges of unowned cats were larger, home range size for some individuals implies that unowned cats have more widespread impacts on potential prey species and greater likelihood of spreading diseases like toxoplasmosis.

Home ranges of male cats were not significantly larger than home ranges of females. Previous research on free-roaming cats has generally reported males to have larger home ranges (e.g., Liberg 1980, Warner 1985, Langham and Porter 1991, reviewed in Liberg et al. 2000), although there have been exceptions (Hall et al. 2000, Molsher et al. 2005). Females often have home ranges overlapping those of related females, whereas males are more solitary, disperse more often, and are often aggressive in defending their territory (Liberg 1980). These behaviors relate to differences in reproductive strategies between the sexes. The lack of a difference in home range size between male and female owned cats might be explained by the neutered status of these individuals; reproductive strategies that affect space use were likely not in play. Five of 6 male and 9 of 10 female unowned cats in our study appeared unneutered. Unexplainably, 2 of these unneutered males and the neutered male had home ranges <10% of the mean home range size of the other 3 unneutered, unowned males. Observed home range differences may reflect age or social rank of individual male cats rather than neuter status. Liberg et al. (2000) noted that subordinate males used smaller home ranges than dominant males. We consistently located the neutered male in a small home range centered on a barn for 3 months, but it disappeared the day after we located one of the unneutered males with a large home range in the same barn. The other 2 unneutered, unowned males with small home ranges also had ranges centered on farm buildings, whereas the wider-ranging males used a variety of habitats including grasslands, crop fields, and forest remnants and were not associated with buildings. Thus, both social rank and the shelter or prey (unowned cats were not intentionally fed) provided by anthropogenic structures likely contributed to the observed dichotomy in home range size of unowned males.

We did not observe seasonal differences in home range size in any sex or ownership category, but our sample sizes in some categories were small. Langham and Porter (1991) reported that home range size of female cats in New Zealand farmland did not vary consistently across seasons but that home ranges of adult males were larger in summer and winter. In contrast, Hall et al. (2000) did not find any effect of sex or season on home range size of feral cats in California. Seasonal variation in home range size likely reflects changes in prey availability, habitat use, environmental (e.g., thermal) stress, and mating strategies. Seasonal variation in home ranges of unowned, unneutered free-roaming cats should be investigated further.

Unowned cats located their home ranges in areas with more urban and grassland area in our analysis of second-order habitat selection. Within their home ranges, unowned cats shifted their habitat use across seasons in a manner that reflected availability of cover. In particular, unowned cats used row-crop fields less than expected after harvest in fall and winter and were associated more with farmsteads, forests, and urban areas at that time, which likely provided greater protection from inclement weather and thermal stress. Coyotes use farmsteads, residential areas, and forests less than other cover types during winter in our area, which has been related to greater use of these habitats by red foxes (*Vulpes vulpes*; Gosselink et al. 2003). The role of predator avoidance in habitat selection by cats is unknown. In summer, unowned cats were most often located in grasslands and row-crops. Small mammals such as voles (*Microtus*), some species of mice (*Mus musculus*, *Peromyscus maniculatus*), and ground-nesting songbirds are typically common in grasslands (Getz 1985, Kleen et al. 2004). Row-crop fields in summer may also provide shaded resting sites, with freedom of movement due to sparse non-crop vegetation at ground level and relative freedom from insect pests, in contrast to forests at this time of year (E. J. Heske, Illinois Natural History Survey, personal observation). We failed to detect habitat selection for owned cats within their home ranges, which were centered on the homes of their owners (Kays and DeWan 2004). Thus, differences in space use by owned and unowned cats will reduce the potential for direct contact, but disease transmission is still possible due to some spatial and temporal overlap in habitat use.

Unowned cats were nocturnal in their diel activity (see also Haspel and Calhoon 1993), possibly reflecting activity patterns of their primary prey. Fitzgerald (1979) and Warner (1985) found that small mammals comprised most of cat diets, and most small mammal activity is nocturnal (Vickery and Bider 1981, Madison 1985, Getz 2009). Unowned cats may also be more active at night to avoid contact with humans. Diel activity of owned cats was likely modified by the activity of their owners. For example, activity of owned cats was slightly greater in early morning and evening, which might reflect times when owners are rising or returning from work. Levels of activity of owned cats were more consistent throughout the day compared to the periodicity shown by unowned cats, and nocturnal activity was reduced. We surmise that supplemental feeding and the availability of reliable shelter lessens the need for owned cats to correspond activity with prey activity patterns.

Differences in diel activity patterns between owned and unowned cats reduce the likelihood of direct interaction, but direct interactions can nonetheless occur over short time intervals. We observed an unowned cat (known to harass one of the owned cats) wait by the deck of a home until the owned cat would come out, at which time it would quickly take aggressive actions toward the owned cat (i.e., hissing, clawing). Thus, owners that allow their pets to roam freely at night, even for a short time, could be exposing them to greater risk of conflict with, and disease transmission from, unowned cats. Although nocturnal activity of unowned cats suggests that their greatest impact will be on nocturnal prey species, their activity in early morning and evening occurs at times when many diurnal prey species such as songbirds are active and available. In addition, transfer of *Toxoplasma* oocytes between owned and unowned cats, or between cats and other wildlife, does not depend on time of activity.

Unowned cats were more active than owned cats throughout the year, reflecting their greater foraging and reproductive activities. Unowned cats also showed an increased amount of activity in the colder months (i.e., Nov–Feb), probably due to higher energetic demands or more time needed to capture prey at those times. Owned cats showed reduced activity during the hottest months of summer and lower activity during the coldest months of winter; because they are fed and cared for, activity of owned cats appears to reflect comfort in response to thermal conditions rather than foraging needs. Overall higher levels of activity suggest that unowned cats are likely having a greater year-round impact on wildlife than owned cats.

Unowned cats in our radiotracked sample showed lower mean survival than owned cats, as reported by Schmidt et al. (2007), but our results are based on small sample sizes. Schmidt et al. (2007) reported survival rates over a 14-month study of 56% for feral (free-roaming, never fed; $n = 28$), 90% for semi-feral (free-roaming but occasionally fed; $n = 14$), and no mortality for their sample of owned cats ($n = 10$), which was similar to the survival rate of 50% for unowned cats and only 1 mortality in our sample of owned cats over a comparable time interval. Our study area included portions of the University of Illinois South Farms, which has a program to remove predators and other mammals for disease prevention. Domestic cats are not removed from these areas, however; survival rates of unowned cats may have been influenced positively by removal of potential predators and competitors.

MANAGEMENT IMPLICATIONS

Overall, greater activity levels and ranging behavior suggest unowned cats have a greater potential impact on wildlife than do owned cats. Our results indicate that feeding and owner care modifies the space use and activity of free-roaming cats, information that is important for making decisions on controlling cat populations and the potential spread of disease. Actual impacts of both categories of cats at the population level of prey need better assessment, however. Owned cats may have less impact on other wildlife than unowned cats because of their localized ranging behavior, or conversely, they may have a very high impact within their smaller home ranges whereas the impacts of unowned cats are more dispersed. Free-roaming cats do kill wildlife and pose a disease risk; cat owners should keep pets indoors.

ACKNOWLEDGMENTS

We thank the field assistants and volunteers who helped with this project; without their work this project could not have been undertaken. We also thank M. Ward and A. Raim for their advice and help throughout the project, R. Schooley for his helpful comments on previous drafts and advice on data analysis, and C. Warwick for help producing the figures.

LITERATURE CITED

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313–1325.

Aramini, J. J., C. Stephen, and J. P. Dubey. 1998. Toxoplasma gondii in Vancouver Island cougars (*Felis concolor vancouverensis*): serology and oocyst shedding. Journal of Parasitology 84:438–440.

Baker, P. J., A. J. Bentley, R. J. Ansell, and S. Harris. 2005. Impact of predation by domestic cats *Felis catus* in an urban area. Mammal Review 35:302–312.

Beckerman, A. P., M. Boots, and K. J. Gaston. 2007. Urban bird declines and the fear of cats. Animal Conservation 10:320–325.

Beyer, H. L. 2004. Hawth's Analysis Tools for ArcGIS. <http://www.spatialecology.com/htools>. Accessed 17 May 2008.

Boutin, S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. Canadian Journal of Zoology 68:203–220.

Calhoon, R. E., and C. Haspel. 1989. Urban cat populations compared by season, subhabitat and supplemental feeding. Journal of Animal Ecology 58:321–328.

Carr, A. P., and A. R. Rodgers. 1998. HRE: The Home Range Extension for Arcview. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.

Conrad, P. A., M. A. Miller, C. Kreuder, E. R. James, J. Mazet, H. Dabritz, D. A. Jessup, F. Gulland, and M. E. Grigg. 2005. Transmission of toxoplasma: clues from the study of sea otters as sentinels of *Toxoplasma gondii* flow into the marine environment. International Journal for Parasitology 35:1155–1168.

Dickman, C. R. 2009. House cats as predators in the Australian environment: impacts and management. Human-Wildlife Conflicts 3:41–48.

Dubey, J. P., and J. K. Frenkel. 1973. Experimental toxoplasma infection in mice with strains producing oocysts. Journal of Parasitology 59:505–512.

Dubey, J. P., R. M. Weigel, A. M. Siegel, P. Thulliez, U. D. Kitron, M. A. Mitchell, A. Mannelli, N. E. Mateus-Pinilla, S. K. Shen, O. C. H. Kwok, and K. S. Todd. 1995. Sources and reservoirs of toxoplasma-gondii infection on 47 swine farms in Illinois. Journal of Parasitology 81:723–729.

Fitzgerald, B. M. 1979. Foods of feral house cats (*Felis catus L.*) in forest of the Orongorongo Valley, Wellington. New Zealand Journal of Zoology 6:107–126.

Getz, L. L. 1985. Habitats. Pages 286–309 *in* R. H. Tamarin, editor. Biology of new world *Microtus*, Special Publication No. 8. The American Society of Mammalogists.

Getz, L. L. 2009. Circadian activity rhythm and potential predation risk of the prairie vole, *Microtus ochrogaster*. Southwestern Naturalist 54:146–150.

Gosselink, T. E., T. R. Van Deelen, R. E. Warner, and M. G. Joselyn. 2003. Temporal habitat partitioning and spatial use of coyotes and red foxes in east-central Illinois. Journal of Wildlife Management 67:90–103.

Granholm, M., B. C. McKusick, F. C. Westerholm, and J. C. Aspegrén. 2006. Evaluation of the clinical efficacy and safety of dexmedetomidine or medetomidine in cats and their reversal with atipamezole. Veterinary Anaesthesia and Analgesia 33(4): 214–223.

Gutilla, D. C., and P. Stapp. 2010. Effects of sterilization on movements of feral cats at the wildlife-urban interface. Journal of Mammalogy 91:482–489.

Hall, L. S., M. A. Kasparian, D. Van Vuren, and D. A. Kelt. 2000. Spatial organization and habitat use of feral cats (*Felis catus L.*) in Mediterranean California. Mammalia 64:19–28.

Haspel, C., and R. E. Calhoon. 1993. Activity patterns of free-ranging cats in Brooklyn, New York. Journal of Mammalogy 74:1–8.

Hill, D., and J. P. Dubey. 2002. *Toxoplasma gondii*: transmission, diagnosis and prevention. Clinical Microbiology and Infection 8:634–640.

Illinois State Water Survey, 2009. Illinois climate. <http://www.isws.illinois.edu/atmos/statecli>. Accessed 4 Dec 2009.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology (Washington DC) 61:65–71.

Jones, E., and B. J. Coman. 1981. Ecology of the feral cat, *Felis catus* (*L.*), in southeastern Australia 1. Diet. Australian Wildlife Research 8:537–548.

Kauhala, K., and K. Holmala. 2006. Contact rate and risk of rabies spread between medium-sized carnivores in southeast Finland. Annales Zoologici Fennici 43:348–357.

Kays, R. W., and A. A. DeWan. 2004. Ecological impact of inside/outside house cats around a suburban nature preserve. Animal Conservation 7:273–283.

Kleen, V. M., L. Cordle, and R. A. Montogomery. 2004. The Illinois breeding bird atlas, Special Publication No. 26. Illinois Natural History Survey, Champaign, Illinois, USA.

Koganezawa, M., and H. Imaki. 1999. The effects of food sources on Japanese monkey home range size and location, and population dynamics. Primates 40:177–185.

Langham, N. P. E., and R. E. R. Porter. 1991. Feral cats (*Felis catus L.*) on New Zealand farmland. 1. Home range. Wildlife Research 18:741–760.

Liberg, O. 1980. Spacing patterns in a population of rural free roaming domestic cats. Oikos 35:336–349.

Liberg, O. 1984. Food habits and prey impact by feral and house-based domestic cats in a rural area in southern Sweden. Journal of Mammalogy 65:424–432.

Liberg, O., M. Sandell, D. Pointer, and E. Natoli. 2000. Density, spatial organization, and reproductive tactics in the domestic cat and other felids. Pages 119–147 *in* D. C. Turner and P. Bateson, editors. The domestic cat: the biology of its behaviour. Cambridge University Press, Cambridge, United Kingdom.

Lord, L. K. 2008. Attitudes toward and perceptions of free-roaming cats among individuals living in Ohio. Journal of the American Veterinary Medical Association 232:1159–1167.

Madison, D. M. 1985. Activity rhythms and spacing. Pages 373–419 *in* R. H. Tamarin, editor. Biology of new world microtus, Special Publication 8. American Society of Mammalogists.

Mateus-Pinilla, N. E., B. Hannon, and R. M. Weigel. 2002. A computer simulation of the prevention of the transmission of *Toxoplasma gondii* on swine farms using a feline T. gondii vaccine. Preventive Veterinary Medicine 55:17–36.

Meireles, L. R., A. J. Galisteo, E. Pompeu, and H. F. Andrade. 2004. *Toxoplasma gondii* spreading in an urban area evaluated by seroprevalence in free-living cats and dogs. Tropical Medicine & International Health 9:876–881.

Mitchell, J. C., and R. A. Beck. 1992. Free-ranging domestic cat predation on native vertebrates in rural and urban Virginia. Virginia Journal of Science 43:198–208.

Molsher, R., C. Dickman, A. Newsome, and W. Mueller. 2005. Home ranges of feral cats (*Felis catus*) in central-western New South Wales, Australia. Wildlife Research 32:587–595.

Nams, V. O. 2006. Locate III user's guide. Pacer Computer Software, Tatamagouche, Nova Scotia, Canada.

Nielson, L. 1999. Chemical immobilization of wild and exotic animals. Iowa State University Press, Ames, USA.

Nogales, M., A. Martin, B. R. Tershy, C. J. Donlan, D. Witch, N. Puerta, B. Wood, and J. Alonso. 2004. A review of feral cat eradication on islands. Conservation Biology 18:310–319.

Nutter, F. B., J. P. Dubey, J. E. Levine, E. B. Breitschwerdt, R. B. Ford, and M. K. Stoskopf. 2004. Seroprevalences of antibodies against *Bartonella henselae* and *Toxoplasma gondii* and fecal shedding of *Cryptosporidium* spp, *Giardia* spp, and *Toxocara cati* in feral and pet domestic cats. Journal of the American Veterinary Medical Association 225:1394–1398.

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.

Plumb, D. C. 2008. Veterinary drug handbook. Sixth edition. Iowa State University Press, Ames, USA.

Rodgers, A. R., A. P. Carr, H. L. Beyer, L. Smith, and J. G. Kie. 2007. HRT: home range tools for ArcGIS. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.

Schmidt, P. M., R. R. Lopez, and B. A. Collier. 2007. Survival, fecundity, and movements of free-roaming cats. Journal of Wildlife Management 71:915–919.

Sims, V., K. L. Evans, S. E. Newson, J. A. Tratalos, and K. J. Gaston. 2008. Avian assemblage structure and domestic cat densities in urban environments. Diversity and Distributions 14:387–399.

Slater, M. R. 2004. Understanding issues and solutions for unowned, free-roaming cat populations. Journal of the American Veterinary Medical Association 225:1350–1354.

Tennent, J., and C. T. Downs. 2008. Abundance and home ranges of feral cats in an urban conservancy where there is supplemental feeding: a case study from South Africa. African Zoology 43:218–229.

Turner, D. C., and P. Bateson. 2000. The domestic cat: the biology of its behaviour. Cambridge University Press, Cambridge, United Kingdom.

Vickery, W. L., and J. R. Bider. 1981. The influence of weather on rodent activity. Journal of Mammalogy 62:140–145.

Warner, R. E. 1985. Demography and movements of free-ranging domestic cats in rural Illinois. Journal of Wildlife Management 49:340–346.

White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California, USA.

Woods, M., R. A. McDonald, and S. Harris. 2003. Predation of wildlife by domestic cats *Felis catus* in Great Britain. Mammal Review 33:174–188.

Associate Editor: Gary Roloff.