Demographic differences between urban feeding groups of neutered and sexually intact free-roaming cats following trap-neuter-return procedure

3 authors, including:

Hilit Finkler
Tel Aviv University
7 PUBLICATIONS   **119** CITATIONS

SEE PROFILE

Demographic differences between urban feeding groups of neutered and sexually intact free-roaming cats following a trap-neuter-return procedure

Idit Gunther, DVM; Hilit Finkler, MSc; Joseph Terkel, PhD

Objective—To examine demographic differences during a 1-year observational period between urban feeding groups of neutered and unneutered free-roaming cats following a trap-neuter-return procedure.

Design—Natural-setting trial.

Animals—Free-roaming adult cats (n = 184) and kittens (76) living in 4 feeding groups in an urban region of Israel.

Procedures—Cats in 2 feeding groups were subjected to a trap-neuter-return (TNR) procedure. Cats in 2 other feeding groups were untreated. Data were collected on a weekly basis before and during feeding time over a 1-year period. Following individual cat identification, presence of adults and kittens was recorded throughout the year. Rates of immigration, emigration, and kitten survival were compared between neutered and unneutered groups.

Results—The number of adult cats in the 2 neutered groups increased significantly during the study period because of higher immigration and lower emigration rates than in the unneutered groups, in which the number decreased. In the neutered groups, annual presence of neutered cats was significantly higher than that of sexually intact cats. Kitten survival in the neutered groups was significantly higher than in the unneutered groups.

Conclusions and Clinical Relevance—Targeting the TNR method mainly at feeding groups in urban residential neighbourhoods may result in increased group size, as a consequence of 2 major changes in group dynamics: sexually intact cats immigrate into the neutered groups more readily and neutered cats reduce their emigration rates, possibly because of a reduction in reproductive and competitive pressures. To maintain a high proportion of neutered cats in such cat groups, persistent TNR campaigns are therefore necessary. (*J Am Vet Med Assoc* 2011;238:1134–1140)

In an urban setting, free-roaming cats usually have access to clumped food resources (eg, garbage cans or feeding sites), and humans control the distribution and availability of those resources.[1] Such cats typically live in groups,[2–4] which are often referred to as cat feeding groups.[4–6]

The continuous abandonment of pet cats to city streets, the high fecundity of stray cats, and the widespread availability of vital resources (ie, food, water, and shelter) have enabled free-roaming domestic cat populations to reach densities as high as 1,000 to 2,500 cats/km² in urban environments.[1] These high densities, combined in many situations with a lack of proper diet and medical care, impair the cats' welfare[4,7–9] and create a public nuisance in that the cats can transmit zoonotic diseases, vocalize loudly, and produce unwanted stray kittens.[1] Consequently, managing stray cat populations and resolving specific nuisances have become a necessity. Fertility control methods, particularly TNR

programs, are gradually replacing or adding to prior attempts at eradication in many western countries.

To date, only a few studies have been conducted to investigate the effects of neutering on the size of free-roaming cat populations and the extent of the associated nuisances. Although findings of some studies[a,b] suggest that the cat population size increases after neutering, others suggest it decreases[10–12,c] or stabilizes.[d] Most of these studies were performed in fairly secluded areas, such as rural neighborhoods,[c] hospitals, or campus grounds,[11,13,14] and, in studies[10,a] involving more urban locations, in parks. Cat populations living in a contiguous urban area will vary greatly from those inhabiting secluded areas. An urban cat population is expected to have a higher turnover because of higher rates of immigration and emigration as well as a higher density.[12,15] Therefore, as opposed to the effect of TNR on the size of secluded cat feeding groups, its effect on urban cat feeding groups is strongly influenced by the surrounding cat populations rather than by the changes within the groups.

In Israel, which has a hot climate and large urban areas abundant in vital resources available for free-roaming cats, such cat populations can reach densities as high as 2,300 to 2,800 cats/km², as was found in Jerusalem in 1989 through 1990.[15] In contrast to the legal restrictions on dogs in Israel, cats are permitted to roam freely and need no individual identification such as tags or electronic chips. Many of these cats live in poor conditions[9]: their diet is based on food leftovers and refuse or food provided by feeders, they rarely receive any medical care and thus develop many infectious diseases[8,16–20] (eg, FIV or FeLV), and they are commonly hit by cars, abused by people, or bitten by dogs.[1,8,20,e] While battling for survival, these cats nonetheless still manage to reproduce, becoming a growing public health concern. This is reflected not only in their potential as a vector for zoonotic diseases[21,22] but also in their tendency to enter restaurant or hotel kitchens, kindergartens, army facilities, and other public places.

In the last decade, there has been increasing public pressure for change in the free-roaming cats' situation. One of the achievements resulting from such pressure was a ruling by the Israeli Supreme Court that any eradication method carried out without proof of the animal constituting a true hazard to public health is illegal.[f] Consequently, today, the only routinely applied method of regulating cat populations in Israel is that of TNR.

Because, in most situations, the TNR method is applied following a caretaker's request, and because trapping feral cats that are not accustomed to being handled is challenging,[c] most TNR procedures are conducted at feeding group sites rather than in the surrounding area. Similar to the situation in other countries, it remains unclear as to whether TNR programs in Israel are succeeding in reducing cat numbers and the associated nuisances. This uncertainty is valid even in cities such as Tel Aviv, where approximately 40,000 free-roaming cats have been neutered since 1994.[g] The purpose of the study reported here was to examine demographic differences during a 1-year observational period between urban feeding groups of neutered and unneutered free-roaming cats following a TNR procedure.

Materials and Methods

Cats and setting—For participation in the study, free-roaming cat groups were required to have regular and fixed feeding hours and a habitat representative of a typical feeding group site in the urban environment in Israel. All locations at each study site had to be accessible to investigators to facilitate observations.

Four defined cat feeding groups were selected (A, B, C, and D) and monitored from October 1999 to October 2000. All groups were situated in residential neighborhoods in the area of the Tel-Aviv metropolis known as Gush Dan, which is a relatively small continuous urban environment. Each neighborhood had similar weather characteristics, human populations (4,900 to 5,200 residents/km²),[23] and free-roaming cat densities. Two of the groups (A and D) were located in quieter neighborhoods with private houses, whereas the other 2 groups (B and C) were located in neighborhoods with apartment buildings. In all 4 neighborhoods, the urban environment, characterized by low traffic, many small streets, backyards, and shelter spaces, facilitates the movement of cats from one place to another.

In all 4 groups, feeding had been performed by cat caretakers at least once a day for several years before the beginning of the study. Because of the long distances between study group sites (7.6 km between A and B, 3.3 km between C and D, and 10 to 14.3 km between both A and B and both C and D) and heavily trafficked roads separating the study group neighborhoods, no immigration of cats between groups was possible. In group A, food was delivered as 1 large pile every morning. In group B, food was delivered in individual portions to each cat every morning. In group C, food was delivered in 2 to 3 bowls every evening. In group D, food was delivered in 3 to 5 bowls every morning.

Cats in groups A and B were trapped, taken to a veterinary clinic, neutered, vaccinated against rabies, and returned to their site of capture (after 24 hours of recovery in the clinic). Females underwent ovariohysterectomy via a flank approach, and males underwent regular castration. While anesthetized, the tip of each cat's left ear was removed to indicate it had been neutered.[24] Much effort was required to achieve maximal trapping rates of these free-roaming cats,[c] many of which were untamed. Therefore, with the assistance of the municipal veterinary services, TNR procedures were initiated a few months prior to onset of the study observational period and ended up to 2 months into the observation period. During the time of the TNR procedures in the feeding groups, an intensive TNR campaign was also conducted in the surrounding neighborhoods of groups A and B.

Cats in groups C and D were neither captured nor treated in any manner. Neither the municipal authorities nor the cat caretakers conducted any management campaign within a radius of 4.7 km around groups C and D before or during the study period.

All cats were characterized as belonging to 1 of 2 age categories: kittens (≤ 6 months old) and adults (> 6 months old). Cats older than 6 months are referred to as adults rather than juveniles[25,d] in this report because females can go through puberty and experience their first estrus as early as 5 months of age, and in free-roaming cats, this can occur even earlier.[26]

Data collection—During the month prior to beginning data collection, cats were individually identified at each feeding group by direct observation or by use of binoculars. The identification process included photographing the cats and recording specific details,[27–29,a] including sex, estimated age, body size, length and pattern of hair coat, date of neutering, and other characteristics such as eye color or any deformities. Sex and neuter status were defined by the presence of testes in sexually intact males, the scrotum in neutered males, enlarged mammary glands of lactating queens, enlarged cheek glands in males, and the overall body size (males are usually larger than females).[15,28] For the purpose of data recording, each cat was assigned a specific number and its picture and number were placed in an album prepared for each group.

On the basis of results of preliminary observations of feeding duration in group A, a duration of 160 minutes was initially chosen as the observation period for

all groups. However, after the study began, it became apparent that 3 of the 4 study groups did not require such a long observation period. Accordingly, the duration of subsequent observations was group specific, ranging usually between 30 and 100 minutes but no longer than 160 minutes. The study started with 5 to 7 weeks of observations performed 2 to 3 times/wk (15 initial observation points), followed by 8 months of once-a-week observations and, at the end of the 8-month period, another 5 to 7 weeks of observations performed 2 to 3 times/wk (15 final observation points). The purpose of the initial and final 15 observation periods was to obtain data regarding group size at the beginning and end of the study. Each observation began when the cats started to gather at the feeding site before the feeder initiated food delivery and ended when only a few cats at most were still eating. A cat was counted as present if it arrived at any time during the observation period.

Cat categorization—Cats in all 4 groups were categorized as residents, transients, immigrants, or emigrants. Resident was defined as a cat seen at > 4 observation points but that did not immigrate into or emigrate out of its feeding group. Transient was defined as a cat that was observed < 4 times at the study site. Immigrant was defined as an adult cat that did not appear at the study site until after the first 15 observations had been made and then continued to be seen later in the study period for > 4 observation points. Emigrant was defined as an adult cat that was present at the study site at the first 15 observation points but was never seen again throughout the last 15 observation points.

Surviving kittens were defined as cats first seen as kittens at the study sites that reached the age of approximately 6 months. Most kittens that did not reach 6 months of age had disappeared from the study site and were presumed dead.[c]

Statistical analysis—Statistical analysis was performed by use of a statistical software package.[h]

To determine whether any changes in numbers of adult cats had occurred during the study period, linear regression analysis was used to test the number of adult cats as a function of time for each of the 4 feeding groups separately. To evaluate the effect of neutering on the annual presence rate of the adult cats, the ratio of the number of observations at which each cat was present in each group was divided by the total number of observations made, which yielded the percentage of observations in which each cat was present. After square-root and arcsine transformation of these data, a 2-way ANOVA (sex and neuter status) was performed for groups A and B separately. The ANOVA could not be performed for groups C and D because those groups had only 1 neutered cat in each.

For analysis of population dynamics, a χ^2 test was used to compare proportions of immigrants and emigrants (with the denominator being the number of cats seen in > 4 observations) between the feeding groups. To test the difference in survival rates between kittens from groups A and B combined and C and D combined, the Kaplan-Meier product limit estimate of the survivor function estimate was used. To examine stability of appearance (consistency of appearance) of the adult cats in all groups, the percentage of adult cats at each observation point that had been present in the previous observation was calculated. For example, for observation point 3, the number of cats at that point that were also present at observation point 2 (nominator) was divided by the number of cats present at observation point 2 (denominator). For the first 15 observation points, the presence of cats was pooled into 1 observation for this computation (ie, for consistency of appearance) and from then on calculated for each observation.

Results

Cats—At the beginning of the study, after the TNR procedure had ended, 27 of 37 (73%) adult cats (13 males and 14 females) had been neutered in group A and 30 of 40 (75%) adult cats (15 males and 15 females) had been neutered in group B.

During the observation period, 89 cats were observed in group A (18 neutered females, 12 sexually intact females, 11 neutered males, 30 sexually intact males, and 18 kittens), 72 cats were observed in group B (21 neutered females, 7 sexually intact females, 16 neutered males, 16 sexually intact males, and 12 kittens), 61 cats were observed in group C (22 sexually intact females, 1 neutered male that had been neutered by the caretaker months before the study had begun, 14 sexually intact males, and 24 kittens), and 38 cats were observed in group D (7 sexually intact females, 1 neutered male that had immigrated into the group from the surroundings, 8 sexually intact males, and 22 kittens).

Group comparisons—The number of adults in the neutered groups (A and B) increased significantly ($P < 0.001$ for both) as a function of time (group A regression line, $y = 0.2x + 26.9$ [$R^2 = 0.4$]; group B regression line, $y = 0.2x + 16.6$ [$R^2 = 0.54$]), whereas the number of adults in unneutered groups (C and D) declined significantly (group C regression line, $y = -0.1x + 11.3$ [$R^2 = 0.4$]; group D regression line, $y = -0.1x + 9$ [$R^2 = 0.6$]).

In groups A and B, the increase in total population size was due to an increase in numbers of both adults and kittens (**Figure 1**). The number of cats in group C remained stable during the study period because of a decrease in the number of adults occurring concomitantly with an increase in the number of kittens. Group D increased in total size, from 10 to > 20 cats, primarily because of an increase in the number of kittens.

Effect of neutering on the annual presence rate—Annual presence rates of adult neutered cats were significantly higher than those of sexually intact cats in neutered groups A (neutered cats [n = 29], 0.7 ± 0.07; unneutered cats [42], 0.4 ± 0.06; $P = 0.001$) and B (neutered cats [37], 0.6 ± 0.05; unneutered cats [23], 0.5 ± 0.07; $P < 0.043$; **Figure 2**). No difference in presence rates was evident between males and females for both neutered and sexually intact cats in these groups. In group D, females had a higher annual presence rate than males (females [n = 7], 0.6 ± 0.1; males [9], 0.2 ± 0.05; $P = 0.02$).

Immigration—Proportions of immigrants in neutered groups A (37%) and B (44%) were significantly
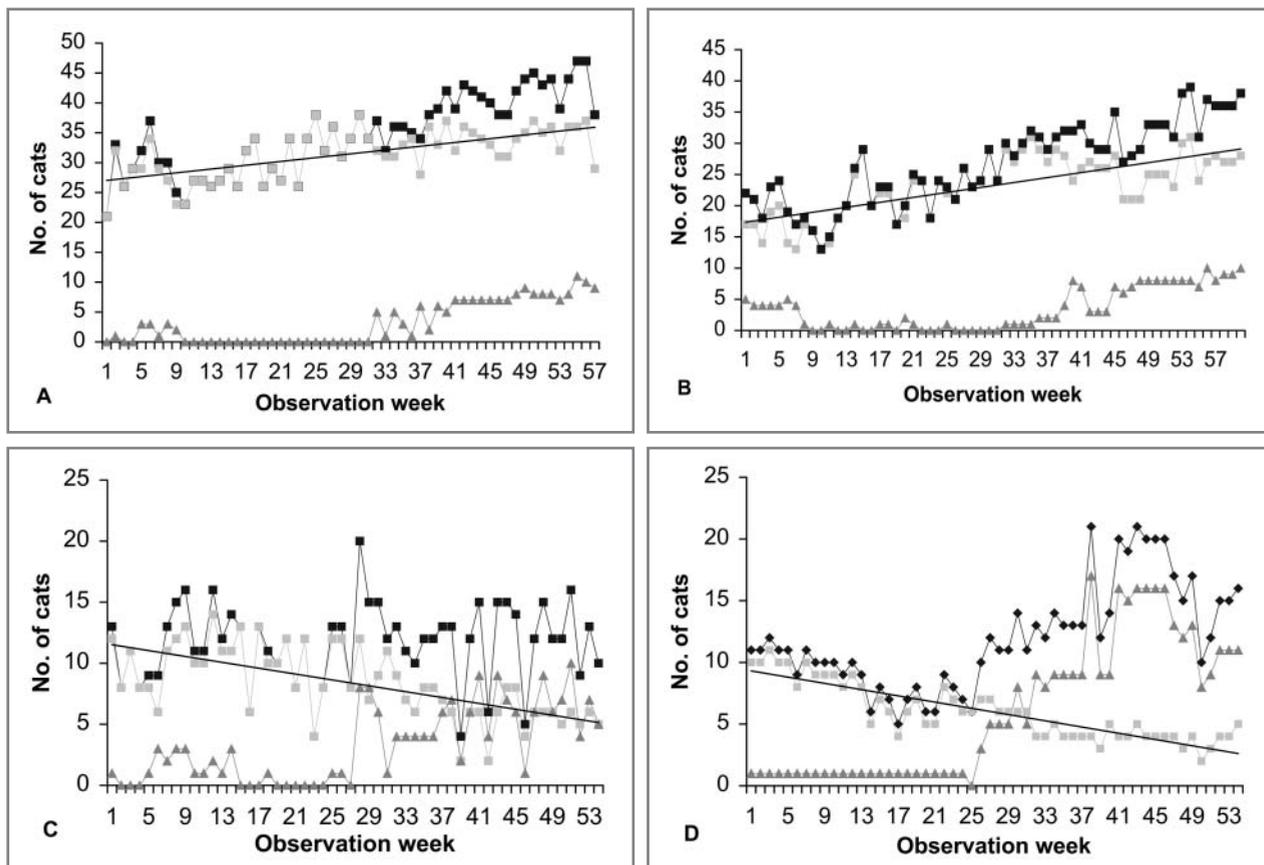
Figure 1—Dot plots of changes in the total number of cats (black squares), adults (gray squares), and kittens (triangles) in free-roaming cats in feeding groups A (A) and B (B) that were neutered as part of a TNR procedure prior to a 1-year study period and those in groups C (C) and D (D) in which neutering was not performed. The diagonal line represents the regression line for adult cat numbers as a function of time.
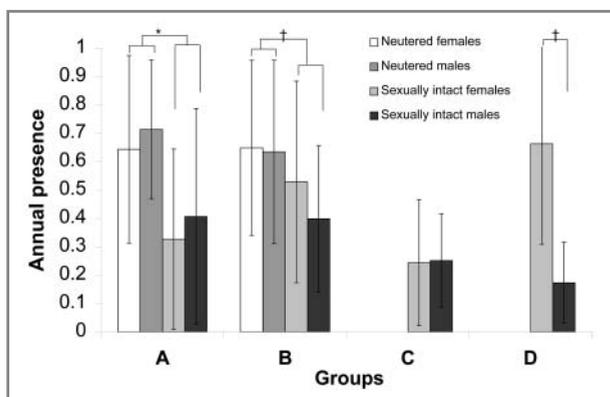

Figure 2—Annual presence rates (proportion of number of observations a cat was present divided by the total number of observations made during the study period ± SD) for free-roaming cats in 4 feeding groups. In groups A (n = 71) and B (60), cats were neutered as part of a TNR procedure prior to the observation period, and in groups C (37) and D (16), they were not. *Values differ significantly (P < 0.01) between groups indicated by the brackets. †Values differ significantly (P < 0.05) between groups indicated by the brackets.

Table 1—Number (%) of immigrant, emigrant, resident, and transient adult cats in feeding groups A and B in which cats that were neutered as part of a TNR procedure prior to a 1-year observation period and groups C and D, in which neutering was not performed.

Group	Immigrants	Emigrants	Residents	Transients
A	21 (37)	11 (19)	25 (44)	14
B	23 (44)	13 (25)	16 (31)	8
C	6 (19)	15 (48)	10 (32)	6
D	0 (0)	9 (75)	3 (25)	4

Percentages of immigrants, emigrants, and residents are relative to the number of cats that were observed at > 4 observation points in each group (ie, immigrants + emigrants + residents).

immigrants were also compared between the neutered groups combined and the unneutered groups combined (χ^2 test with a Bonferroni correction), revealing that the neutered groups had a significantly (P = 0.02) greater proportion of immigrants than the unneutered groups.

Emigration—Proportions of emigrants in neutered groups A (19%) and B (25%) were also significantly (P < 0.001) less than those in unneutered groups C (48%) and D (75%). Therefore, proportions of emigrating cats were compared between groups A and B and between groups C and D. Again, these differences were not significant (P = 0.49 for A vs B and P = 0.17 for C vs D). After a Bonferroni correction, the proportion of emigrants in the

(P < 0.001) greater than those in unneutered groups C (19%) and D (0%; **Table 1**). Therefore, a decision was made to test[30] for differences in immigration proportions between groups A and B and between groups C and D. These differences were not significant (P = 0.44 for A vs B and P = 0.16 for C vs D). Proportions of

combined neutered groups was significantly ($P < 0.001$) greater than that of the combined unneutered groups.

Kitten survival—Seventy-three kittens were observed in the study groups, with the earliest age being approximately 4 weeks. Survival data were available for 56 kittens (34 from neutered groups A and B and 22 from unneutered groups C and D; **Figure 3**). Survival time was significantly ($P < 0.001$) greater for kittens
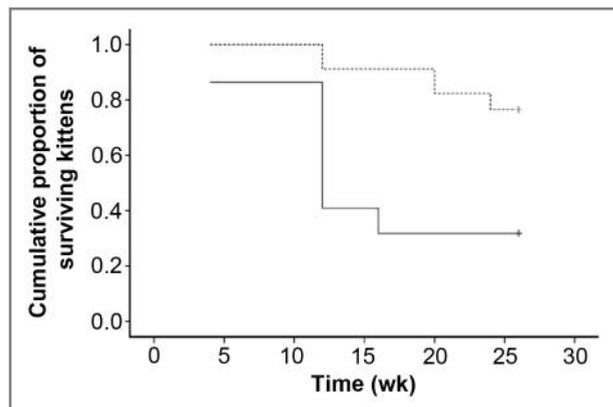

Figure 3—Kaplan-Meier survival estimates for free-roaming kittens observed in feeding groups A and B (dotted line; n = 34) and feeding groups C and D (solid line; 22). In groups A and B, adult cats were neutered as part of a TNR procedure prior to the observation period, and in groups C and D, they were left sexually intact. Hatch marks indicate time of censoring (ie, at 26 weeks).

originating from a neutered group than for those originating from an unneutered group. Overall, 41% of kittens (n = 68 in the unneutered groups and 24 in the neutered groups) from all groups died or disappeared before reaching 6 months of age.

Consistency of appearance—Adult cats in all 4 groups had differing consistencies of appearance over the 1-year study period (**Figure 4**). The magnitude of changes and fluctuations in the consistency of appearance appeared least in group A (range, 65% to 100%), followed by group B (range, 55% to 90%), group D (range, 55% to 100%), and group C (range, 15% to 100%).

Discussion

The present study is one of the few studies conducted to examine the effects of a TNR procedure on urban cat feeding groups located in crowded residential neighborhoods. The feeding groups used in the study had been established years before the study began and no changes other than application of the TNR procedure to the experimental groups were made during the study period. Similar to another study[12] carried out in an urban area, our study revealed that despite the variability between the 2 neutered groups in the food delivery method and feeding site characteristics, both groups increased in size. This increase in total number was due to the increase in adult cat numbers, which in turn resulted from higher immigration and lower emigration rates than in
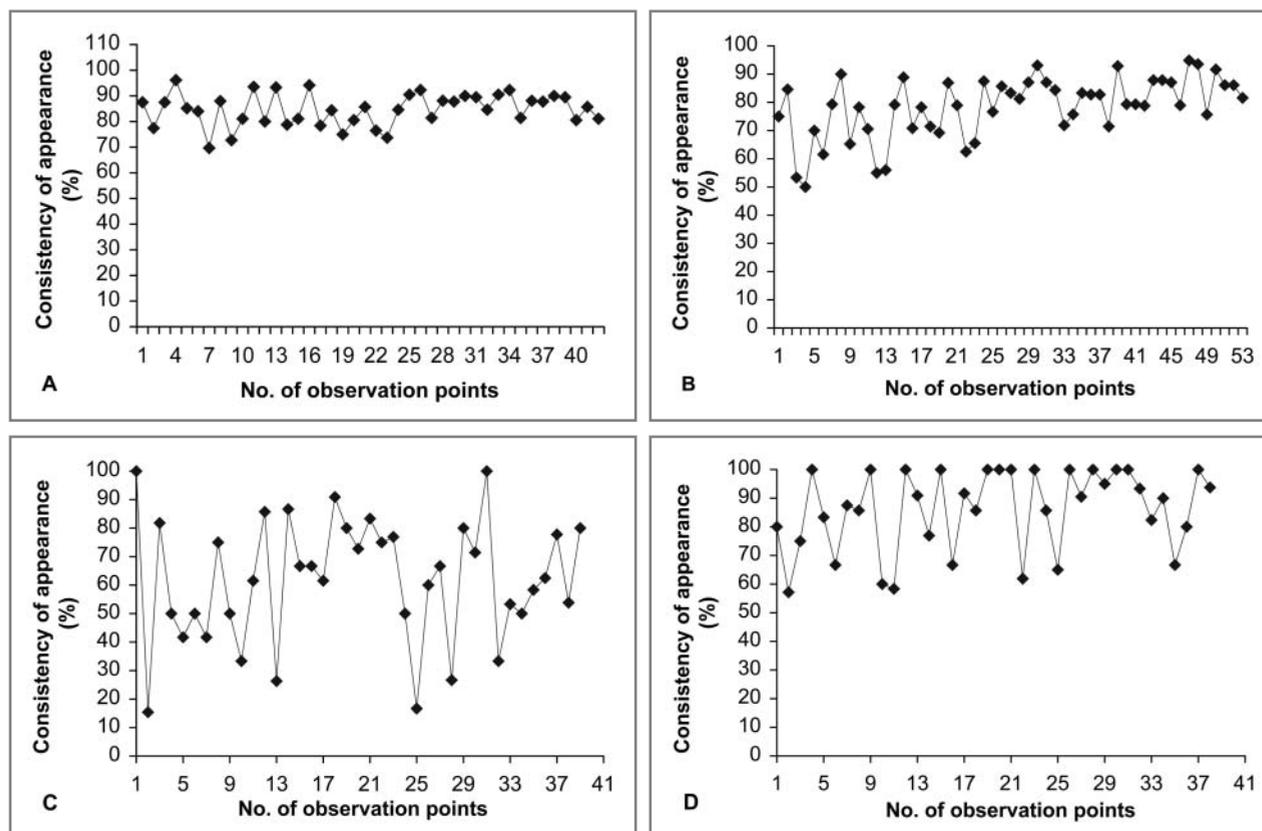
Figure 4—Consistency of appearance (%) of free-roaming adult cats in feeding groups A (A; n = 71) and B (B; 60) and feeding groups C (C; 37) and D (D; 16). In groups A and B, cats were neutered as part of a TNR procedure prior to the observation period, and in groups C and D, they were left sexually intact. Consistency was calculated as the percentage of adult cats at each observation point that had been present in the previous observation.

the 2 unneutered groups. Because almost all immigrant cats were not tamed and succeeded to integrate into the groups (as opposed to the almost impossible integration of abandoned house cats into such groups[8]), we suggest that these cats were not abandoned but were free-roaming cats that had moved from the surroundings into the groups. These findings are in contrast to those of other investigators[12,a] who claimed that the observed increase in population size in their studies was due to abandonment of house cats by their owners, although these claims were not supported by their data. Moreover, we suggest that the main reason for the higher immigration rates in the neutered groups derived from the reduction in agonistic behavior of the neutered cats, resulting in a so-called behavioral vacuum that enabled the existence of a larger population size in the same habitat.[31]

The neutered cats in groups A and B had significantly higher annual presence rates than the sexually intact cats in the same groups. Moreover, the consistency of appearance across the year of adult cats in the neutered groups (A and B) was higher than that of cats in group C. We suggest that, in these neutered groups, the neutered cats formed a stable feeding core, resulting from the decreased roaming and increased survival rates of cats after neutering. After neutering, males lose interest in mating with females,[32] which considerably reduces their inclination to roam,[13,30,33,34] and may accordingly have appeared more regularly at the feeding sites in our study.[10] In addition, after neutering, females have no need to disperse from their original group at the age of 1 to 2 years because of competition for favorable nesting sites.[i] However, cats may become permanently absent from a feeding site because of death or temporarily because of sickness.[13,35,36] A previous study[36] showed that sexually intact cats, particularly males, which can roam great distances, get hit by cars more commonly than do neutered cats. Moreover, neutered cats may live 2- to 3-fold longer than sexually intact cats because of fewer deaths attributable to trauma or infectious diseases.[37]

The higher than expected rate of consistency of appearance of adult cats in unneutered group D versus unneutered group C as well as the higher annual rate for females versus males can be explained by the fact that in group D, several of the cats belonged to 1 female lineage. A possible explanation for the higher consistency and female annual presence rate found in this group, compared with group C, may be that group D was smaller and located in a neighborhood of private houses. Consequently, cats in group D might have had behavioral patterns similar to those observed in female lineages in more rural areas, where females rarely disperse.[33,i]

Although, at the beginning of the study, 98% of the females in group A and 77% of females in group B were neutered, kittens still appeared in the groups toward the beginning of summer, most of them probably from immigrating females. A similar pattern was evident in the unneutered groups. Having a seasonal polyestrous reproductive cycle, domestic cats in warm and temperate countries breed throughout most of the year,[15,26,38] with a peak in kitten numbers during summer.[39,d] During the summer months, kitten numbers were similar in groups A, B, and C (range, 0 to 11 kittens/observation) and slightly higher in group D (range, 5 to 17 kittens/obser-

vation). However, whereas in the neutered groups, kittens comprised up to 27% of the total population, in the unneutered groups, they comprised up to 67% in group C and up to 80% in group D. Moreover, in contrast to the situation in the neutered groups, adult cat numbers in the unneutered groups dropped concomitantly with the increase in kitten numbers. In the unneutered groups, some of the adult cats dispersed, probably because of reproductive activity of both males and females.[40,i]

The kitten survival rate of 32% in the unneutered groups was similar to that in another study,[41] in which 75% of the kittens in the less crowded rural or suburban residential neighborhoods died or disappeared before reaching 6 months of age. Other studies conducted to examine the survival rate of kittens in high-density populations of free-roaming cats found lower survival rates: 16% of kittens reached 6 months of age in an Israeli urban environment,[15] and 9.5% of kittens reached 10 months of age in a Japanese fishing village.[42] The somewhat higher survival rate in the present study is probably an overestimation of the true rate because kittens were observed at the study site from the age of approximately 4 weeks and kitten deaths in the early postnatal period were not documented. Moreover, many kittens were born toward the end of the study period and their future survival could not be predicted. In contrast to their survival rates in the unneutered groups, only 24% of the kittens in the neutered groups died or disappeared before reaching 6 months of age. However, this difference between kitten survival rates is not necessarily a direct result of neutering. Environmental[41] and social factors may also influence kitten survival rates, including prevalence of viruses,[8,15] availability of vital resources,[15] feeding site size and habitat carrying capacity, and tolerance by the other cats.[43,44] Because the environmental factors were noticed but not studied in our groups, we can only speculate that the decreased aggression in the neutered groups relative to aggression in the unneutered groups detected in our concurrent study[45] may have indirectly contributed to increased kitten survival through increased tolerance toward them by the group cats. We suggest that this tolerance was expressed not only in decreased direct agonistic interactions with the kittens but also in the higher rate of the neutered adults' presence at the feeding sites, contrasting that in the unneutered groups, in which the adult cats left the groups when kitten numbers increased.

As hypothesized by Courchamp and Cornell,[44] vertebrate populations that undergo reproduction control may compensate through an increase in fertility of the sexually intact females, increase in survival rate, and increase in immigration into the population. We suggest that the neutered cat groups in the present study had at least some of these compensating demographic changes, which did not occur in the unneutered groups. Immigration rates were significantly higher and emigration rates significantly lower in the neutered groups than in the unneutered groups, which in turn increased the number of adults and thus the population size. Kitten survival rates were significantly higher in the neutered groups. Moreover, the TNR procedures stabilized the appearance of neutered cats in the groups, as indicated by their prolonged presence and more consistent appearance. We also found variability in the demography of free-roaming cat feeding groups, even in similar situations and environments. Consequently, in order to determine the

effectiveness of the TNR method in reducing free-roaming cat populations and their related nuisances, additional studies on a larger scale are still needed.

a. Castillo D. *Population estimates and behavioral analysis of managed cat* (Felis catus) *colonies located in Miami-Dade country, Florida parks*. MSc thesis, Department of Environmental Studies, Florida International University, Miami, Fla, 2001.

b. Xemar V, Pontier D, Artois M. Attempt to control stray cats in an urban area (abstr), in *Proceedings*. 8th Conf Changing Role Anim Soc 1998.

c. Nutter FB. *Evaluation of a trap-neuter-return management program for feral cat colonies: population dynamics, home ranges, and potentially zoonotic diseases*. PhD thesis, Comparative Biomedical Science, North Carolina State University, Raleigh, NC, 2005.

d. Rees P. The *ecological distribution of feral cats and the effects of neutering a hospital colony*. PhD thesis, School of Studies in Environmental Science, University of Bradford, Bradford, West Yorkshire, England, 1982.

e. Ben-Dov D, Animal Protection Law Veterinary Services Official, State of Israel. Jerusalem, Israel: Personal communication, 2006.

f. Israeli Supreme Court, 2004. "Let the Animals Live" and The Cat Welfare Society in Israel versus the Veterinary Services, the Ministry of Agriculture 4884/00.

g. Galin Z, Municipal Veterinarian, Tel Aviv-Yafo Municipality, Tel Aviv, Israel: Personal communication, 2008.

h. SPSS, version 16.0, SPSS Inc, Chicago, Ill.

i. Courchamp F. *Epidemiological study of feline immunodeficiency virus in domestic cat populations* (Felis catus). PhD thesis, University Claude Bernard, Lyon, France, 1996.

References

1. Gunther I, Terkel J. Regulation of free-roaming cat (*Felis silvestris catus*) populations: a survey of the literature and its application to Israel. *Anim Welf* 2002;11:171–188.

2. Izawa M, Doi T. Flexibility of the social system of the feral cat, *Felis catus*. *Physiol Ecol Jpn* 1994;29:237–246.

3. Kerby G, Macdonald DW. Cat society and the consequences of colony size. In: Turner DC, Bateson P, eds. *The domestic cat, the biology of its behaviour*. Cambridge, England: Cambridge University Press, 1988;67–82.

4. Macdonald DW. The ecology of carnivore social behaviour. *Nature* 1983;301:379–384.

5. Izawa M. Daily activities of the feral cat *Felis catus* LINN. *J Mammal Soc Jpn* 1983;9:219–228.

6. Natoli E, De Vito E, Pontier D. Mate choice in the domestic cat (*Felis silvestris catus* L.). *Aggress Behav* 2000;26:455–465.

7. Bronson RT. Age at death of necropsied intact and neutered cats. *Am J Vet Res* 1981;42:1606–1608.

8. Natoli E. Urban feral cats (*Felis catus* L.): perspectives for a demographic control respecting the psycho-biological welfare of the species. *Annali dell Istituto Superiore Di Sanita* (*Roma*) 1994;30:223–227.

9. Remfry J. Strategies for control, in *Proceedings*. Symp Ecol Control Feral Cats 1981;73–80.

10. Neville PF, Remfry J. Effect of neutering on 2 groups of feral cats. *Vet Rec* 1984;114:447–450.

11. Zaunbrecher KI, Smith RE. Neutering of feral cats as an alternative to eradication programs. *J Am Vet Med Assoc* 1993;203:449–452.

12. Natoli E, Maragliano L, Cariola G, et al. Management of feral domestic cats in the urban environment of Rome (Italy). *Prev Vet Med* 2006;77:180–185.

13. Rees P. The ecological distribution of feral cats and the effects of neutering a hospital colony, in *Proceedings*. Symp Ecol Control Feral Cats 1981;12–22.

14. Hughes KL, Slater MR. Implementation of a feral cat management program on a university campus. *J Appl Anim Welf Sci* 2002;5:15–28.

15. Mirmovitch V. Spatial organization of urban feral cats (*Felis catus*) in Jerusalem. *Wildl Res* 1995;22:299–310.

16. Longcore T, Rich C, Sullivan LM. Critical assessment of claims regarding management of feral cats by trap-neuter-return. *Conserv Biol* 2009;23:887–894.

17. Levy JK, Crawford PC. Humane strategies for controlling feral cat populations. *J Am Vet Med Assoc* 2004;225:1354–1360.

18. Robertson SA. A review of feral cat control. *J Feline Med Surg* 2008;10:366–375.

19. Slater RS. The welfare of feral cats. In: Rochlitz I, ed. *The welfare of cats*. Cambridge, England: Springer, 2005;141–175.

20. Maruyama S, Kabeya H, Nakao R, et al. Seroprevalence of *Bartonella henselae*, *Toxoplasma gondii*, FIV and FeLV infections in domestic cats in Japan. *Microbiol Immunol* 2003;47:147–153.

21. Patronek GJ, Glickman LT, Beck AM, et al. Risk factors for relinquishment of dogs to an animal shelter. *J Am Vet Med Assoc* 1996;209:572–581.

22. Breitschwerdt EB. Feline bartonellosis and cat scratch disease. *Vet Immunol Immunopathol* 2008;123:167–171.

23. Israel Central Bureau of Statistics. *Statistical abstract of Israel 2008: localities, population and density per sq km, by metropolitan area and selected localities*. Jerusalem: Israel Central Bureau of Statistics, 2008.

24. Cuffe DJ, Eachus JE, Jackson OF, et al. Ear-tipping for identification of neutered feral cats. *Vet Rec* 1983;112:129.

25. Macdonald DW, Yamaguchi N, Passanisi WC. The health, haematology and blood biochemistry of free-ranging farm cats in relation to social status. *Anim Welf* 1998;7:243–256.

26. Feldman EC, Nelson RW, Feldman EC, et al. Feline reproduction. *Canine and feline endocrinology and reproduction*. St Louis: WB Saunders Co, 1996;741–742.

27. Haspel C, Calhoon RE. Home ranges of free-ranging cats (*Felis catus*) in Brooklyn, New York. *Can J Zool* 1989;67:178–181.

28. Dards JL. The behaviour of dockyard cats: interactions of adult males. *J Appl Ethol* 1983;10:133–153.

29. Natoli E. Spacing pattern in a colony of urban stray cats (*Felis catus* L.) in the historic centre of Rome. *Appl Anim Behav Sci* 1985;14:289–304.

30. Devillard S, Say L, Pontier D. Dispersal pattern of domestic cats (*Felis catus*) in a promiscuous urban population: do females disperse or die? *J Anim Ecol* 2003;72:203–211.

31. Knol BW, Egberinalink ST. Treatment of problem behavior in dogs and cats by castration and progestagen administration—a review. *Vet Q* 1989;11:102–107.

32. Bradshaw JWS. The cat-human relationship. In: *The behaviour of the domestic cat*. Wollingford, Oxfordshire, England: CAB International, 1992;163–176.

33. Hart BL, Eckstein RA. The role of gonadal hormones in the occurrence of objectionable behaviours in dogs and cats. *Appl Anim Behav Sci* 1997;52:331–344.

34. Scott KC, Levy JK, Gorman SP. Body condition of feral cats and the effect of neutering. *J Appl Anim Welf Sci* 2002;5:203–213.

35. Childs JE, Ross L. Urban cats: characteristics and estimation of mortality due to motor vehicles. *Am J Vet Res* 1986;7:1643–1648.

36. Hamilton JB, Hamilton RS, Mestler GE. Duration of life and causes of death in domestic cats: influence of sex, gonadectomy and inbreeding. *J Gerontol* 1969;24:427–437.

37. Wallace JL, Levy JK. Population characteristics of feral cats admitted to seven trap-neuter-return programs in the United States. *J Feline Med Surg* 2006;8:279–284.

38. Beaver BV. *Feline behavior: a guide for veterinarians*. St Louis: WB Saunders Co, 1992.

39. Say L, Pontier D. Spacing pattern in a social group of stray cats: effects on male reproductive success. *Anim Behav* 2004;68:175–180.

40. Nutter FB, Levine JF, Stoskopf MK. Reproductive capacity of free-roaming domestic cats and kitten survival rate. *J Am Vet Med Assoc* 2004;225:1399–1402.

41. Izawa M, Ono Y. Mother-offspring relationship in the feral cat population. *J Mammal Soc Jpn* 1986;11:27–34.

42. Yamane A, Emoto J, Ota N. Factors affecting feeding order and social tolerance to kittens in the group-living feral cat (*Felis catus*). *Appl Anim Behav Sci* 1997;52:119–127.

43. Bonanni R, Cafazzo S, Fantini C, et al. Feeding-order in an urban feral domestic cat colony: relationship to dominance rank, sex and age. *Anim Behav* 2007;74:1369–1379.

44. Courchamp F, Cornell SL. Virus-vectored immunocontraception to control feral cats on islands: a mathematical model. *J App Ecol* 2000;37:903–913.

45. Finkler H, Gunther I, Terkel J. Behavioral differences between urban feeding groups of neutered and sexually intact free-roaming cats following a trap-neuter-return procedure. *J Am Vet Med Assoc* 2011;238:1141–1149.