The influence of neighbourhood socio-demographic factors on densities of free-roaming cat populations in an urban ecosystem in Israel

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The Impact of Anthropogenic Factors on the Behavior, Reproduction, Management and Welfare of Urban, Free-Roaming Cat Populations

Hilit Finkler[*], Erez Hatna[†] and Joseph Terkel[*]

[*] *Zoology Department, George S. Wise Faculty of Life Sciences, Tel Aviv University, Tel Aviv 69978, Israel*

[†] *Institute for Management Research, Radboud University, The Netherlands*

Address for correspondence: Hilit Finkler, Zoology Department, George S. Wise Faculty of Life Sciences, Tel Aviv University, Ramat Aviv, Tel Aviv 69978, Israel. E-mail: hilit.finkler@gmail.com

ABSTRACT Free-roaming domestic cats constitute an integral part of many urban ecosystems worldwide; their presence results from undisturbed natural reproduction, abandonment by pet owners, and abundant food resources. These cats present controversial and emotional issues regarding management of their high densities, hygiene and epidemiologic risks to humans, and predation of wildlife. Improved urban cat management requires greater knowledge of the anthropogenic factors affecting free-roaming cat populations. In this study, we explored the relationship between caretaker treatment levels and the socio-economics of the caretakers and neighborhoods, and free-roaming cat reproduction management, behavior, and physiology in urban populations. Eight free-roaming cat feeding groups, from eight neighborhoods in Tel Aviv, Israel, were observed for six months. Neighborhoods displayed differences in socio-economic status and housing type, and cat feeding groups reflected different levels of caretaker treatment with regard to neutering, physical interaction with the cats, and medical treatment. We examined whether agonistic behaviors, neutering rates, pregnancy rates, and cortisol levels of the cats differed between groups. We found a strong socio-economic effect on neutering and pregnancy rates: low-income neighborhoods had lower neutering and higher pregnancy rates. Higher-level caretaking was associated with lowered aggression, as well as lower cortisol levels of neutered females. Additionally, analysis of data from 622 registered cat feeding groups from north (high-income) and south (low-income) Tel Aviv, obtained from the municipal veterinary department, revealed a socio-economic influence on reproduction management. Our results indicate that, in urban environments, both the neighborhood's socio-economic status and the caretaker treatment level affect management of these cat populations.

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We conclude that, to improve cat management success, municipalities should consider addressing these socio-economic differences, while, just as importantly, raising awareness and encouraging caretaker involvement in neutering efforts. Improved caretaker treatment levels can lead to reduced cat aggression, with consequent improved cat welfare and reduced noise disturbance to humans.

Keywords: caretakers, free-roaming cats, population management, socio-economic status (SES), TNR, urban ecosystem

Free-roaming domestic cats constitute an integral part of many urban ecosystems worldwide. Their presence is the result of many years of undisturbed natural reproduction, abandonment by pet owners, and an abundance of food resources, intentionally or unintentionally supplied by the human population (Strula 1993; Natoli 1994; Gunther and Terkel 2002). The management of these cats is a controversial and emotional issue, leading to concerns about cat welfare (Natoli 1994), hygiene and epidemiologic risks to the human population (Slater 2001), potential predation risk to wildlife (Clarke and Pacin 2002; Jessup 2004), and the best methods of control (Wallace and Levy 2006).

The co-existence of free-roaming cats with humans in the urban ecosystem has been studied from numerous perspectives, such as cat activity patterns (Haspel and Calhoon 1993), food preferences and availability (Church, Allen and Bradshaw 1996; Bradshaw et al. 1999), and cat and feeder interrelationships (Natoli et al. 1999; Centonze and Levy 2002). However, a much smaller number of studies (Calhoon and Haspel 1989; Alves et al. 2005; Schmidt, Lopez and Collier 2007) has incorporated anthropogenic factors, attempting to solve issues related to free-roaming cat overpopulation. Such incorporation of human factors was recently acknowledged by several authors as crucial to the efficient management of human–wildlife conflicts in urbanized environments (Baker and Harris 2007; Markovchick-Nicholls et al. 2008), and in the case of managing the cat population, it is assumed to play an equally important role.

Part of the free-roaming cat population in urban areas is cared for, to varying extents, by voluntary cat caretakers: from food delivery alone, to comprehensive care including neutering and medical treatment (Haspel and Calhoon 1990; Centonze and Levy 2002). The caretakers deliver food to feeding groups, where the cats gather to feed and where they interact (Izawa 1983; Natoli, De Vito and Pontier 2000). The extent of contact between these caretakers and cats, and the selective behaviors that caretakers choose to engage in, can vary, with probable consequent varying effects on the cat population (Toukhsati, Bennett and Coleman 2007). Some caretaker behaviors are likely to contribute to the maintenance of the free-roaming cat population, as, for example, many of them engage in feeding but not in neutering (Natoli et al. 1999; Centonze and Levy 2002; Toukhsati, Bennett and Coleman 2007). In addition to the effect of caretaker behaviors, the particular socio-economic status (SES) of a neighborhood or region of a city can also affect the cat population. For example, the socio-economic status of neighborhoods surrounding urban parks in Phoenix, Arizona, was recently shown to predict bird species richness and abundance in those parks (Kinzig et al. 2005; Shaw, Chamberlain and Evans 2008). Furthermore, Beck (2002) showed that in Baltimore, Maryland, more free-roaming dogs were found in poor neighborhoods compared with wealthier ones, partially due to the former having more available refuse and open trash cans in the streets.

If cat behavior, reproduction, and welfare parameters are affected by the behaviors of humans (the caretakers of a feeding group), the measures of such parameters in the cats should, to some extent, consequently reflect the cultural, social, or economic differences pertaining to their caretakers. In addition, larger-scale effects on free-roaming cats, as on other animals,

derive from city-level management decisions (Kinzig et al. 2005). In order to better understand the effects of anthropogenic factors on these cat feeding groups, we therefore selected several parameters of cat reproduction, behavior, and physiology, and measured them against the different types of neighborhood housing, the socio-economic status of the caretakers and neighborhood, and the level of caretaking.

Our four hypotheses were as follows:

1. Frequency of agonistic behaviors of the cats before and during food delivery would be influenced by behaviors of the caretakers, and also, to a smaller extent, by the neighborhood housing type, which reflects density of human presence and consequent level of human activity.
2. Neutering rates would be largely influenced by city-level management of the cat population, but might also be influenced by the involvement level of the caretaker him/herself.
3. Pregnancy rates would be affected by the same factors affecting neutering rates.
4. Cortisol levels, as a stress indicator, would be affected by the level of caretaking as well as by the SES of the neighborhood, which could affect the general attitude of residents towards the cats.

Thus, this research is the first step in achieving a greater understanding of the impact of anthropogenic factors on free-roaming, urban cat populations and their relevance to cat population management.

Methods

Tel Aviv is the main city of the greater Tel Aviv metropolitan area and Israel's largest urban region, ca. 53 km^2 (Tel Aviv population census of 1995–1998). The study areas were located in high SES residential neighborhoods of north Tel Aviv, and low SES residential neighborhoods of south Tel Aviv (Porat, Frenkel and Shoshany 2008) (northern neighborhoods in the survey comprised ca. 12 km^2 and southern neighborhoods ca. 15 km^2). The process of selecting low- and high-SES neighborhoods for the study is elaborated below. In stage 1 of the study, we examined whether these two contrasting SES areas differed in cat feeding group disposition and characteristics. In stage 2, we compared reproductive, behavioral, and physiological parameters of cats from feeding groups located in eight different neighborhoods, four in north and four in south Tel Aviv.

Stage 1: Characteristics of Cat Feeding Groups in Tel Aviv

Active cat feeding is a widespread phenomenon throughout the city. The municipal veterinary services cooperate with the cat caretakers in neutering the cat populations, and 40,000 cats are reported to have been neutered since 1994 (Z. Galin DVM, Tel Aviv chief municipal veterinarian, personal communication). Following cat caretakers' requests, the animals are taken by the veterinary services from the feeding group for a TNR (Trap-Neuter-Return) procedure. Each cat entering the procedure is registered according to the feeding group from which it was taken, and its sex, age, sexual status, and any injuries are noted. The tip of the left ear is cut, as in other countries (Natoli et al. 2006), to allow identification of neutered cats. After neutering, cats are returned to their group. This procedure is done at no cost to the caretaker. The relevant data from the Tel Aviv Veterinary Services for 2000–2005 were uploaded to an Excel database and were subsequently used to compare the following parameters between north and south Tel Aviv: (1) number

of feeding groups, (2) number of neutered cats, (3) number of visits made to feeding groups by the veterinary municipal services, (4) rates of pregnancies, and (5) rates of rabies vaccinations.

Stage 2: Field Study

Selection of Neighborhoods: According to the most recent Tel Aviv population census (1995–1998), Tel Aviv comprises 63 neighborhoods. To select the neighborhoods for this study, five socio-economic variables were determined from the population census for each neighborhood (matriculation rates, employment rates, number of new immigrants, computer ownership, and income level) and entered into a factor analysis (using the principal axis factoring extraction method in SPSS). This analysis takes all the variables and produces, according to the correlation between them, a smaller set of factors. The first factor in the analysis explained 75% of the variance in the data, and was interpreted as the socio-economic status. All five variables had a loading of 0.74 or above on the first factor. The other factors had eigenvalues lower than 1 and were therefore not considered further. The scores of the neighborhoods from the first factor were used to choose the neighborhoods for the study.

Of the 63 neighborhoods, 49 were analyzed (there were missing data for the other 14). Figure 1 shows the neighborhood scores, produced by the factor analysis on the SES data (the first factor in the factor analysis), for the Tel Aviv neighborhoods. Neighborhoods that received a low score were labeled "low SES" and those that received a high score were labeled "high SES." Finally, eight neighborhoods were selected according to the factor analysis (presented in Figure 2), as well as according to the type of housing characteristic of the neighborhood (neighborhoods with a mean of more than two stories per building were labeled "apartment-building neighborhoods;" those with a mean of two or fewer stories per building were labeled "private-home neighborhoods"). Table 1 summarizes the SES, the type of housing of the neighborhoods, and the five socio-economic variables, according to which neighborhoods were assigned to low or high SES.

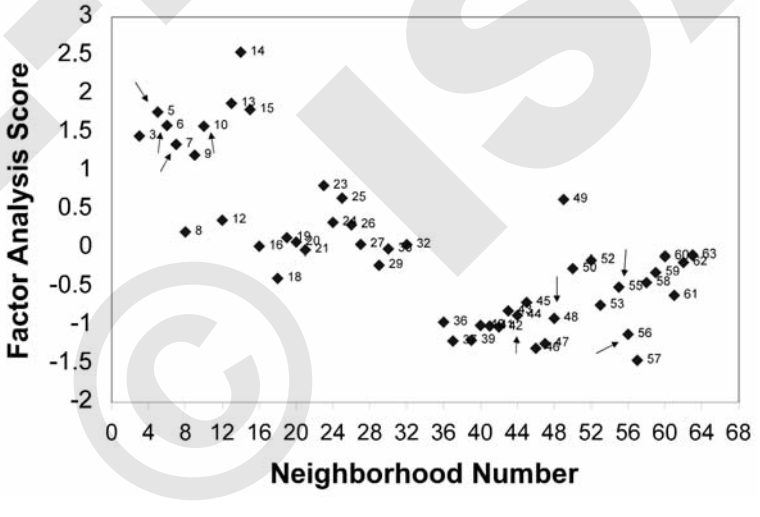

Figure 1. Scores for each of the Tel Aviv neighborhoods from the factor analysis. Neighborhood numbers are neighborhood identifiers from the population census of 1995–1998. The eight neighborhoods selected for the study are marked by arrows (on the lower right side, southern low-SES neighborhoods, and on the upper left side, northern high-SES neighborhoods).

Figure 2. The eight selected neighborhoods and the distribution of 622 registered cat feeding groups (for 2000–2005) (dots) in north and south Tel Aviv. The numbers are the neighborhood identifiers: 1–4 in north Tel Aviv and 5–8 in south Tel Aviv. Map prepared using ArcView GIS 9 software.

Selection of Feeding Groups: In order to select feeding groups, cat caretakers from the eight neighborhoods were contacted and asked if they would be willing to participate in a study consisting of observing their cat groups for six months. An initial screening process consisting of a short telephone interview with 55 caretakers was followed by 25 visits to potential feeding groups. During the visits, the following criteria for inclusion of groups in the study were examined:

1. Adequate amount and type of food delivered to the cats (diet based on dry commercial food).
2. A cooperative caretaker.
3. A group comprising at least 10 cats.
4. No objection by neighbors to our presence or to the feeding of the cats.
5. Access to all parts of the feeding site area, in order to easily observe all the cats.

Table 1. Socio-economic status, type of housing of the neighborhoods selected for the study, and the five socio-economic variables used in the neighborhood selection process.

Neighborhood	Neighborhood Identifier	SES	Type of Housing	Income Scale*	Employed (%)	New Immigrants (%)	Matriculated (%)	Owns a Computer (%)
Neot Afeka Bet	1	H	A	164	60.0	7.9	51.4	48.6
Afeka	2	H	P	186	52.4	10.9	51.9	44.5
Ramat Aviv Gimel	3	H	A	185	55.7	9.8	51.0	48.6
Neve Avivim	4	H	A	169	53.0	14.9	53.0	43.0
Yad Eliyahu	5	L	A	74	46.3	15.3	41.9	25.7
Hatikva	6	L	P	53	44.6	26.0	35.7	17.2
Kiryat Shalom	7	L	A	60	45.6	23.0	33.5	20.4
Dakar	8	L	A	56	43.8	26.0	31.7	19.6

For SES: L = low, H = high.

For type of housing: P = private, A = apartment building.

Neighborhood identifiers are the same as those in Figure 2, detailing the geographic locations.

* Average monthly income per capita, normalized so that 100 is the Tel Aviv average.

Figure 3. One of the eight feeding groups in the study, showing the cats gathering to eat from a communal food source.

According to these criteria, eight feeding groups were selected, one in each of the eight neighborhoods of the field study. Before the start of observations, the Tel Aviv veterinary municipal services were informed of the field study, in order to ensure continuous and well-arranged observation periods, and to prevent any unexpected changes in neutering status of the cats. Feeding groups were chosen with no preliminary knowledge of the proportion of neutered cats. A typical feeding station is shown in Figure 3.

Determination of Caretaker Treatment Level: Cat caretakers from the eight feeding groups were interviewed to determine their level of treatment of the cats. They answered five questions on a five-point Likert scale (where 1 equals the strongest negative reply and 5 equals the strongest positive reply). The interview comprised the following questions:

1. What is your level of closeness to the cats (as expressed by individually identifying and being able to pet or otherwise handle most of the group cats) (1 = not close at all, 5 = very close)?
2. How often do you contact the veterinary municipal services for TNR (1 = once a year, 5 = every 3 months)?
3. How often do you pay privately to neuter your group cats (1 = never, 5 = every 3 months)?
4. How long do you stay with the cats when you deliver them food (1 = little beyond time needed for food delivery, 5 = long beyond time needed for food delivery)?
5. Do you provide medical treatment to sick or injured group cats (1 = never, 5 = I try to give medical assistance to every sick or injured cat)?

According to the total sum, each caretaker was classified on the caretaking scale as giving maximal (18–25), medium (10–17), or minimal (0–9) treatment.

Experimental Procedure: Prior to the beginning of the study, cats were individually identified at each feeding group by direct observation. The identification process included photographing them and recording specific details (Dards 1983; Natoli 1985; Calhoon and Haspel 1989): sex, estimated age, body size, fur pattern, and other characteristics such as eye color and deformations. For the purpose of data recording, each cat was given a specific identification number. Observations in all study groups took place twice weekly, during daytime hours, upon food delivery, for 30-min sessions, over a total period of six months, between January and August 2007. 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. Numbers of adult individuals (> 1-year-old) identified and recorded in each feeding group during the period of group identification are shown in Table 2 (n = 193). During the study period, new cats migrated into the groups, and therefore the eventual number of cats as given in some of the results is greater than those originally presented in Table 2.

Table 2. Numbers of neutered and intact adult males and females in the eight feeding groups in Tel Aviv during the initial period of group identification.

Feeding Group	Intact Females	Intact Males	Neutered Females	Neutered Males	Total Cats
1	1	1	14	5	21
2	3	4	5	5	17
3	7	6	16	6	35
4	3	4	9	4	20
5	9	8	3	2	22
6	6	4	2	1	13
7	5	16	1	1	23
8	7	6	18	11	42

Studied Parameters: 1) Agonistic Behaviors: During observation sessions, agonistic behaviors were recorded using the all-occurrences recording method (Altman 1974). Each agonistic behavior performed by a cat during an interaction with another cat (whether this cat was on the initiating or the receiving end of the interaction), was recorded on paper. Since presence of the cats in the feeding groups varied among individuals, the frequencies of agonistic behaviors were regressed as a function of the relative presence of each cat during the six months of observations. Standardized residual values from this regression were used for the statistical analysis. The agonistic behaviors recorded were: slapping, chasing, vocalizations (hiss, yowl and growl), threat displays (approach and stare), and physical attacks.

2) Pregnancy Rate: The number of pregnancies in each feeding group was recorded during the six months of observations. The number of kittens could not be recorded accurately since not all kittens appeared at the feeding group site.

3) Neutered Cats: After the individual cat identification process, the proportion of the total number of cats which were observed as neutered in each feeding group was calculated from the first month of observations.

4) Hair Collection and Extraction for the Measurement of Cortisol Concentrations: Hair samples were collected from 101 cats. Hair sample collection, method validation, cortisol extraction, and the determination of cortisol concentrations (pg/mg hair) are fully described in Finkler and Terkel (2010).

Statistical Analysis

Regression analyses were performed to evaluate the effect of the various anthropogenic factors on the number of neutered cats and cortisol levels. The effect of the anthropogenic factors on agonistic behaviors and number of pregnancies was analyzed using non-parametric tests. Statistical analysis was performed using SPSS 16.0 software.

Results

Characteristics of Feeding Groups in Tel Aviv

General Characteristics: Between the years 2000 and 2005, 622 cat feeding groups were registered by the municipal veterinary services in 46 neighborhoods in north and south Tel Aviv (as noted earlier, central Tel Aviv was not included in this study) (Figure 2). During this period, 3,771 cats (2,052 females and 1,719 males) were trapped, neutered, and returned to their feeding group. Only 490 (13%) of the 3,771 cats had been vaccinated for rabies. This vaccination is given only if the caretaker is willing to pay for it. Of the 2,052 females cats caught during the six-year period, 305 (about 15%) were found to be pregnant. In November to January, the highest mean number of estrous females was recorded. Pregnancies were observed throughout the year, but peaked in February and March.

Characteristics of North vs. South Feeding Groups: Of the 622 feeding groups, 392 feeding groups were located in north Tel Aviv and 230 in south Tel Aviv. The density of feeding groups was 33.45 groups/km^2 in the north (12 km^2), compared with 14.72 groups/km^2 in the south (15 km^2). In northern feeding groups, 2,283 cats were neutered compared with only 1,488 cats in southern groups. In northern neighborhoods, significantly more cats were vaccinated against rabies compared with southern neighborhoods (chi square of observed [339 and 151 respectively] vs. expected frequencies [according to the ratio of north:south neutered cats, expected frequencies were 193.34:296.65] is 15.32, $p < 0.001$).

Visits by the Veterinary Municipal Services: During the veterinary visits to the feeding groups, only the number of cats taken for neutering was recorded (and not the number of all cats present), so the actual group size could not be determined. We therefore present the mean number of cats (± *SD*) captured per visit, which was significantly higher in south compared with north Tel Aviv (numbers of cats: 4.92 ± 3.44 and 3.96 ± 2.88, in south and north, respectively, *t*-test, $t = -3.70$, $p < 0.01$). Significantly more visits by the veterinary municipal services were made to northern compared with southern groups (chi square of observed [number of visits in north and south: 575 and 288, respectively] vs. expected frequencies [according to the ratio of north:south feeding groups, the expected frequencies were 545:320] is 5.03, $p < 0.05$), as well as per group (visits per group in the north: 1.39 ± 0.05; in the south: 1.26 ± 0.05, *t*-test for square root transformed values, $t = 2.58$, $p < 0.05$). Of the 622 feeding groups visited for the TNR procedure between 2000 and 2005, only 127 groups received a second visit. The number of second visits to the northern feeding groups was three times that of the southern groups (95 compared with 32).

Field Study: Caretaker Treatment Level and Neighborhood Socio-Economic Status

Since each of the eight feeding groups was located in either a high- or low-SES neighborhood, we refer to these groups correspondingly as either high or low SES feeding groups. Of the four high SES feeding groups, three caretakers scored between 18 and 25 points (maximal treatment level) and one caretaker scored between 10 and 17 (medium treatment level). The mean interview score (± *SD*) for caretaker treatment level in the northern groups was 20 ± 5.29. Of the four low SES

feeding groups, three caretakers scored between 0 and 9 points in the interview (minimal treatment level), and one caretaker scored between 18 and 25 points (maximal treatment level). The mean interview score (± *SD*) for caretaker treatment in the southern groups was 12.25 ± 8.53.

Field Study: Effect of Anthropogenic Factors on Behavior, Reproduction Management, and Physiology of the Cats

Agonistic Behaviors: Agonistic behavior values (which are the residuals after regression of agonistic behavior frequencies on cat presence rates) were not normally distributed. Therefore, we used non-parametric tests to examine the effect of sex, neuter status, and anthropogenic variables (type of housing, SES of neighborhood, and caretaker treatment level), separately, on the frequency of agonistic behaviors.

Neutered cats showed lower frequencies of agonistic behaviors compared with intact cats (Mann-Whitney *U* test, Z = –2.72, $p < 0.01$). Caretaking level also had a significant effect on frequency of agonistic behaviors (Kruskal-Wallis, $\chi^2 = 12.99$, $p < 0.01$, maximal ($n = 161$) = –0.18 ± 0.05, medium ($n = 31$) = 0.12 ± 0.18, minimal ($n = 74$) = 0.35 ± 0.16, see Figure 4), and a post-hoc test revealed that aggression was higher among cats receiving the minimal treatment level compared with those receiving the maximal treatment level ($p < 0.01$). To further examine the difference between the caretaking levels, we summed the positive agonistic behavior values for each treatment level and compared them (in relation to the total population) between levels (Figure 4). At the minimal and medium caretaking level, more cats exhibited high agonistic behavior values out of the total number in that treatment level (30 of 74 and 12 of 31 cats, respectively) compared with cats at the high caretaking level (36 of 161 cats). The contribution of the neutered and intact cats to this high aggression was equal at all caretaker levels (Mann Whitney *U* test for the minimal caretaking level, $Z = –0.16$, $p = 0.89$, for the medium level $Z = –0.48$, $p = 0.7$, and for the maximal level, $Z = –0.21$, $p = 0.85$).

Type of housing and SES had no effect on the frequency of agonistic behaviors.

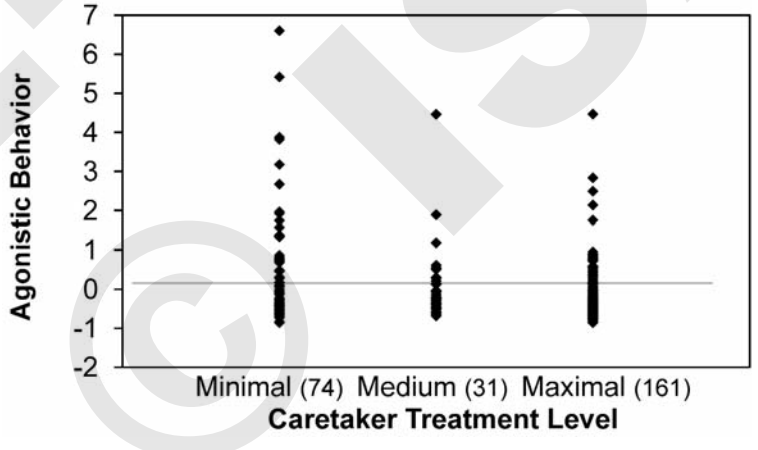

Figure 4. Agonistic behaviors of cats from the eight study groups, at each of the caretaker treatment levels. Agonistic behavior values are the residuals from a regression of agonistic behavior frequencies on cat presence rates. To analyze the difference between the treatment levels, only positive values (above the x axis) were considered. The numbers in parentheses represent numbers of cats.

Pregnancies: The frequencies of pregnancy were not normally distributed. Therefore, we examined the effect of type of housing, SES of neighborhood, and caretaker treatment level, separately, on the frequency of pregnancies, using non-parametric tests. We found that in high-SES groups, the frequency was significantly lower compared with the low-SES groups (Mann-Whitney *U* Test, $Z = -2.31$, $df = 64$, $p < 0.05$). The mean number of pregnancies (± *SD*) was 0.6 ± 0.12 ($n = 23$) and 0.95 ± 0.09 ($n = 41$) in high and low-SES feeding groups, respectively. Type of housing and caretaker treatment level did not significantly affect pregnancy frequencies.

Proportion of Neutered Cats: At the beginning of the study, the proportion of neutered cats of the total number of cats in all the high SES feeding groups was higher than 50% (a range of 58–90% neutered cats). However, while three of the four low-SES groups had neutering proportions of 8–23%, one low-SES group had a similar proportion to those found in the high-SES groups (69% neutered cats) (Figure 5).

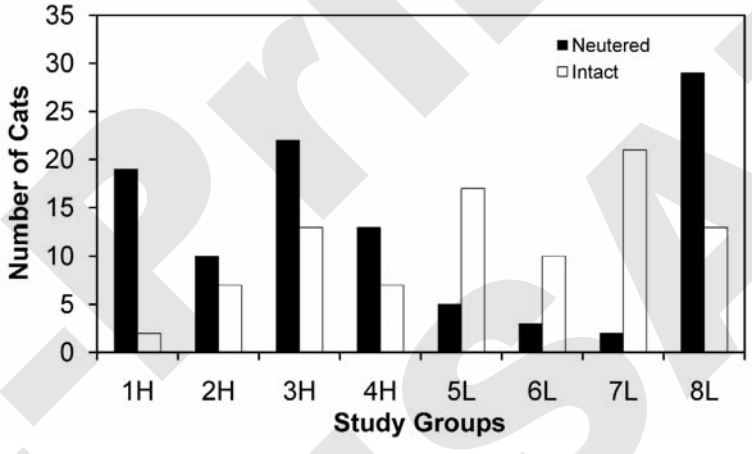

Figure 5. Number of neutered and intact cats in the study groups (groups 1–4: H = high SES, groups 5–8: L = low SES) at the beginning of the study.

A logistic regression was performed to determine whether neighborhood SES and type of housing are good predictors of whether a cat will be neutered or not (caretaker level was not used in this analysis because their involvement in TNR had already been evaluated in their interviews—see Methods). Socio-economic status was found to be a significant predictor of whether a cat would be neutered ($n = 193$, logistic regression, B = 1.24, $SE = 0.30$, R^2 (Nagelkerke) = 0.12, $p < 0.001$). Neutering of cats was 3.5 times (= Exp(B)) more likely to occur in high-SES (north Tel Aviv) groups compared with low SES-groups (south Tel Aviv). The type of neighborhood housing was not a good predictor of neutering status in the regression model.

Cortisol Concentrations: Multiple hierarchical regression analysis was used to examine the effects of sex, neuter status, SES, caretaker treatment level, and type of housing on cortisol levels. In the first block, neutering and sex were entered using the enter method. In the second block, caretaker treatment level, SES, and type of housing were entered using the forward stepwise method. Intact cats ($n = 46$) had significantly higher cortisol levels compared with

neutered cats ($t_{(101)} = -3.47$, $n = 55$, $p < 0.001$, $R^2 = 0.14$). Since the effect of caretaker treatment level was close to significant ($t_{(101)} = 1.96$, $p = 0.053$), and since the four combinations of sex and neutering status showed different trends for cortisol as a function of caretaker treatment level (see Figure 6), we tested the effect of this factor on cortisol levels in each combination (of neutering × sex) separately. Cortisol levels in neutered females with minimal caretaker treatment level were significantly higher compared with those in neutered females with medium and maximal caretaker treatment levels (minimal: 7.91 ± 5.22 pg/mg hair, medium: 1.45 ± 0.38 pg/mg hair, maximal: 1.89 ± 0.79 pg/mg hair, Figure 6, one-way ANOVA, $F = 3.78$, $p < 0.05$). Cortisol levels of intact females, intact males, and neutered males did not differ significantly between caretaker treatment levels.

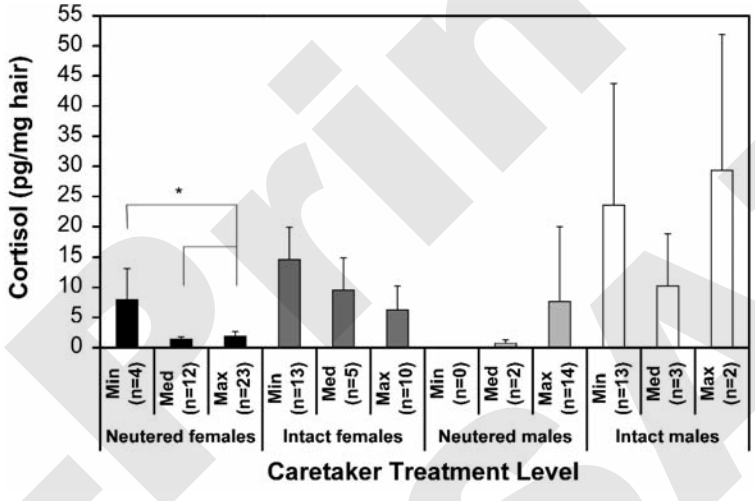

Figure 6. Cortisol levels in neutered females (a) intact females (b) neutered males (c), and intact males (d) as a function of caretaker treatment levels. No hair samples were obtained from neutered males at the low caretaking level, and therefore are absent from the figure.

Discussion

The results of this study support our hypothesis that anthropogenic factors, specifically socio-economic status and caretaker treatment level, influence the reproduction management, behavior, and welfare of urban free-roaming cats. Only a small number of studies (e.g., Oppenheimer 1980; Calhoon and Haspel 1989; Childs 1990; Haspel and Calhoon 1990; Alves et al. 2005) have considered the effect of human behaviors and actions on free-roaming, urban cat overpopulations. The present study adds to this body of knowledge and, together with the feeding stations survey, constitutes one of the few rigorous, academic attempts to evaluate the efficacy of allocating selectively targeted financial and manpower resources in order to achieve the most effective management of free-roaming cat populations in Israel.

Descriptive Characteristics of Feeding Groups in Tel Aviv

The number of registered feeding stations is considerably high (622 over a six-year period) for a city the size of Tel Aviv (53 km²). Divided by the total combined area of the northern and

southern neighborhoods (27 km^2), the mean number of feeding stations is 23/km^2. Natoli et al. (2006) reported 3,533 registered colonies in Rome's D area (517 km^2) (Azienda USL Roma D) over a period of four years, which reflects a colony density of about 7 stations/km^2. This difference may simply reflect the higher population density in Tel Aviv (7,500 people/km^2) (Israeli Central Bureau of Statistics 2008) compared with Rome (2,500 people/km^2) (ISTAT, Instituto Nazionale Di Statistica 2005). Beck (2002) suggests that urban stray dog population densities are higher in areas where human density is higher, perhaps due to more abundant resources. We suggest that where human density is higher, more food is also available to the cats, as more people feed cats for a given area, and the result is a higher density of feeding stations in Tel Aviv compared with Rome.

Most registered feeding groups (for TNR) were only visited once by the veterinary services during the surveyed six-year period. Without continuous neutering, the proportion of neutered cats in such groups will quickly become insignificant due to the immigration of intact cats (Levy and Crawford 2004), and the potential long-term efficacy of this method on a city-scale is thus jeopardized. In addition, the mean neutering rate found in our groups was 50%. Previous authors have suggested that in order to manage a population successfully, an annual neutering rate of at least 75% should be continuously maintained (Xemar, Pontier and Artois 1998; Andersen, Martin and Roemer 2004). Thus, although the city-operated TNR program is a step in the right direction, it may not be enough in itself for efficient cat management in a city with such a successful free-roaming cat population as Tel Aviv.

Rabies is a major zoonotic disease in Israel, and many measures are taken to prevent human exposure to the disease (Gdalevich et al. 2000). It is therefore surprising that only 13% of the surveyed cats were vaccinated and that such vaccination is not mandatory. However, this number is probably an under-estimate, since it only represents the cats from registered colonies. As far as optional vaccination for rabies is concerned, we are not aware of references to other studies of free-roaming cats and therefore cannot compare our own results with other findings. Compared with the optional vaccination, in other studies that initiated or followed TNR programs, rabies vaccination was part of the routine procedure (Levy, Gale and Gale 2003; Wallace and Levy 2006), as the name of the program implies (TTVARM: Trap-Test-Vaccinate-Alter-Return-Monitor) (Hughes and Slater 2002).

The proportion of pregnant females in the survey was about 15%. This figure is identical to that found in a 12-year survey of 103,643 feral cats from seven TNR programs in the United States (Wallace and Levy 2006). Pregnancies were mainly observed between January and September, peaking in February and March, similar to previous reports (Nutter, Levine and Stoskopf 2004; Wallace and Levy 2006). Lower rates of pregnancies were observed in the fall months, between October and December, similar to other studies (Nutter, Levine and Stoskopf 2004; Wallace and Levy 2006).

A greater number of females than males was found in the current study, which was also reported by Wallace and Levy (2006) and in a survey in England of 192 feeding groups (Rees 1981; Remfry 1981). The reason for this skewed ratio is not clear. Perhaps the possibility of capturing females is higher than that of capturing males, because females usually roam less than males and are therefore more likely to be present at the feeding site (Liberg and Sandell 1988; Mirmovitch 1995). In addition, due to their greater territorial behavior and roaming habits, male mortality may be higher than that of females (Remfry 1981).

SES Effects on Reproduction and Neutering Rates and the Relationship between the Veterinary Services and Caretakers

Several important differences were revealed in the current study between north (high SES) and south (low SES) Tel Aviv in the characteristics, dispersion, and number of cat feeding groups, as well as in neutering and pregnancy rates. According to our survey, feeding group density in north Tel Aviv was more than two times that of south Tel Aviv. However, the mean human population density does not differ between the northern and southern neighborhoods (population census of 1995–1998 of Tel Aviv). Since the urban cat is directly dependant on humans for its food supply, whether this is supplied intentionally (i.e., by caretakers) or unintentionally (i.e., from refuse or trash cans), we expect both geographical areas to be similar "food-rich environments" (Mirmovitch 1995) and thus support a similar number of cats. In south Tel Aviv, where fewer feeding stations are registered, the unintentional food supply may be of greater importance for the cats. In 2006, the Green Forum of Tel Aviv, of the Society for the Protection of Nature in Israel, issued a report on environmental health risks in south Tel Aviv. One of the findings was that there are more large, collective trash cans and fewer small, individual trash cans in the area compared with north Tel Aviv. The former are several meters long and are usually open, and thus can easily accommodate the nutritional needs of several cats. It is possible that "natural" feeding groups form around these cans (as opposed to the "artificial" ones fed by caretakers). The former are probably not registered by the TNR service, since they do not have a daily caretaker, and thus although the number of cats in the south might be equal to their number in the north, there are fewer registered feeding stations.

High SES is often correlated with higher education levels (Cohen, Doyle and Baum 2006), and has also been found to be linked to higher awareness or concern regarding various health and social issues (de Walle and de Jong-van den Berg 2007; Morley et al. 2008). Cat caretakers in the north, due to their higher education levels, may thus have been more aware of the cat management possibilities and, consequently, more involved in neutering activities, through registering their feeding group and requesting repeated veterinary visits, as well as engaging in privately-funded TNR (resulting in more neutered cats, as was found in the field study). Several reports suggest that the higher the education level, the higher the trust people have in the government or civil services (Christensen and Leaegreid 2002; Delhey and Newton 2002). South Tel Aviv residents, of lower education levels, may have a lesser degree of trust in the TNR public service, which is expressed in lower registration rates of feeding stations. Indeed, from in-depth interviews conducted by the authors (Finkler and Terkel in press), some south Tel Aviv caretakers reported their lack of trust as a reason for not using the veterinary public services for TNR (i.e., saying that the veterinary department takes the cats but does not return them), as was also noted by caretakers in studies conducted in Rome (Natoli et al. 1999; Natoli et al. 2006).

Neutering rates were higher and reproduction rates lower in feeding groups located in high-SES areas compared with low-SES areas. It is possible that in cases where caretakers had a long wait for the arrival of the TNR veterinary services team, as was previously reported (Natoli et al. 2006), more resourceful caretakers, from high-SES neighborhoods, had neutered the cats at their own expense, as was found in the current study. In addition to the cost of neutering, another potential cost—for rabies vaccination—may pose a financial burden for the less affluent caretaker. A single rabies vaccine is offered to the caretaker at a cost of NIS 12 (ca. US$3), and can be given to the cat during anesthesia for TNR, with the caretaker's consent. Less affluent caretakers were probably more reluctant to pay for the rabies vaccine—hence, the lower number of vaccinations in the south.

Residents of lower SES neighborhoods may be discriminated against in terms of access to certain municipal and social services (Williams 1998; Altschuler, Somkin and Adler 2004). In the present study, the number of veterinary visits per cat group in northern groups was significantly higher compared with the southern groups. It is possible that the veterinary services responded differently to the requests received from south and north Tel Aviv, due to discrimination against poorer neighborhoods. However, we consider this unlikely.

Caretaker Effects on Aggression and Cortisol Levels

In the current study, at least two aspects of good caretaking may be related to the reduced aggression and cortisol levels. First, from the interviews with the caretakers, high-level caretakers spent more time with the cats, before, during, and after feeding, and second, these caretakers also admitted to being more bonded with the cats they feed, which they expressed in naming each cat and being able to easily pet and approach most of them. Although the relationship between free-roaming cats and their caretakers has been previously examined (Haspel and Calhoon 1990; Natoli et al. 1999), and many caretakers report a strong bond with the cats they feed (Centonze and Levy 2002), the potentially ameliorating effect of good caretaking on the welfare of these cats has not been studied. Some relevant ideas on the possible enrichment effect of good caretaking on free-roaming cats, specifically of time "invested" in the cats and physical interaction with them, can be derived from studies on other species. "Low" aggression dogs were reported to be groomed more often by their owners, and owners spent more time with them and had greater attachment to them compared with "high" aggression dogs (Podberscek 1997). In the case of military dogs, being taken to the handler's home (i.e., spending more time with the handler) was associated with improved welfare (Lefebvre et al. 2007).

Good caretaking was also shown to be related to reduced cortisol levels, indicating lower stress levels. Other studies have also shown this link: for example, a study on captive clouded leopards showed that the more time keepers spent with the animals, the lower the animals' cortisol levels (Wielebnowski et al. 2002). Another study showed that positive human interaction had a moderating effect on the hypothalamic-pituitary-adrenal (HPA) activity of sheltered dogs (Hennessy et al. 1998; Hennessy et al. 2002). These studies all demonstrate the importance of positive animal–owner/handler interactions in reducing aggression and improving welfare. Our own findings show that this may also be the case for the cat–human relationship, as evidenced in the reduced aggression of the cats in the areas with high caretaking. However, the extent of such influence deserves further attention. If aggression levels can be reduced by better caretaking, the noise nuisance caused to humans by the cats' social activity, especially during the reproductive season (Gunther and Terkel 2002), can be minimized.

Cortisol levels of neutered females were lower at higher caretaking levels. There was also a tendency for this in intact females, but this was not significant. Females may be more influenced by the caretaker's actions and behaviors because they roam less compared with males (Liberg and Sandell 1988) and therefore are more consistently present at the feeding site, and thus may be in daily contact with the caretaker (Wallace and Levy 2006). Additionally, neutered females, not needing to search for nesting sites or to have to raise kittens (Bradshaw 1992; Devillard, Say and Pontier 2003), are expected to roam less than intact females and be more present at the study site, and thus be more bonded to the caretakers. Consequently, neutered females can benefit from good caretaking more than other cats in the group, which may be expressed in reduced cortisol levels, as was previously demonstrated for other species

(Hennessy et al. 1998; Wielebnowski et al. 2002). Another explanation for the reduced cortisol levels of the neutered females is that of reduction of the excitatory effect of gonadal steroids on the HPA axis (Seale et al. 2004).

Conclusions

The results of this study demonstrate the need to account for anthropogenic factors when determining appropriate solutions to cat overpopulation. We recommend that municipal and private organizations, as well as other individuals involved with cat management and caretaking, include in their TNR method consideration of the socio-economic status of city areas, and focus more on those areas that rely mainly on the city's free-of-charge services, which according to this study's results may currently not be sufficient to control the cat populations. Educational campaigns can help caretakers to learn about the neutering options available from the municipal veterinary services. High caretaker treatment can contribute to lowering cats' aggression levels, thereby both reducing disturbance to people and leading to improved welfare of the cats. As people in urban areas interact with the cats on a daily basis, it is in our interest to find new ways to effectively incorporate an understanding of the factors that influence this interaction into practical cat management, for the benefit of both the human and the cat populations.

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