**Population compensation mechanisms counteract the effectivity of high-intensity free-roaming cat sterilization - A 12-year city-scale longitudinal experiment**

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**Abstract**

The domestic cat (*Felis sylvestris catus*) has been listed among the 100 worst invasive alien species in the world. Apart of ecological damage, free-roaming cats (FRC) cause nuisances and public health risks. On the other hand, cats are considered as highly popular companion animals. This ambiguity led to the common use of fertility control as a humane population management strategy as an alternative to culling. However, to date, there is no controlled evidence for the long-term effectiveness of fertility control for management of FRC metapopulations as well as for the management of other open large-scale populations of vertebrate species.

Here we present the results of a long-term, large-scale experiment, examining the outcome of a commonly used fertility control method, the Trap-Neuter-Return (TNR) program of an open urban metapopulation of FRC. The study was conducted in a large city in Israel and progressed in three phases: (1) ‘control period’, three years preceding the TNR program (years 2007-2009), (2) ‘mixed treatment period’, five years of TNR in randomly allocated neighborhoods spanning half of the city (years 2010-2014) resulting in high and low neutered neighborhoods, and (3) ‘full treatment period’, four years of implementation of the TNR program over the entire city (years 2015-2018). Population dynamics were determined by analysis of five indicators: cat and kitten counts along random transects, kitten per queen ratio as well as municipal records of carcasses and reproduction reports. In addition, the effect of anthropogenic co-factors was assessed.

Overall, 13,718 cat-observations from annual samplings and a further total of 36,544 carcasses and 12,217 reproduction reports were collected for analysis. During the TNR program a total of 22,144 FRC were neutered, reaching a median of 76% and a range of 28-100% neutering percentage in the city neighborhoods at the end of the study.

During the control phase of the study, an increase in FRC population was indicated. In the mixed treatment phase, an annual growth of ca. 21% was observed in the low neutering neighborhoods (up to 30% neutering level). In the high-TNR neighborhoods (ca. 75% median neutering level), population size was stabilized but not reduced, possibly due to migration of cats from low-neutering neighborhoods. In the full treatment phase, an annual reduction of 7% was observed. However, it was accompanied by an increase in kitten per queen ratio, reproduction reports, and reduced carcasses reports. These findings suggest accelerated fertility and survival as possible compensatory mechanisms, diminishing the effect of TNR.

Our study illustrates the importance of long-term experimental studies in understanding the full ecological consequences (or implications) of management programs. We conclude, that in order for a TNR program to be effective for reducing the size of an open FRC population size it demands an investment of significant resources for achieving spatial contiguity of high neutering percentage over long periods. As we showed, even under such conditions it is limited by the effect of population compensation mechanisms. Its use for diminishing ecological adverse effects of FRC is therefore questionable.

Abbreviations:

FRC=Free-Roaming Cats

TNR=Trap-Neuter-Return

SA=Statistical Areas

**Introduction**

Invasive alien species are acknowledged as the second most common threat to biodiversity after habitat lost. As such, are a growing driver of species extinction, and their damage is one of the most difficult to reverse (Van Ham, Genovesi et al. 2013, Bellard, Cassey et al. 2016). As a generalist predator, the domestic cat (*Felis sylvestris catus*) has been listed among the 100 worst non-native invasive species in the world (Lowe, Browne et al. 2000).

The domestic cat is a fast life-history species (i.e. early maturation, smaller body size, rapid reproduction) (Feldman and Nelson 1996, Scott, Levy et al. 2002, England and Heimendahl 2010), which had been distributed around the globe mainly as a pet (Serpell 2000). Along the years it formed nondomiciliary and often human-independent populations known as Free-Roaming Cats (FRC) which were shown to cause adverse environmental effects (Lowe, Browne et al. 2000, Slater, Di Nardo et al. 2008, Dabritz and Conrad 2010, Medina, Bonnaud et al. 2011, Gerhold and Jessup 2013, Gunther, Raz et al. 2015, Loss and Marra 2017). The most prominent ecological adverse effect of cats is on islands, where they are considered as responsible for at least 14% of the global bird, mammal, and reptile extinctions and are the principal threat to almost 8% of critically endangered birds, mammals, and reptiles (Medina, Bonnaud et al. 2011). Moreover, cats also cause a significant ecological effect on mainland, not only due to direct predation but also due to the transmission of diseases to other species, fear-related effect, and alteration of demographic processes such as source–sink dynamics (Loss and Marra 2017). By the potential to transmit certain zoonotic diseases and by direct aggressive attacks toward humans, FRC constitute a hazard to public health (Dabritz and Conrad 2010, Gerhold and Jessup 2013), and further might cause nuisance to humans, mainly by impairing sanitation (Slater, Di Nardo et al. 2008, Gunther, Raz et al. 2015). These human-cat negative interactions are further enhanced by the increased urbanization over the last decades, and the formation of FRC metapopulations (Boone 2015).

The adverse effects caused by FRC and other invasive alien species raised the motivation to artificially manage their populations, aiming either to diminish their related-nuisances and their damage to agro-systems (Doerr, McAninch et al. 2001, Prokopy 2003, Ramsey 2005, Donnelly, Wei et al. 2007, Dalla Villa, Kahn et al. 2010, Pinter-Wollman 2012, Linz, Bucher et al. 2015, Massei, Kindberg et al. 2015), or to preserve natural ecosystems (Twigg, Lowe et al. 2000, Bester, Bloomer et al. 2002, Parkes and Murphy 2003, Campbell and Donlan 2005, Grarock 2013). Population management is usually performed by modifying two natural processes: the ‘bottom-up’ process, which refers to resource limitation in the habitat, and the ‘top-down’ process that refers to actions that are applied on individuals (e.g. predation)(Sinclair and Krebs 2002, Sinclair 2003, Gandiwa 2013).

Of the top-down control programs, culling affects population dynamics by an increase in mortality above the natural rate, whereas fertility control methods aim at decreasing the natural reproduction rate (Schmidt, Swannack et al. 2009). There are several examples for failure of culling to accomplish population control offast life-history species, such as voles (Hein and Jacob 2019), mice, rats, jirds (Shilova and Tchabovsky 2009), rabbits (Williams, Parer et al. 1995), and foxes (Baker and Harris 2006). On the other hand, information on the efficacy of fertility control on vertebrate populations is scarce (Ransom, Powers et al. 2014). Specifically for FRC, theoretical studies predicted that culling performs better than Trap-Neuter-Return (TNR), which is the common fertility control method (Schmidt, Swannack et al. 2009, Loyd and DeVore 2010, McCarthy, Levine et al. 2013, Miller, Boone et al. 2014). However, despite these predictions, the TNR method has been progressively implemented in FRC populations over widespread areas, mainly due to moral considerations (Longcore, Rich et al. 2009, Denny and Dickman 2010, Boone, Miller et al. 2019, Wolf and Schaffner 2019).

Several field studies, which aimed to determine the association of TNR management programs with FRC population dynamics, demonstrated a decrease in population growth indicators (Neville and Remfry 1984, Hughes and Slater 2002, Hughes, Slater et al. 2002, Levy, Gale et al. 2003, Nutter 2005, Natoli, Maragliano et al. 2006, Algar, Hilmer et al. 2011, Jones and Downs 2011, Levy, Isaza et al. 2014, Swarbrick and Rand 2018, Zito, Aguilar et al. 2018, Kreisler, Cornell et al. 2019), while others showed a stabilization or an increase in indicators for population growth (Castillo and Clarke 2003, Mannhart 2007, Gunther, Finkler et al. 2011, Kilgour, Magle et al. 2017). These inconsistent results might stem from differences in management efforts, in the examined populations (e.g., close versus open populations, small versus large-scale populations) and in their environment. The inference of the overall population consequences of TNR is further limited due to: absence of control (Neville and Remfry 1984, Hughes and Slater 2002, Hughes, Slater et al. 2002, Castillo and Clarke 2003, Levy, Gale et al. 2003, Natoli, Maragliano et al. 2006, Mannhart 2007, Jones and Downs 2011, Swarbrick and Rand 2018, Kreisler, Cornell et al. 2019); combining TNR with other top-down control tactics (i.e. adoption and euthanasia of clinically ill or retrovirus positive cats) (Neville and Remfry 1984, Hughes and Slater 2002, Hughes, Slater et al. 2002, Levy, Gale et al. 2003, Algar, Hilmer et al. 2011, Jones and Downs 2011, Levy, Isaza et al. 2014, Swarbrick and Rand 2018, Zito, Aguilar et al. 2018, Kreisler, Cornell et al. 2019); short-term follow-up (Neville and Remfry 1984, Hughes and Slater 2002, Castillo and Clarke 2003, Mannhart 2007, Gunther, Finkler et al. 2011, Jones and Downs 2011, Levy, Isaza et al. 2014, Kilgour, Magle et al. 2017, Zito, Aguilar et al. 2018); small sample size (Neville and Remfry 1984, Hughes and Slater 2002, Castillo and Clarke 2003, Levy, Gale et al. 2003, Nutter 2005, Gunther, Finkler et al. 2011, Jones and Downs 2011, Swarbrick and Rand 2018); relying on indirect indices of population growth (Hughes and Slater 2002, Hughes, Slater et al. 2002, Levy, Isaza et al. 2014, Zito, Aguilar et al. 2018); and examining populations in secluded areas (Algar, Hilmer et al. 2011, Kreisler, Cornell et al. 2019).

To close the knowledge gap and overcome the shortcomings of previous studies Boon et al. (2014) call for a long term and a large scale study in a FRC meta-population. Here we present the results of a 12-year longitudinal experiment designed to assess the effect of neutering‒a top-down process‒and anthropogenic environmental‒ bottom-up processes on the long-term temporal and spatial dynamics of FRC metapopulation. The comparisons of FRC dynamics before, at partial, and at full TNR programs suggest that population compensation mechanisms counteract the effectivity of this top-down strategy.

**Materials and Methods**

**Study site**

The study was conducted during 2007-2018 in the city of Rishon-LeZion, Israel. The city human population comprised 240,666 residents at the end of 2014 (Central Bureau of Statistics, Israel), living in a jurisdiction area of 50 km2. Rishon-LeZion is located within the greater Tel-Aviv metropolis and is divided into 64 statistical residential areas. Determined by the Israeli Central Bureau of Statistics, each statistical area (SA) (which is similar to commonly used city blocks) that consists of ca. 4000 residents, which form an approximately homogeneous sub-division of the city’s neighborhoods. Four statistical areas comprised mainly of commercial, industrial or research facilities and were excluded from this study, since they substantially differed from the rest of the city.

**Study design**

The study period was divided into three consecutive phases: (1) ‘control period’, prior initiation of the TNR program, between January 2007 to the end of 2009; (2) ‘mixed treatment period’, implementing a multi-annual TNR (Trap-Neuter-Return) program over half of the city’s neighborhoods, since the end of 2009 until October 2014. The city SA’s were then classified according to the observed neutering percentage at the end of this period: Group-1, low-TNR, including all SA’s in the first quartile, and Group-2, high-TNR, including all SA’s in the fourth quartile; (3) ‘full treatment period’, applying the TNR program into the entire city, between November 2014 to December 2018 (**Figure 1**). A total of 22,144 FRC were neutered during the entire study period. Trapping was routinely performed with a trigger-plate trap. Where neutering percentage reached high levels ca. 70%, and in order to catch trap-shy cats, specific trapping procedures were selectively used: nets, traps that were triggered by remote control, shooting sedative drugs by blow-pipe, and accepting assistance from feeders of FRC that gained personal trust of specific cats.

FRC that underwent ovariohysterectomy or castration procedures were marked by cutting their ear tip. Marking was performed under general anesthesia during sterilization (Cuffe, Eachus et al. 1983). Following recovery, FRCs were released back at the same location where they had been trapped. The veterinary services kept meticulous records for each neutered FRC, including the date and the location of trapping (documented as the street address closest to the trapping location).



**Figure 1**: Dot plot (1) and heat map (2) showing locations and intensity of Trap-Neuter-Return locations during two consecutive phases: **(A)** Phase-2, mixed treatment period between the end of 2009 to end of 2014. During this phase, 10,925 FRC were neutered with a male:female ratio of 1:1.07, and **(B)** Phase-3,full treatment period, since the end of 2014 to the end of 2018. During this phase, 11,219 FRC were neutered with a male:female ratio of 1:1.06.

**Data collection**

FRC population dynamics in each SA were determined by using the following variables: counts of FRC, kittens, neutered cats, and reports regarding carcasses, and reproduction. Cat, kitten and neutered counts were collected in 50 SA via repeated annual surveys performed along fixed walking transects using a stratified random sampling design. Sample surveys were performed in years 2012, 2013, 2014, and in 2018. For each observed cat, individual characteristics were documented including the neutering status (according to ear marks). A comprehensive description of this sampling method is detailed in Gunther *et al.* (2020).

Reports regarding carcasses and reproduction of FRC had been documented by the municipal emergency call center during 2007 to 2018. The call center was continuously available and received voice reports from concerned residents regarding real-time events for the entire study area. The following data were recorded for each reported event: time and date of the call, location of the event, personal details about the calling resident, and synopsis of the reported event.

Data on the anthropogenic environmental covariates were collected and generated per each SA as follows:

1. The *number of residents* in 2014 and 2017 was determined by the Central Bureau of Statistics, Israel. Data were divided by the area of each SA in km2, and used as the *human* *population density*.
2. The *socio-economic-status* in 2008 was determined by the Central Bureau of Statistics, Israel based on the 2008 national census. The estimated socio-economic status was measured on a continuous scale ranging from 389 to 1395. These ranks were calculated by the Israeli Central Bureau of Statistics and represent a combination of variables including demographic composition, education, labor, housing and income.
3. Number of *waste bins* as documented by the municipal maintenance department for the end of 2012 and 2018. Waste bins data consist of the location, volume and type of each bin (e.g. closed bins, closed and open dumpsters, underground waste containers, and garbage compactors). Data were divided into three sub-categories according to the potential accessibility of waste for cats: Un-accessible (underground waste containers and garbage compactors), partial accessibility (close bins and close dumpsters), and full accessibility (open dumpsters). In addition to testing each sub-category separately, the partial and full accessible waste bins were combined and tested together. Data were geographically coded, summarized as total waste bin volume per each SA, and then standardized by the number of residents. Prior to inclusion of the sub-categories in the multivariable model, correlation was tested between each pair of sub-categories.
4. *FRC feeding locations* were reported in the 2013-telephone survey that was performed among feeders of FRC (for more details see Gunther *et al*. 2016). Locations were geographically coded, summarized per each SA, and standardized by the number of residents. Due to the length of the study period, thisvariable was excluded from the 2018 analyses.
5. The location, number and type of *educational institutes* were documented for 2014 and for 2017 by the municipal GIS department. Educational institutes were summarized per each SA, and standardized by the number of residents.
6. The type and location of *food marketing businesses* (e.g. butcher shops, restaurants, supermarkets, catering) were documented for 2012 and 2018 by the municipal department for businesses registration and by the municipal veterinary services. Food marketing businesses were geographically coded, summarized per each SA, and standardized by the number of residents.
7. *Area of buildings*, and *area of parks* were documented for 2014 and for 2017 by the municipal GIS department.Data were summarized per SA and standardized by the area of the SA in km2.
8. The *age of each neighborhood* was documented by the municipal information and research center. This is relevant to the study as the sanitation and potential hiding places that are available to the cats depend on the architecture and infrastructure, which differ substantially between neighborhoods according to the year of development; from the oldest neighborhood established at 1882 to the youngest at 2008.
9. *TNR actions* were geographically coded and summarized per SA and month. 345 trapped cats were omitted due to missing or unclear capturing location. Further 3479 cat-trapped locations were randomly chosen from a specific reported area, such as parks or blocks.

**Statistical analysis**

Geographical data was summarized and presented by ARCGIS map. Statistical analysis was performed using the following packages in R software (R Core Team 2014): ‘nlme’ for Generalized-Liner-Mixed-Models (Pinheiro, Bates et al. 2017); ‘MuMIn’ for model average analysis (Barton and Barton 2015); ‘forecast’ for time series analysis ; ‘broom’ and ‘ggplot2’ for model diagnostics analysis and for generating figures (Silge and Robinson 2016, Hyndman and Athanasopoulos 2018); ‘MASS’ for spatial auto-correlation analysis ; ‘Car’ for model diagnostics analysis (Fox and Weisberg 2011, Ripley, Venables et al. 2013) . Unless stated otherwise, in all analyses a 5% significance level α was applied.

*The effect of the intensity and spatial contiguity of TNR on FRC and kitten counts*

Outcome variables were analyzed as follows:

1. Annual counts of *FRCs, kittens and queens along fixed walking transects* were summarized per SA and year.
2. Annual *neutering percentage* was calculated by dividing the total number of neutered cats observed in each SA and year by the total number of observed cats with identified neutering status.

For examining the overall annual differences, counts of FRC, kittens, neutered cats, and the kitten per queen ratio in 2012-2014 and in 2018 (dependent variables) were modeled using generalized linear mixed models (GLMM) with a negative binomial distribution. ‘Year’ was a fixed effect, and ‘SA’ was a random effect. The log-transformed ‘Transect length’ was included as an offset for FRC and kitten models, ‘FRC’ was used as an offset for neutered cats, and log-transformed ‘Queens’ (with an addition of 0.5 to all counts) was set as an offset for kitten counts in the kitten per queen ratio model. The same model was used to test contrasts between years, and results were adjusted for multiple testing using the Bonferroni method.

For demonstrating the association of TNR intensity with cat population trend, the FRC, kitten counts and kitten per queen ratio (dependent variables) were modeled using GLMM with a negative binomial distribution. In these models ‘Group’ (low vs. high TNR) was a fixed effect. The trend in each phase was modeled by including the first and last year of each phase, as fixed effect (i.e., phase-2: 2012 to 2014, phase-3: 2014 to 2018), as well as the interaction with ’Group’. The annual change was calculated by dividing the relevant estimated beta by the number of years in each phase (i.e., two for phase-2, and four for phase-3 (years 2012 and 2014 were not included in the calculations of phase-2 and phase-3, respectively, since observations took place on the end of these years)). ‘SA’ was a random effect. The log-transformed ‘Transect length’ was used as an offset for the FRC and kitten models, and log-transformed ‘Queens’ (with an addition of 0.5 to all counts) was set as an offset for kitten counts in the kitten per queen ratio models.

*The effect of the intensity and spatial continuity of TNR on cat carcasses and reproduction*

Outcome variables were analyzed as follows:

1. Resident *reports regarding FRC carcasses* were removed from the general animal related reports. Duplicate reports for an event were omitted. The remaining reports were geographically coded, and summarized per each SA.
2. Resident *reports regarding FRC reproduction* were analyzed similarly to the carcasses reports. Reports retained for analysis were those that explicitly contained key-words as “kitten” and “parturition” (for a more comprehensive explanation see Gunther *et al*. 2015).

To examine the association of municipal TNR actions with the trend of cat reports in the entire city (64 SA) during years 2007-2018, a time-series decomposition using the STL method (Cleveland, Cleveland et al. 1990) was performed for the monthly number of reports. Furthermore, differences in trends between low-TNR vs. high-TNR SA’s (the described above Group-1 and Group-2) were demonstrated. STL decompositions were generated separately for the monthly count time series of carcasses and reproduction reports of these two SA groups.

To examine the association of TNR intensity with trends of population indicators, the carcasses and reproduction reports were modeled using mixed negative binomial regression models (GLMM). The trend in each phase was modeled by including an interaction between the fixed variable ‘Phase’ (i.e., Phase-1 control period, Phase-2 mixed treatment period, and Phase-3 full treatment period) and ‘Group’. The annual change was calculated by dividing the relevant estimated beta by the number of years in each phase (i.e., three for phase-1, five for phase-2, and four for phase-3). ‘SA’ was modeled as random effect and log-transformed ‘Street length’ as the offset.

*The effect of neutering and anthropogenic environmental factors on the spatial population dynamics of FRCs*

Association of anthropogenic environmental factors with population indicators (i.e. the counts of FRCs, kittens, carcasses and reproduction reports) in the different SA’s was performed using a negative binomial regression model. ‘Street length’ was an offset for the carcasses and reproduction-reports models. ‘Transect length’ was an offset for the cat and kitten models.

Analysis was performed according to the following steps: first, a univariable analysis was conducted separately for each covariate. Second, statistically significant covariates were included in a multivariable analysis, after ruling-out collinearity. Third, interactions between covariates with the annual estimated neutering percentage were included in the models. Forth, by using ‘model average analysis’, the most parsimonious model was selected using the Akaike-Information-Criterion (AIC). Finally, for examining spatial dependence between the SA, an exponential variogram model was fitted to the distances between the centroids (central point of the SA polygons). Then, the fitted variogram was included into the ‘selected model’.

Analysis was repeated for each year separately, i.e. for years 2012-2014 and 2018.

**Results**

Overall, 13,718 cat-observations were documented, of which 1,486 were of kittens. 36,544 carcasses reports and 12,217 reproduction reports were analyzed in the current study. The neutering status of the observed cats was successfully recorded for 96% of the cat-observations, based on the detection of ear marks.

*The effect of the intensity and spatial contiguity of TNR on FRC and kitten counts*

At the end of the mixed treatment period the observed median neutering percentage in the entire city reached approximately 60% (rang 9-92%). At that phase, the overall count of cats increased by 26.5%. At the end of the following full treatment phase, the observed neutering percentage increased to a median of 76% and a range of 28-100%. During this phase a significant reduction by ca. 25% in the total counts of cats was observed (**Table S1, Figure 2**).

Further classification of the SAs into low and high TNR groups according to 2014 observations, resulted in twelve SA with up to 30% neutering rate (Group-1, low-TNR) and 15 SA with above 75% neutering rate (Group-2, high- TNR). After implementation of TNR to the entire city, neutering rate in Group-1 ranged between 28-100% with a median of 76%, and in Group-2 ranged between 30-89% with a median of 75.5% (**Figure 3**). This classification reveals an annual increase of approximately 21% in the FRC counts in Group-1 during phase-2. Though the annual trend in Group-2 was significantly lower than in Group-1, FRC counts in this group remained stable and did not decline. During phase-3, when spatial contiguity was maintained due to the performance of TNR in the entire city, a significant and similar reduction of ca. 7% per year was observed in both groups, (**Table 1**).

As opposed to FRC, no significant reduction was observed in the count of kittens during phases 2 and 3 in the entire city (**Table S1**). During phase-2 there is a large difference in the trend of kitten counts between Groups 1 and 2. However, it is not significant due to the large variability between the SAs within each group (probably caused by the low number of observed kittens). In phase-3 the trend in Group-1 is negative and significantly reduced compared to phase-2 while, the kittens count stabilize in Group-2 (**Table 1**).

To further examine the occurrence of possible compensation mechanisms such as increased fertility and/or kitten survival we analyzed the ratio of kitten to intact queens over the course of the study. Interestingly, during phase-3 the ratio of kitten to queen increased by 2.25 fold (**Table S1, Figure 2**). As shown in Table 2, this increase occurred primarily in the SAs of Group-1, which changed during this phase from low TNR to high TNR.



**Figure 2**: Parallel boxplots of the crude annual prevalence ofthe observedFRC counts, kitten counts, neutering percentage, and kitten to queen ratio in the city of Rishon LeZion (n=50 statistical areas), Israel in 2012-2014 and in 2018. The superscript letters represent statistically significant different years.

**Table 1:** The annual trend of FRC and kitten counts in phases 2 and 3 of the study: conducting TNR in half of the city neighborhoods (phase-2 during years 2012-2014), and implementing the TNR program into the entire city (phase-3 during years 2014-2018). In low-TNR SA’s (Group-1, n=12, initiating TNR program at the end of 2014) versus high-TNR SA’s (Group-2, n=15, initiating TNR program at the end of 2009). The letters a–b represent comparisons between pairs of phases within each group of SA’s (pairs with no significant difference are signed by the same superscript letter).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Variable | Phases | Annual trend Group-1 (CI95%) [%] | Annual trend Group-2 (CI95%) [%] | P-value |
| FRC counts | Phase-2  Phase-3 | 20.71 (8.21 to 34.65) a1  -7.28 (-9.81 to -4.67) b1 | 1.71 (-7.78 to 12.17) a2  -6.94 (-9.25 to -4.57) a2 | 0.022  0.923 |
| Kitten counts | Phase-2  Phase-3 | 19.78 (-13.41 to 65.69) a1  -17.84 (-30.49 to -2.89)b1 | -11.92 (-36.69 to 22.53) a2  0.18 (-14.20 to 16.97) a2 | 0.194  0.088 |
| Kitten to queen ratio | Phase-2  Phase-3 | -16.75 (-42.94 to 21.46) a1  25.11 (0.27 to 52.41)b1 | -5.13 (-34.52 to 37.45) a2  8.37 (-9.75 to 30.13) a2 | 0.628  0.295 |



**Figure 3**: Distribution of the (**A**) observed neutering percentage in the low-TNR (Group-1, n=12) and high-TNR SA’s (Group-2, n=15), and their spatial prevalence during the mixed treatment period (**B1**) and during the full treatment period (**B2**). (\*) Excluded commercial areas

*The effect of the intensity and spatial continuity of TNR on cat carcasses and reproduction*

The decomposition of the monthly time series data using the STL method revealed different trends along the study period for both the carcasses and reproduction reports in the entire city. These trends are linked to the application of the TNR program in the city: A positive trend was observed during the first phase (prior to initiation of the TNR program at the end of 2009). This was followed by a high magnitude negative trend, starting shortly after the onset of phase-2 and lasting until one year after it ends (years 2011 to 2015). One year after the onset of phase-3 (2016-2018), a stabilization of the carcasses reports and an increased trend of reproduction reports were observed (**Figure 4**). Both report types showed prominent seasonal pattern: Carcasses peaked twice, in May-June, and in October, whereas reproduction reports peaked only once during April-May. The seasonal pattern decreased gradually during the first years of the TNR program (2011-2014, phase-2) until its disappearance in the carcasses reports, which coincided with the implementation of TNR in the entire city (2015-2018, phase-3) (**Figure 4**).



**Figure 4:** (**A**)Monthly-based time series plots of municipal TNR actions (n=22,144), cat carcasses (n=36,544) and reproduction reports (n=12,217) from January 2007 to December 2018 across the entire city. And their (**B**) STL decomposition graphs of carcasses and reproduction reports linked with cumulative TNR percentage. Phase-1 refers to the period preceding the TNR program, during phase-2 the TNR program was conducted in Group-2, and in phase-3 it was implemented into both groups of SA’s.

Both the time series decomposition and the GLMM results of the carcasses and reproduction reports (**Figure 5**, **Table 2**) demonstrate a clear division of the study into three periods, coinciding with the TNR efforts in each group in each of the three phases. In phase-1, an increase in the number of carcasses reports was observed in both groups, while reproduction reports were stable in Group-1 and decreased slightly in Group-2. During this phase no significant difference in the annual trend of carcasses and reproduction reports were noted between the two groups (p=0.757 and p=0.229, respectively). In the second phase, the trends of carcasses and reproduction reports differed significantly between the two groups (p<0.001 for both carcasses and reproduction): In Group-2 a statistically significant negative trend of the carcasses and reproduction reports was observed while they remained stable in Group-1 SA’s. In phase-3, a further significant difference was found between the groups in the trend of carcasses and reproduction reports (p<0.001 for both): The carcasses reports decreased in Group-1 and stayed stable in Group-2, whereas the reproduction reports stayed stable in Group-1 and increased in Group-2.



**Figure 5**: Cumulative TNR percentage with month-based decomposition graphs of (A) cat carcasses and (B) cat reproduction reports in Group-1 SA’s (n=12, initiation of the TNR program at the end of 2014) versus Group-2 SA’s (n=15, initiation of the TNR program at the end of 2009), during 2007-2018 in the city of Rishon-LeZion, Israel. In the SA’s of Group-1, overall 2517 cats were neutered by the municipality and in Group-2 SA’s, 5410 cats were neutered. Phase-1 refers to the period preceding the TNR program, during phase-2 the TNR program was conducted in Group-2, and in phase-3 it was implemented into both groups of SA’s.

**Table 2**: The annual trend of carcasses and reproduction reports in three consecutive phases: preceding TNR program (phase-1 during years 2007-2010), conducting TNR actions in half of the city neighborhoods (phase-2 during years 2011-2014), and implementing the TNR program to the entire city (phase-3 during years 2015-2018). In low-TNR SA’s (Group-1, n=12, initiating TNR program at the end of 2014) versus high-TNR SA’s (Group-2, n=15, initiating TNR program at the end of 2009). The letters a–c represent comparisons between pairs of phases within each group of SA’s (pairs with no significant difference are signed by the same superscripted letter).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Variable | Phases | Annual trend Group-1 (CI95%) [%] | Annual trend Group-2 (CI95%) [%] | P-value |
| Carcasses reports | Phase-1 | 7.96 (-1.38 to 18.19)a1 | 6.00 (-1.60 to 14.17) a2 | 0.757 |
| Phase-2 | 0.90 (-2.99 to 4.95) a1 | -12.02 (-15.16 to -8.77) b2 | <0.001 |
| Phase-3 | -13.46 (-18.89 to -7.67)b1 | 0.63 (-4.74 to 6.29) a2 | <0.001 |
| Reproduction reports | Phase-1 | 7.84 (-8.34 to 26.88) a1 | -5.81 (-18.70 to 9.12) a2 | 0.229 |
| Phase-2 | 3.97 (-2.96 to 11.38) a1 | -24.57 (-30.06 to -18.64) b2 | <0.001 |
| Phase-3 | -6.95 (-17.04 to 4.37) a1 | 22.19 (9.59 to 36.25)c2 | <0.001 |

*The effect of neutering and anthropogenic environmental factors on the spatial population dynamics of FRCs*

While neutering percentage was negatively associated with kitten counts and reproduction reports, the human population density and accessed waste bins were positively correlated with cat population growth parameters, such as FRC counts, carcasses and reproduction reports. Other covariates as well as spatial dependence were not consistently associated with the measured parameters (**Table S2**).

**Discussion**

The unique experimental design of the current study, including its division into three phases and spatial units enables pinpointing the long- and short-term effects of TNR intensity and spatial continuity on FRC metapopulation dynamics. As expected, TNR actions resulted in a significant short-term reduction in kitten counts and reproduction reports. However, the long-term reduction in FRC population size was only mild (though significant). The findings of reduced carcasses and increased kitten to queen ratio support counteraction by population compensatory mechanisms, such as increased survival and reproduction of queens, which enhance population recovery.

Overall, kitten counts and reproduction reports showed a fast decline after applying TNR. However, exploration of the long-term trends of these variables revealed complex dynamics. Comparison of the two SA groups over the different study phases demonstrates a significant negative trend during the first years after initiating intensive neutering. As shown in the time series analysis, this trend was partially masked by seasonality. In addition, the negative trend was counteracted by a rebound elevation. This elevation is possibly explained by two processes—increased fertility and decreased mortality of juveniles and adults—that were previously reported to follow fertility control in domestic cats (Nutter, Levine et al. 2004, Gunther, Finkler et al. 2011, Gunther, Raz et al. 2018, Boone, Miller et al. 2019) and other vertebrates (Chambers, Singleton et al. 1999, Twigg, Lowe et al. 2000, Turner and Kirkpatrick 2002, Williams, Davey et al. 2007, Ransom, Powers et al. 2014, Smith, Hartmann et al. 2019). Both processes are supported by two observed trends in the current study. The first trend is an elevation of the kitten to queen ratio at the end of the study period. The second trend is the short- and long-term decrease of carcasses reports (in a greater magnitude than the overall FRC reduction) during the implementation of the TNR program. Both compensatory processes can be a result of the higher food availability and decreased resource competition, following population decline (Scott, Levy et al. 2002, Gunther, Raz et al. 2018). They can also be a result of diminished agonistic behavior of neutered cats (Finkler, Gunther et al. 2011), thus reducing competition. Regardless of the exact mechanism, the consequences are an improved mean body condition and higher survival of adults, kittens, or both (Nutter, Levine et al. 2004, Gunther, Finkler et al. 2011, Gunther, Raz et al. 2018, Boone, Miller et al. 2019).

Another potential population compensation process that was documented in other managed species is immigration to vacant niches from untreated surrounding (Ransom, Powers et al. 2014). The same process was reported in FRC populations, where the behavioral changes associated with sterilization enhanced immigration from low- into high-neutering populations (Gunther, Finkler et al. 2011). The design of the current study enables examining the occurrence of immigration phenomenon in a large scale. A reduction of population size was observed only during the full treatment period, while it remained stable in the treated SA’s during the mixed treatment period, despite a similar neutering percentage of ca. 70-75%. This neutering percentage was previously shown by mathematical models to be sufficient for reducing FRC population size (Foley, Foley et al. 2005, McCarthy, Levine et al. 2013). It can be thus concluded that for achieving reduction in population size, spatial contiguity should be maintained.

The current study was performed on an open-population of FRC, which might be influenced by other processes such as cat abandonment and migration from adjacent cities (Natoli, Maragliano et al. 2006, Gunther, Finkler et al. 2011, Miller, Boone et al. 2014). However, the city boundaries consist of the Mediterranean Sea on the west, and vast natural ground and highways on the south and east, which enable migration of cats only on the north. The small home range of urban cats (Metsers, Seddon et al. 2010, Thomas, Baker et al. 2014) limits their potential to immigrate over large distances and thus diminishes the influence of this process. As for abandonment, in comparison to other countries, the density of FRC population in Israel is among the highest in the world (Mirmovitch 1995, Finkler, Hatna et al. 2011). Therefore, the magnitude of cat abandonment should have been extremely high in order to contribute to the elevation of these populations. Since, abandonment and cat adoption depend on human behavior, and the demographic changes were only mild over the study period, it is unlikely to assume that human behavior changed dramatically over the years. Thus, abandonment and adoption probably had only mild effect on the trends of cat numbers during the mixed and the full treatment periods.

Considering the bottom-up processes, the human population density and accessed waste bins were found to be positively correlated with the FRC population size, carcasses, and reproduction reports. Increased food availability (e.g. leftovers and caretakers that feed the cats) is probably the biological explanation for these positive associations. However, a further explanation is related to the higher potential for human-cat encounter in denser human populations, increasing the likelihood for reports on cat carcasses, kittens, parturition, pregnant or lactating queens.

In summary, to date, this study is the largest and longest to test the influence of TNR on FRC metapopulation. Its unique experimental design, which control for both temporal and spatial effects, shows that the effect of fertility control on the size of open FRC metapopulations may be limited by rapid compensation mechanisms and occupancy of immigrant FRC. It can therefore be concluded that maintaining a very high neutering rate for a prolonged period and in spatial contiguity is necessary in order to counteract the effect of these compensatory mechanisms and to achieve a long-term reduction in population size. In the case of the current study, more than one million $US were invested in the TNR project during the study period, with a limited success. The significant reduction of carcasses and reproduction have several merits, such as improved welfare, reduction in cat-related nuisances and in zoonotic diseases. However, the study findings together with the fact that neutered FRC might still continue to hunt (Loyd, Hernandez et al. 2013, Bruce, Zito et al. 2019), questions the effectiveness of TNR for diminishing the predation of urban wild animals species by FRC. In the wild nature settings, fertility control might be even more challenging to apply and maintain. This might preclude this strategy for controlling FRC metapopulation or any other fast life history species in order to achieve a diminished ecological adverse effect.

**Acknowledgement**

The authors are thankful to Y. Even-Zor head of the municipal veterinary services, E. Gian head of the municipal GIS department, S. Keidar principle at the maintenance department, I. Ashkenazy from the municipal call center, E. Levi head of the municipal information and research center at the city of Rishon-LeZion.

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**Supplementary**

**Table S1:** Overall annual counts of FRC, kittens, neutered cats and queens, and municipal carcasses and reproduction reports in 50 SA in the city of Rishon LeZion, Israel.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Year | FRC | Kittens | Neutered | Queens | Neutering percentage | Kitten per queen ratio |
| 2012 | 3211 | 435 | 1517 | 387 | 47.24% | 1.12 |
| 2013 | 3233 | 318 | 1647 | 411 | 50.94% | 0.77 |
| 2014 | 4062 | 396 | 2054 | 513 | 50.57% | 0.77 |
| 2018 | 3122 | 337 | 2256 | 194 | 72.26% | 1.74 |

**Table S2**: Predicting factors for the annual spatial prevalence of FRC and kitten counts and for cat carcasses and reproduction reports in 2012-2014 and 2018. The ‘population density’ variable is presented per 10,000 residents, and ‘educational institutes’ per 1000 residents.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Outcome variable | Year | Predicting variables | Coefficient estimates (CI95%) | P-value | Distance of spatial correlation [m] |
| FRC counts | 2012 | Measured neutering ratio  Human population density | 0.658 (0.130 to 1.186)  0.204 (0.040 to 0.367) | 0.015  0.015 | Ng |
| 2013 | Human population density | 0.294 (0.134 to 0.454) | <0.001 | NA |
| 2014 | Full accessed waste bins | 0.041 (0.005 to 0.077) | 0.025 | NA |
| 2018 | Measured neutering ratio  Human population density | 0.603 (-0.210 to 1.416)  0.152 (-0.044 to 0.347) | 0.146  0.128 | Ng |
| Kitten counts | 2012 | NA | NA | NA | NA |
| 2013 | Measured neutering ratio | -1.630 (-2.600 to -0.661) | <0.001 | Ng |
| 2014 | Measured neutering ratio | -1.899 (-2.857 to -0.941) | <0.001 | 191 |
| 2018 | Measured neutering ratio  Educational institutes | -1.799 (-3.293 to -0.305)  -0.401 (-0.734 to -0.069) | 0.018  0.018 | Ng |
| Carcasses reports | 2012 | Human population density  Area of parks | 0.2581 (0.115 to 0.402)  -1.025 (-1.753 to -0.297) | <0.001  0.006 | Ng |
| 2013 | Human population density  Zero accessed waste bins | 0.409 (0.286 to 0.532)  -0.019 (-0.035 to -0.004) | <0.001  0.013 | Ng |
| 2014 | Measured neutering ratio  Human population density  Seniority of neighborhood  Interaction of human population density and seniority | -0.991 (-1.358 to -0.624)  0.620 (0.389 to 0.851)  0.012 (0.006 to 0.018)  -0.004 (-0.007 to -0.001) | <0.001  <0.001  <0.001  0.009 | Ng |
| 2018 | Total accessed waste bins | 0.020 (0.012 to 0.028) | <0.001 | 220 |
| Reproduction  reports | 2012 | Measured neutering ratio  Human population density | -1.794 (-2.489 to -1.099)  0.476 (0.262 to 0.691) | <0.001  <0.001 | 74 |
| 2013 | Measured neutering ratio | -1.437 (-2.279 to -0.595) | <0.001 | Ng |
| 2014 | Measured neutering ratio  Human population density | -2.519 (-3.111 to -1.927)  0.460 (0.282 to 0.639) | <0.001  <0.001 | 79 |
| 2018 | Measured neutering ratio  Total accessed waste bins | -1.119 (-1.918 to -0.319)  0.017 (0.006 to 0.027) | 0.006  0.002 | 214 |

Ng = Negligible distance (less than 50 m)

NA = Not Applicable