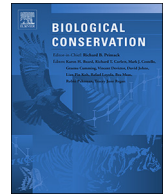




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Where there are girls, there are cats

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ABSTRACT

The growing population of outdoor free-ranging cats poses an increasingly serious threat to biodiversity. Identifying the strategies that outdoor free-ranging cats apply to live with humans is an interesting research topic. In this study, we provided robust estimates of free-ranging cat density in 30 universities in Nanjing, Jiangsu Province, China. We found that the population density of free-ranging cats is linearly related to the proportion of female students in the university. An online questionnaire confirmed that human females were more concerned about the living conditions of free-ranging cats than human males in China. By contrast, a socialization test on 27 free-ranging cats suggests that the cats may have the ability to distinguish human sex and adopt a sociable skill to human females. This study leaves an interesting coevolution story between humans and cats and suggests that human sex may be an important factor to consider in cat population managements and wildlife conservation.

1. Introduction

Free-ranging cats (*Felis catus*) are predators that humans introduce globally (Fitzgerald, 1990; Gehrt et al., 2010). The earliest evidence of cat–human association is their co-occurrence in 9500-year-old Cyprus deposits (Vigne et al., 2004). Cats likely developed specific abilities during this time, thereby allowing them to communicate with human beings. To obtain the attention of humans when soliciting food, cats can make a particular purr mixed with a high-pitched cry, which mimics the distressed cry of a human baby (Bornstein, 1986; McComb et al., 2009). Humans are naturally sensitive to baby's cry (Dessureau et al., 1998). Hence, they respond to the cats' purr.

However, as predators, outdoor free-ranging cats are a major threat to global biodiversity (Hutchings, 2003; Karl and Best, 1982; Krauze-Gryz et al., 2019; Lazenby et al., 2015; Loss et al., 2013; Woolley et al., 2019). Extensive evidence suggests that free-ranging cats caused numerous localized population declines and extirpations of prey species (Christensen, 1980; Fancourt, 2014; Risbey et al., 2000). As a novel and invasive predator, free-ranging cats can reduce the prey populations and even drive the extinction of local vertebrates (Baker et al., 2005; Bonnaud et al., 2012; Frank et al., 2014; Loss and Marra, 2017; Medina and Nogales, 2009) and invertebrates (Gillies and Clout, 2003; Medina and García, 2007; Nogales and Medina, 2009). Quantifying the potential impacts of feral cats and devising management strategies to reduce those impacts require population information of outdoor free-ranging

cats. Such information is generally lacking in most Chinese regions. Several natural factors can influence the population density of outdoor free-ranging cats (Hohnen et al., 2016). However, the most important factor may be humans who feed cats. In comparison with human males, human females have greater concern for animal welfare and rights (Herzog, 2015; Phillips et al., 2011) and raise pets mainly due to companionship and emotional purposes (Al-Fayez et al., 2003; Herzog, 2015). Hence, the proportion of human females may affect the cat population in a certain area.

Can cats distinguish human sex, and use this knowledge to increase survival rate by reacting more positively to human females than human males? If so, then positive feedback between cats and human females should lead to increased cat density. Therefore, the relationship between cat and human sex ratio must be studied to verify if the claim “where there are girls, there are cats” is true. It also helps manage the explosive population of free-ranging cats in China. In contrast to general communities, universities in China are usually enclosed and independent. They have different sex ratios but maintain a relatively stable age structure. For example, police academies and teachers' universities have similarly aged student bodies, however, police academies are predominantly males, whereas teachers' universities are primarily females. This difference gives us an excellent opportunity to study the effect of human sex ratio on the population density and survival strategies of outdoor free-ranging cats. This study proposes and tests the following hypotheses:

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- 1) cat density is negatively related to human sex ratio (human male/human female);
- 2) human females are more concerned with free-ranging cats and have higher tendency to feed them than human males;
- 3) cats react more positively to human females than human males.

2. Methods

2.1. Population census of free-ranging cats

2.1.1. Study area

Our investigations were carried out in Nanjing, Jiangsu Province, China (32° 03' N, 118° 46' E), which has an area of about 1398.69 km² and a permanent resident population about 8.44 million. Nanjing is one of the three mega-cities in the Yangtze River Delta and East China. It has 53 colleges and universities, and 30 of them were selected as our focal samples.

Cat population censuses were carried out from June 2018 to June 2019, usually 2 h before the sundown on a sunny or cloudy day. We started our survey from the front gate of the university and then headed to the dormitories and canteens. Prior to our arrival at each campus, we determined the location of the key points, such as the canteens and dormitories on the map. We then based on these points selected the routes randomly. In the transect line determining, we would try to cover all types of habitats in that campus, including roads, sidewalks, alleys, grasslands, ponds, groves, and garbage dumps. During the transect line walking, we recorded every cat we saw using a camera (Canon 5D III) equipped with telephoto lens (Canon EF100-400 mm f/4.5–5.6 L II IS USM) to document individually identifiable markings or patterns. Every survey we conducted in one area would not be too many days apart. Hence, we would distinguish those cats with similar colors via their physique and demeanor. We only recorded adult cats to eliminate the difference brought by reproductive seasons to a certain extent. We processed our transect line census at least twice for each campus.

The data on the number of students of each campus and the proportion of female students in each college and university in 2018 were obtained from the university website. The feeding stations of each campus were counted during the census, and an area of the food bowl with no obvious trace of deserted was considered a feeding station. Cats may use green land as their shelter. Hence, we calculated the percentage of greenery coverage of each campus using a high-resolution aerial photograph.

2.2. Online questionnaires

We used an online questionnaire to examine the attitudes of human males and human females towards outdoor free-ranging cats. We administered the questionnaire produced via Tencent through the Internet from April 2019 to June 2019 in China (<https://wj.qq.com/>). Weblinks to the questionnaire were distributed through WeChat and QQ (<https://wj.qq.com/s2/3482595/cbbc/>), which have the largest user database in China. The participants were chosen randomly. A total of 2066 questionnaires were collected, and the survey area covered all the provinces in China. Unusable questionnaires, such as those falsely filled out or with answers from countries outside China, were excluded. We ended up with 2038 questionnaires in our analysis. Participants were asked up to 19 questions about their general information and their cats. We reported only the related questions here: “Did you ever feed or rescue outdoor free-ranging cats” and “Do you regularly feed outdoor free-ranging cats”. The sex of the respondents was also recorded.

2.3. Socialization of cats

2.3.1. Study area

This experiment was carried out in December 2018 and January

Table 1

Definition and assignment of socialization index of free-ranging cats.

Cat behavior	Score
Actively approaches the tester	2
Comes within 1 m	1
Stays within 1 m	1
Allows petting	1
Allows holding	3
Meows at tester	3
Purrs	4
Reacts to toys	1
Plays with toys	2
Approaches for affection (rubbing legs)	2

2019 at Xianlin Campus of Nanjing University, Jiangsu Province, China (32° 06' 57.91" N, 118° 57' 17.88" E). Sixteen volunteers (nine male students and seven female students, all aged 20–21 years old) conducted the experiment. They walked around the campus and conducted socialization tests on randomly selected cats. Each behavior was scored according to previous studies (Siegford et al., 2003; Slater et al., 2013a; Slater et al., 2013b; Slater et al., 2013c), and socialization index was defined as the sum of each socialized behavior the cat expressed to the volunteers (Table 1). High socialization index indicates high potential of communication with humans. A total of 60 identifiable cats were tested, but only 27 were tested both by male students and female students. Thus, only 27 cats were included in analysis. Environmental factors, including weather (rainy or rainless), date, and time, were also recorded.

2.4. Data analysis

We collected the density data of cats from 30 colleges and universities. The study area was about 2964 ha, and the transect lines were 445.32 km. The population of cats was estimated via noninvasive capture–recapture analysis using the “capwire” library in R. This package can fit the models to the data to obtain the maximum likelihood estimate (MLE) of the population size, perform a likelihood ratio test to select between the even capturability model (ECM) and the two innate rates model (TIRM), perform a parametric bootstrap to estimate confidence intervals for the MLE, and simulate data under these and other models. “Capwire” accommodates data with multiple observations of an individual within a single session, accounts for capture heterogeneity, and appears to work well, especially for small populations (Miller et al., 2005). For the model selection, the ECM should be accepted when samples are independent, and all individuals have equal capture probability. However, TIRM should be chosen instead of ECM when the population has capture heterogeneity. The density of cats in each university or college is calculated by dividing the number of cats on the campus by the area of the campus.

First, we used Pearson correlation to evaluate if the cat density was closely related to the proportion of female students of each campus, the student density, the density of feeding stations, and the percentage of greenery coverage of each campus. Second, the factors with significant correlation to the regression were included. Finally, the stepwise method was used to determine which combination of variables can explain dependent variable variation under linear conditions.

A total of 2038 questionnaires were received for the attitudes of human males and human females towards outdoor free-ranging cats with the males/females respondent rate of 0.62. A chi-square test was used to determine if the treatment of human males and females to free-ranging cats differ significantly.

A general linear model was used to determine if the sex of tester or/and weather influenced the socialization score of cats. Cat ID and the interaction between sex and weather was also included in the model. All statistical analyses were carried out using SPSS (version 25.0), and

the level of statistical significance was set at $p = 0.05$.

3. Results

We surveyed free-ranging cat populations in 30 universities in Nanjing from June 2018 to June 2019. The population of cats on each campus was estimated via noninvasive capture–recapture analysis using the “capwire” library in R. The TIRM was selected for the analysis based on the heterogeneity of our subjects in 30 campuses (Supplementary Table 1). The total cat density of all campuses was 37.65 individuals per km^2 . The Pearson correlation test showed that the density of cats was significantly correlated with the proportion of female students ($N = 30$, $r = 0.614$, $p < 0.001$), the student density ($N = 30$, $r = 0.636$, $p < 0.001$), and feeding station density ($N = 30$, $r = 0.855$, $p < 0.001$). However, it was not correlated with the percentage of greenery coverage of each campus ($N = 30$, $r = 0.132$, $p = 0.49$). Only the proportion of female students and the feeding station density were kept in the final model via stepwise linear regression ($R^2 = 0.75$, $p < 0.001$) (Fig. 1). Cat density was positively related to the proportion of female students ($B = 0.542 \pm 0.257$, $t = 2.109$, $p = 0.044$) and feeding station density ($B = 6.273 \pm 0.925$, $t = 6.779$, $p < 0.001$).

We attempted to explain this human female effect in the following aspects: whether Chinese human females are more concerned about free-ranging cats than human males and whether cats react more sociably to human females than human males. The 2038 online questionnaires showed that more females had fed or rescued outdoor free-ranging cats than males ($\chi^2 = 94.692$, $p < 0.001$, $df = 1$, Fig. 2). Similarly, more females feed outdoor free-ranging cats regularly ($\chi^2 = 19.345$, $p < 0.001$, $df = 1$, Fig. 2).

We performed a socialization test on 27 free-ranging cats to identify if cats react more positively to human females than human males. The general linear model showed that experimenter's sex ($F_{1,89} = 4.001$, $p = 0.049$), weather condition ($F_{1,89} = 11.803$, $p < 0.001$), their interaction ($F_{1,89} = 12.226$, $p < 0.001$), and cat ID ($F_{26,89} = 2.221$, $p = 0.003$) significantly affected the socialization index of cats. In general, these cats behaved more sociably or friendlier to human females than human males (not considering the weather conditions). And in bad weather conditions, such as rainy days, cats behaved more sociably or friendlier to humans compared to normal weather (not considering the human sex). While considering the weather condition and human sex simultaneously, the interaction test showed that cats reacted

to human males and human females similarly in normal weather conditions, but they were much friendlier to human females in bad weather conditions (Fig. 3).

4. Discussion

To the best of our knowledge, this study is the first to find the correlation between the population of free-ranging cats and human sex ratio. Cats have a long history of coevolution with humans. Hence, we attempted to explain this finding through the following aspects: human to cat, whether human males and human females have adopted different attitudes to free-ranging cats; and cat to human, whether cats behave differently to human males and to human females.

Considering the transect method we used, an estimated bias on the cat population estimations is possible due to the spatial distribution or unobservability of the cats (Glennie et al., 2015; Nomani, 2012). However, because we used the same method for each campus, we believed that the cats population density ranks of these campuses could not be too different from the actual situation. That is, in the relationship between the proportion of human females and the density of cats, the flaws of the transects method would not substantially impact the results. However, those specific parameters in the model should be treated carefully.

The population density of free-ranging cats on campus was positively correlated with the proportion of female students. This situation is likely because human females give more attention and care to free-ranging cats than human males, as shown in Fig. 4, where a girl is feeding a group of free-ranging cats. Numerous studies also claimed that, in comparison with human males, human females were more humanistic and moralistic about animals and more negativistic and even less supportive of using animals for research (Franklin et al., 2001; Hagelin et al., 2003; Kellert and Berry, 1987; Pifer et al., 1994). In addition, animal hoarding, which refers to people's behavior of living with more pets than they can adequately support, was more rampant among human females than human males (Herzog, 2015; Patronek, 1999; Worth and Beck, 1982). Virtually, all studies on animal rights movement noted that human females outnumber human males among rank and file activists (Herzog, 2015).

The food source of cats that share living space with humans is mostly depending on humans, particularly human females. On the basis of our results and those of previous studies (Einwohner, 1999; Herzog, 2015; Phillips et al., 2011; Phillips and McCulloch, 2005), human females gave more attention and care to cats. Hence, under the powerful selective pressure from humans, cats probably learned to socialize while communicating with human females to efficiently get as much food and care as possible. The socialization test reveals that cats were more sociable to human females than human males, especially under the condition of bad weather. We found that cats behaved similarly to human males and human females in normal weather conditions, which is probably because cats have enough food resources on sunny days, and they do not need to ask for food urgently. However, their food resources are greatly reduced in bad weather conditions because the artificial feedings are reduced and the natural predation becomes difficult. Therefore, accurate and effective food sourcing becomes important. Hence, the high interaction of sex and weather exist. Apparently, getting food from human females is easier and safer in comparison with human males (Flynn, 2000).

Few studies focused on the effect of human sex on the response of companion animals towards humans, not to mention the wild animals. Certain studies showed that a dog's reaction towards a human is influenced by the sex of the person (Lore and Eisenberg, 1986; van der Borg et al., 1991). Hence, they can identify human sex in visual/olfactory and auditory modalities (Ratcliffe et al., 2014). Certain studies also showed that human sex affected dogs' barking and eye orientation (Wells and Hepper, 1999). Dogs showed behaviors suggestive of defensive-aggressive reactions, such as barking and maintained eye

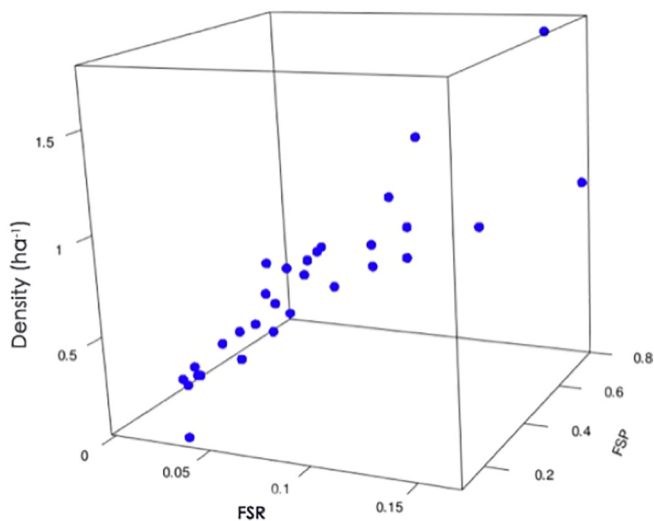


Fig. 1. Relationship between density (the population density of outdoor free-ranging cats) and the FSP (proportion of female students of each campus) and the FSR (the ratio of feeding stations to campus area) in 30 universities of Nanjing, China (constant = -0.111 , $b_{FSR} = 6.273$, $b_{FSP} = 0.542$).

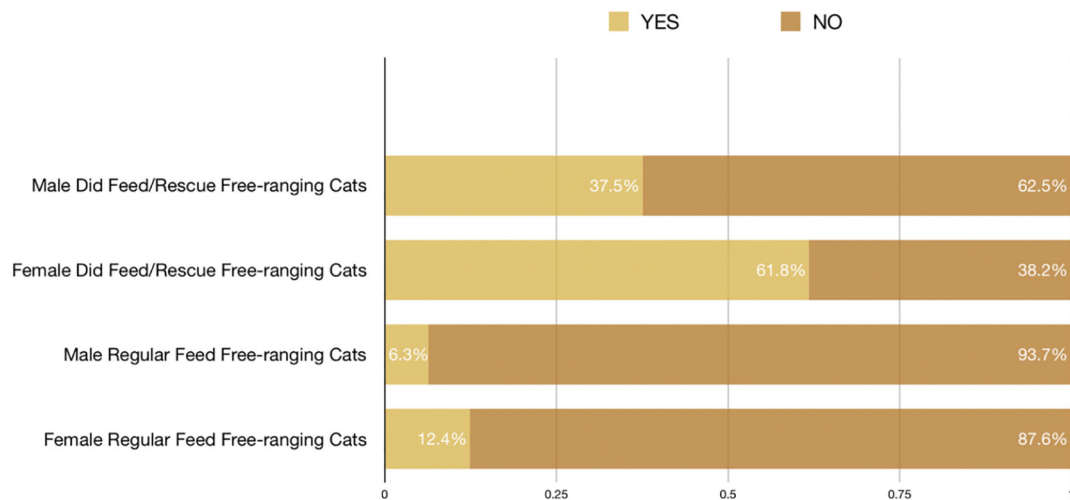


Fig. 2. Difference between human males and human females in the attitude of caring free-ranging cats (“Have you ever fed or rescued free-ranging cats?” and “Have you fed the free-ranging cats regularly?”) on the basis of an online survey involving 2038 questionnaires.

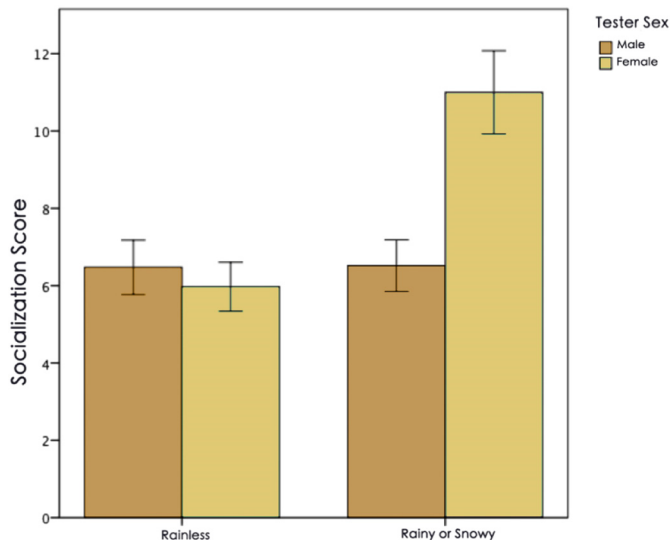


Fig. 3. Effect of weather (rainy or sunny) and experimenter sex on the socialization index of 27 free-ranging cats on Xianlin Campus of Nanjing University. A greater difference showed under severe weather conditions (rainy or snowy).

contact (Millot, 1994) towards human males than human females. They also bite human males significantly more often than human females (Rosado et al., 2009). Our socialization index test shows that cats may potentially distinguish human males from human females. The ability to distinguish human sex is one of the predominant aspects of categorization—a key cognitive mechanism that determines how we perceive and process sensory information (Rosch et al., 1976). Our result may provide a new idea for subsequent studies to explore spontaneous category formation in nonhuman species. Previous works only focused on a few nonhuman species (Murai et al., 2005; Murai et al., 2004; Ratcliffe et al., 2014), but none of them studied cats.

Our results indicated that human females would give more care to free-ranging cats than human male do and mutually, free-ranging cats also tend to act more social towards human females than towards human males. That leads to a more interesting question, who is the initiator of this interrelationship? Is the cats who are attracting females or is human females who are attracting cats? At our socialization experiments, we required both our male and female volunteers conducted with same behavior pattern and intensity, so that we can make sure at least in our test, cats did separate the sex of volunteers only by sex itself



Fig. 4. A girl was surrounded by a group of cats.

but not their specific behavior. But what we cannot determine is whether the cause is the cat's preference towards human females or towards the behaviors of human females, obviously the former indicates human females attracting cats and the latter indicates cats attracting human female. It seems like that it is cats that attracting females since the result of our questionnaires and previous studies indicated that human females gave more attention and care to cats, and because of that free-ranging cats may learn to recognize the characteristics of that kind of humans would provide them more food and

more care. But we still cannot say it for sure since we don't know would the results of the attitude that cats towards different human sex remain so if we remove those behaviors that expressing more care and friendliness from human females. Either way, we believe cats were not just responding to the friendlier behavior of human females towards them at the moment of decision-making, there should be a special cognitive mechanism in it. Further researches are needed for the explanation.

Free-ranging cats are adaptable and invasive predators that threaten global biodiversity (Clements, 2009; Keitt et al., 2011; Medina et al., 2011). They contribute to the collapse of the population of numerous wild animals in the US (Loss et al., 2013), Australia (Hohnen et al., 2016), and Poland (Krauze-Gryz et al., 2019). Even low-density populations of cats can have considerable impacts. For example, native Australian rats (*Rattus villosissimus*) were hunted to extinction soon after the release of only one or two individual cats (Frank et al., 2014). This result may be partly due to the ability of cats to selectively hunt in habitats where prey is vulnerable (McGregor et al., 2014) and specialize on particular preys (Fitzgerald et al., 2000), which somehow proves why they are friendlier to human females than human males and indulge in excess killing (Peck et al., 2008). In addition, bird mortality far exceeds any other direct source of anthropogenic mortality, including collisions with windows, buildings, communication towers, vehicles, and pesticide poisoning (Banks, 1979; Longcore et al., 2012; Manville, 2016; Pimentel, 2005; Risbey et al., 2000).

The systematic research on outdoor free-ranging cats hunting wild animals is currently limited in China. However, this fact does not mean that outdoor free-ranging cats are not destroying China's biodiversity. The assessment of the current population of free-ranging and domestic cats in China is a basic but urgent need. Human sex ratio is an important factor that may affect the population of free-ranging cats. Hence, this factor should be considered not only in the population estimation but also in the population managements of free-ranging cats in China. For human females-dominated colleges, campuses, and communities, the managements and control works of free-ranging cats, such as sterilization and infectious disease surveillance, require further attention. At the same time, the potential impact of popular science education and awareness promotion of free-ranging cats on biodiversity should be studied as well.

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CRedit authorship contribution statement

Yuhang Li: Conceptualization, Data curation, Investigation, Formal analysis, Methodology, Writing - original draft. **Yue Wan:** Data curation, Investigation, Formal analysis, Methodology. **Yigui Zhang:** Data curation, Investigation. **Zhaomei Gong:** Data curation, Investigation. **Zhongqiu Li:** Conceptualization, Formal analysis, Methodology, Funding acquisition, Project administration, Supervision, Writing - review & editing.

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Declaration of competing interest

The authors have no competing interests.

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