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# Spatial ecology of free-ranging domestic dogs in an agroecosystem and its implications for wildlife conservation

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ABSTRACT

Domestic dogs (*Canis familiaris*) are a pervasive threat to biodiversity in developing countries. India has nearly 59 million domestic dogs, many of which are free-ranging. Free-ranging domestic dogs (FRDD) in rural areas often interact with wildlife that inhabit areas outside protected areas in fragmented and human-dominated landscapes. Understanding the spatial ecology of FRDD is crucial for targeted management, as not all FRDD exhibit free-ranging behavior that negatively impacts wildlife. We used location data from GPS-collared FRDD (n = 31; 177,251 locations) to determine how space-use patterns and habitat selection differ between two categories of FRDD – village and farm – in an agroecosystem in central India. Annual 95 % home ranges for farm FRDD (mean = 0.87 $km^2$ ±0.18 SE) were significantly larger than village FRDD (mean = 0.11 $km^2$ ±0.03 SE) but with high individual variation (0.02–2.21 $km^2$). During movement, farm FRDD used various habitats (including natural grasslands) whereas village FRDD primarily used built areas. The top-ranked habitats in a compositional analysis for both FRDD types at the home range level (2nd order) were built, agriculture, and fallow lands, which reflects the broad association of FRDD with humans. However, farm FRDD had a higher selection of grassland, which represents an important habitat for wildlife in the region. Our study highlights that farm FRDD are more likely to interact with wildlife than village FRDD due to their space-use behavior. Therefore, we emphasize the need for responsible dog ownership and practices that limit the free-ranging behavior of farm FRDD that are compatible with their roles in farm management in the region.

## 1. Introduction

Many of the world's species persist outside protected areas in human-dominated landscapes (Chapron et al., 2014; Ferreira et al., 2018; Linnell et al., 2020; Nori et al., 2015). These landscapes often include a matrix of multiple land uses and wildlife habitats and can serve as important areas in maintaining and conserving biodiversity (Anand et al., 2010; Arroyo-Rodríguez et al., 2017; Coelho et al., 2014; Cox and Underwood, 2011; Harvey et al., 2008; Perfecto and Vandermeer, 2008; Ranganathan et al., 2010). Various studies have

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highlighted the role of wildlife habitats in human-dominated landscapes for dispersal and gene flow, especially in the case of wide-ranging species such as jaguars (*Panthera onca*) and Asian elephants (*Elephas maximus*) (Boron et al., 2016; Kumar et al., 2010). Additionally, remnant natural areas in these landscapes are crucial for supporting populations of species whose habitats are inadequately represented in current protected area networks (Punjabi et al., 2013; Madhusudan and Vanak, 2023). For instance, grasslands are the least protected terrestrial biome in the world, with limited continuous and intact grasslands still remaining (Scholtz and Twidwell, 2022). Remnant grassland patches in regions with limited suitable habitat and high anthropogenic pressure hold significant conservation value. These patches are essential for conserving threatened grassland birds such as the streaked horned lark (*Eremophilia alpestris strigata*) in the Pacific Northwest United States (Wintle et al., 2019), habitat specialists such as the Indian fox (*Vulpes bengalensis*) in central India (Punjabi et al., 2013; Katna et al., 2022), and various species of mammals in central Brazil (Coelho et al., 2014).

However, wildlife that moves outside protected areas and inhabits habitats in fragmented and human-dominated landscapes face several conservation challenges (Athreya et al., 2015; Kuijper et al., 2019; Madhusudan et al., 2015; Tucker et al., 2018), one being their increased proximity to a highly successful invasive mammal – the domestic dog (*Canis familiaris*) (Doherty et al., 2017; Hughes and Macdonald, 2013). Domestic dogs are known to exploit fragmented landscapes (dos Santos et al., 2017; Lacerda et al., 2009; Malhotra et al., 2021; Manor and Saltz, 2004; Marshall et al., 2023; Paschoal et al., 2020; Vanak et al., 2014), where they frequently interact with wildlife at multiple levels through predation, competition, disease transmission, and hybridization (Doherty et al., 2017; Vanak and Gompper, 2009b).

With a near-global distribution, domestic dogs are considered the world's most common and abundant carnivore species (Gompper, 2014). Their close association with humans and evolved adaptability through multiple domestication processes have enabled them to survive and persist in a wide range of habitats (Axelsson et al., 2013; Butler et al., 2014; Wynne, 2021). Although they are highly associated with humans through their dependence on human-derived resources, there is still a loose sense of their ownership across much of their range due to cultural differences in dog ownership and roles (Jackman and Rowan, 2007). One of the most prominent categories of domestic dog populations is "free-ranging domestic dogs" (FRDD), comprising approximately 75 % of the global domestic dog population, which was estimated to be ~ 1 billion (Gompper, 2014; Hughes and McDonald, 2013). The majority of domestic dogs in developing countries have few to no restrictions in movement (Jackman and Rowan, 2007). In particular, domestic dogs in rural areas commonly exhibit some form of free-ranging activity regardless of their ownership status (Vanak and Gompper, 2009b; Wandeler et al., 1993). This free-ranging behavior may facilitate their interactions with wildlife living in rural landscapes. However, not all FRDD display free-ranging behavior that may negatively impact wildlife nor do their impacts occur uniformly across all landscapes (Gompper, 2021; Meek, 1999; Sepúlveda et al., 2015). Some categories of FRDD may have a larger impact on wildlife. For example, FRDD with wider-ranging territories in rural areas were found to have a higher opportunistic diet and thus a higher probability of interacting with wildlife than FRDD with limited ranges (Vanak and Gompper, 2009b). Moreover, various studies have shown that dog-wildlife interactions are mediated by the level of care provided (Ruiz-Izaguirre et al., 2015; Silva-Rodríguez and Sieving, 2011), accessibility and presence of anthropogenic food sources (Newsome et al., 2014), roles in farm management/household (Sepúlveda et al., 2014), human accompaniment (Woodroffe and Donnelly, 2011), and accessibility and proximity to specific landscape attributes such as roads (Sepúlveda et al., 2015; Vanak and Gompper, 2010).

India has the fourth-largest population of domestic dogs but likely the highest population of FRDD in the world (Gompper, 2014). They are ubiquitous and occur in high densities in some areas of the country due to poor ownership rules, culture and religious beliefs and perceptions, ineffective population control efforts, and the availability and accessibility to humanized subsidies (Home et al., 2018; Sensharma et al., 2025; Tiwari et al., 2019a). This is particularly concerning when they are present in rural areas and near protected areas that host a diversity of wildlife species, especially mammalian carnivores (Athreya et al., 2013; Carricondo-Sanchez et al., 2019). FRDD in rural areas are mixed breeds and can be generally categorized as village or farm FRDD, although some areas may contain feral dogs and FRDD that exhibit completely wild behavior and are independent of human-derived food sources (Vanak and Gompper, 2009b). Village FRDD are unconfined, unowned dogs that reside in the immediate vicinity of villages and are primarily dependent on communal human-derived resources, such as garbage disposals or direct feeding. Whereas farm FRDD are unconfined, typically owned dogs (3–8/household) that roam freely around farm hamlets (Vanak and Gompper, 2009b, 2010).

Although limited, there is growing evidence documenting the negative impacts of FRDD on wildlife in India (Home et al., 2018). Studies suggest that the presence of FRDD can influence the spatial and temporal space-use patterns of mesocarnivores such as the Indian fox (*Vulpes bengalensis*) in highly fragmented landscapes (Carricondo-Sanchez et al., 2019; Vanak and Gompper, 2010). In addition, they have been recorded as predators (Home et al., 2018; Mahar et al., 2024; Vanak and Gompper, 2009b), pathogen transmitters (Belsare et al., 2014), competitors (Reshamwala et al., 2021), agents of hybridisation (Tyagi et al., 2023), and prey in India (Athreya et al., 2016; Kumbhojkar et al., 2021). However, there is still a poor understanding of the movement ecology and habitat use of FRDD in India, particularly in relation to wildlife habitats. The space-use of FRDD may influence the likelihood and types of interactions they may have with wildlife (Gompper, 2014). Therefore, understanding how FRDD use and move in human-dominated landscapes is important for developing targeted and context-specific strategies to mitigate their negative impacts on wildlife (Paschoal et al., 2020; Gompper, 2021).

In the past decade, there has been growing knowledge of the movement ecology and habitat use of FRDD throughout the world (e.g., Jin et al., 2017; Ladd et al., 2023; Ruiz-Izaguirre et al., 2015; Saavedra-Aracena et al., 2021; Schüttler et al., 2022; Sepúlveda et al., 2015; Sparkes et al., 2014, 2022; Wilson-Aggarwal et al., 2021). Previous studies have shown that FRDD are strongly associated with human infrastructure, indicating a strong selection for human proximity in rural areas (Cunha Silva et al., 2022; Ladd et al., 2023; Ruiz-Izaguirre et al., 2015; Vanak and Gompper, 2010; Woodroffe and Donnelly, 2011). However, there have been various cases where some FRDD occasionally foray into wildlife habitats (Ladd et al., 2023; Schüttler et al., 2022; Sepúlveda et al., 2015). FRDD exhibiting this behavior are of special concern, as they may negatively impact wildlife living in these habitats. We examined the space-use patterns of two categories of FRDD using GPS telemetry data in rural west-central India, which hosts a diverse array of native wildlife. In particular, we examined how (1) home ranges, (2) distance moved within an hour (3) the proportional habitat use during movement, and (4) habitat selection at the second order may vary between village and farm FRDD in a highly fragmented agro-ecosystem in central India. The results were then compared to patterns of space-use by wildlife from previous studies in the region to infer the potential dog-wildlife interactions.

## 2. Methods

### *2.1. Study area*

The study was conducted in and around the rural areas of the Shirsuphal village of Baramati Taluka, Pune District, Maharashtra, in west-central India (Fig. 1). The human population in the study area is estimated to be ~5500 and is largely dependent on agro-pastoralism, commercial poultry farming, and nomadic pastoralism (Carricondo-Sanchez et al., 2019; www.census2011.com). Set within a matrix of multiple land-use types, the study area includes grasslands (also used as common grazing lands), fallow lands, irrigated agriculture, seasonal agriculture, state-managed forestry plantations, asphalt and non-asphalt roads, canals, railway lines, poultry farms, and human residences. The remnant patches of grasslands are unprotected native savannahs that include grasses (e.g., *Aristida spp*., *Heteropogon spp.*, *Chrysopogon spp.*, *Cymbopogon spp.*) and scrub vegetation (e.g., *Zizyphus mauritiana*, *Acacia leucophlea,* and *Acacia nilotica* among others) (Carricondo-Sanchez et al., 2019). Various mammalian species that have been observed utilising this matrix include the Indian fox (*Vulpes bengalensis*), golden jackal (*Canis aureus*), jungle cat (*Felis chaus*), striped hyena (*Hyaena hyaena*), Indian grey wolf (*Canis lupus pallipes*), palm civet (*Paradoxurus hermaphrodites)*, small Indian civet (*Viverra zibetha)*, grey mongoose (*Herpestes edwardsii)*, Indian gazelle (*Gazella bennettii)*, and Indian hare (*Lepus nigricollis)* (Carricondo-Sanchez et al., 2019; Katna et al., 2022; personal observations). The land use land cover (LULC) map of the study area was classified into six habitat types: water (2.56 %), built (5.47 %), agriculture (24.03 %), fallow (32.63 %), grassland (34.22 %), and plantation (1.09 %) (Fig. 1). The agriculture class consists of irrigated and rainfed crops and the plantation class consists of the Maharashtra state-managed tree plantations as part of reserve forests (Katna et al., 2022). Fallow lands are open areas that have not been actively ploughed for approximately two-three years and have some early successional vegetation (Vanak and Gompper, 2010). For further details about the LULC classification, see Katna et al. (2022). The study area experiences a cool-dry season from November to February, a hot-dry season from

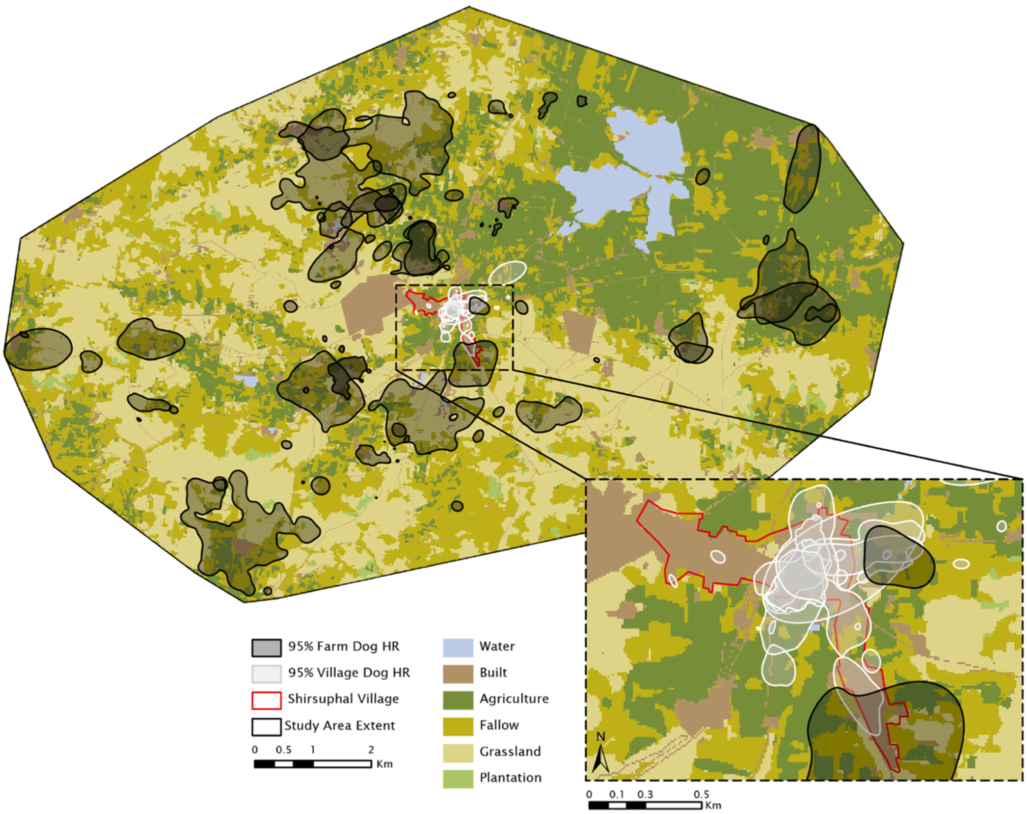


**Fig. 1.** Land use land cover (LULC) map of the study area and the 95 % weighted Autocorrelated Kernel Density Home Ranges (HR) of farm (n = 20) and village (n = 11) free-ranging domestic dogs (FRDD) (*Canis familiaris*) in and around Shirsuphal village, Baramati, Maharashtra, India.

March to June, and a wet season with annual rainfall (~ 500 mm, 95 % precipitation) from July to October (Carricondo-Sanchez et al., 2019; Todmal and Kale, 2016).

### 2.2. Animal capture and telemetry

A total of 31 FRDD were fitted with GPS collars (model d-cell, Africa Wildlife Tracking, Pretoria, South Africa). The set of FRDD (~8 % of the total population; Tiwari et al., 2019b) was either selected from the Shirsuphal village or farm residences and hamlets outside the village. Based on their location of capture and information from owners and villagers, the FRDD were classified as either village (10 males, 1 female) or farm FRDD (19 males, 1 female). We were able to collar only two female FRDD in our study area, which we believe is representative of the study population given the heavily skewed sex ratio toward males (1:2.45; 71 %) in the study area (Tiwari et al., 2019b). This skewness likely reflects a general preference for male FRDD among owners and farmers and/or high mortality rates among female FRDD (Tiwari et al., 2019b). Additionally, given the even spatial distribution of the samples (Fig. 1; Figure S1), we believe this sample size is an adequate representation of the population. Owned FRDD were restrained and captured by their respective owners, whereas we restrained unowned or village FRDD using a net and immobilized them with a combination of Ketamine and Xylazine hydrochloride when necessary (Belsare and Vanak, 2013). The FRDD were fitted with GPS collars that weighed less than 3 % of their body weight and vaccinated for rabies before release. Additionally, no FRDD in our study area were sterilised. The total study period spanned from April 2017 to September 2018 (17 months). Collars were programmed to record a location every 10 min during the breeding season (August-November) and every 60 min at all other times during the study period. Using a handheld receiver, the location data were downloaded every 15 days and uploaded to www.movebank.org. The study was conducted under the approval of the Animal Ethics Committee of the Ashoka Trust for Research in Ecology and the Environment (ATREE), Bangalore, India, with permit number AAEC/101/2016. Verbal permission was obtained from the FRDD owners or the village council before handling the FRDD. The potential risks associated with the procedure were explained, and a phone number was shared in case of emergency or clarify any further questions. The project was reviewed by the internal review board and it was deemed unnecessary to obtain human ethics approval since no personal information from the owners/responsible persons was collected.

### 2.3. Data analysis

#### 2.3.1. Home range estimation and comparisons

Location data were first screened to remove duplicate records using the package *move* in the R environment (Kranstauber et al., 2023; R Core Team, 2025). We used the Autocorrelated Kernel Density Estimation (AKDE) in the *ctmm* package to calculate 95 % annual home ranges (Fleming and Calabrese, 2017; 2023). AKDE was chosen over traditional home range estimators due to its ability to explicitly account for autocorrelation (Fleming et al., 2015), mitigating biases arising from over-smoothing (Fleming and Calabrese, 2017), unrepresentative sampling in time (Fleming et al., 2018), and small absolute and effective sizes (Fleming et al., 2019; Silva et al., 2022). In particular, we used the weighted AKDE (wAKDE) to correct for irregular sampling intervals due to common tracking-related hindrances such as signal loss and transmitter malfunctions (Fleming et al., 2018). To account for implausible error-parameter estimates, we used an informative prior (12.92 m) due to the absence of calibrated data following the recommendations of Fleming et al. (2021). Gross outliers were manually detected and removed using the *ctmm* package.

We confirmed range residency for all FRDD, a key assumption for estimating home ranges with AKDEs, using the empirical variograms for each FRDD (Fleming and Calabrese, 2017). Using the recommended perturbative Hybrid Residual Maximum Likelihood (pHREML – Fleming et al., 2019) method, we fitted isotropic and anisotropic versions of Ornstein-Uhlenbeck (OU) and OU Foraging (OUF) processes, which assume autocorrelation. In addition, the movement data were also fitted under the assumption of independent and identically distributed (IID) data. The Akaike Information Criterion adjusted for small sample size (AICc) with the lowest score was used to select the best movement model and estimate each individual's 95 % weighted home ranges (Burnham and Anderson, 2002). However, if the IID model was selected as the movement model, the estimation returned a 95 % Kernel Density Estimate (KDE). We used the Mann-Whitney U-test to compare annual home range sizes between the two categories of FRDD, as the data were not normally distributed. We also estimated 95 % Minimum Convex Polygon (MCP) home ranges for comparison with other studies and historal datasets.

#### 2.3.2. Distance moved within an hour

To determine the mean distance moved by a FRDD within an hour, we calculated the average linear distances between successive location points recorded at 60-minute intervals ('*step*'). For standardization purposes, we calculated step lengths for steps created only between 60-minute intervals (±10 min) using the R package *move* (Kranstauber et al., 2023). Since we were interested in comparing the average distance traveled when the FRDD moves from one location point to another within a 60-minute interval, we excluded 0 m lengths from the mean calculation. A 0 m step length between two consecutive location points would indicate that the FRDD was in the same location and did not move within the 60 min, thereby skewing the mean. We also recognise that it might exclude short forays and a return to "home-base" within a 60-minute time frame. We used a two-sample *t*-test to compare the mean step length and maximum step length between the FRDD of both the categories – farm and village.

#### 2.3.3. Proportional habitat use during movement

To determine the proportional use of habitat during movement, we extracted the LULC proportions underlying the space through which the individual selected to travel from one location point to another using ArcGIS Pro Version 3.2 (Fig. 2). Due to the irregularity in the dataset, which sometimes resulted in long time intervals between location points, there was an inherent risk of creating linear steps that may largely differ from the true path of the individual (Abouelezz et al., 2018). Since most location points were recorded at either 60-minute or 10-minute intervals, the data were screened to select only steps created between consecutive location points that were less than 65 min apart, using the R package *move* (Kranstauber et al., 2023). To provide an estimate of the used movement space, the created movement paths were encapsulated by a buffer, with the size determined by each individual's half-mean distance traveled. The half-mean distance traveled was calculated by taking the half-mean of the step lengths of each individual FRDD. We then calculated the mean and standard error of each LULC type proportions used while moving for both categories of FRDD.

*2.3.4. Second-order habitat selection*

We then determined habitat selection at the second order by evaluating habitat use within home ranges to availability within the study area (Johnson, 1980). The study area extent of 103 km$^2$ was defined by creating a 100 % minimum convex polygon (MCP) around all telemetry locations of the FRDD (Fig. 1; Cunha Silva et al., 2022; Katna et al., 2022; Vanak and Gompper, 2007). We used compositional analysis (Aebischer et al., 1993) with a modification that incorporates the 95 % Utilization Distribution (UD) to determine second-order habitat selection (Millspaugh et al., 2006). To obtain a UD-weighted proportion of use, we overlaid the individual UDs on the LULC raster, summed the raw UD values by LULC type, and divided that by the total UD value of all patches (i.e., 0.95) for each FRDD using ArcGIS Pro Version 3.2 (Millspaugh et al., 2006). The proportion of each LULC type 'available' at the landscape (study area) was compared to the UD-weighted proportion of use for each LULC type within the individual home range using a Wilks' lambda distribution. Following the recommendations of Aesbicher et al. (1993), in the R package *adehabitatHS* (Calenge, 2006), a habitat type available, but not utilized by an animal (0 %) was replaced by a value that was distinctively less than the smallest non-zero value (in our case replaced by 0.0001 %). Lastly, since our sample did not have enough female FRDD, we pooled all FRDD by

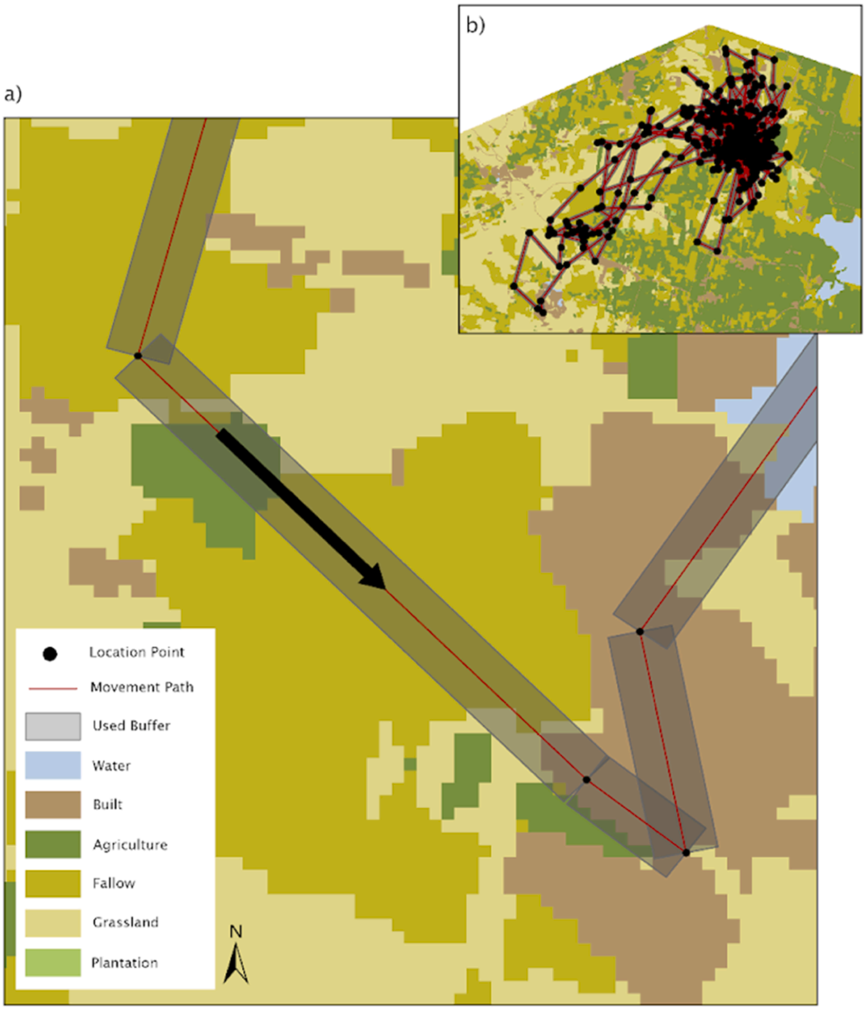


**Fig. 2.** a) Sample movement path of a farm free-ranging domestic dog (FRDD) traveling in the study area, b) all the screened movement paths of the same farm FRDD (Dog 38).

category and did not test for the effects of sex on habitat selection and home range size.

## 3. Results

We collected 100,715 locations (range = 451–9286/individual) from 20 farm FRDD and 76,536 locations from 11 village FRDD (range = 376 –17,954/individual) (Figure S1). On average, farm FRDD were tracked for 7.55 ± 1.41 SE months (range = 0.67 – 28.26), and village FRDD were tracked for 7.46 ± 1.96 SE months (range = 0.54 – 16.57). A few FRDD were tracked for a short period of time due to collar failure, the owner's request to remove the collar, and/or the FRDD dying or disappearing from the study area (Table S1). However, we included all the FRDD (n = 31) in our analysis after we confirmed the range residency assumption using empirical variograms.

### 3.1. Home ranges

As expected, farm FRDD annual home range sizes were much larger than village FRDD ($U = 184$, $p = 0.00155$). The annual home range size for farm FRDD varied from 0.021 to 2.210 $km^2$, and those of village FRDD varied from 0.004 to 0.444 $km^2$ (Table 1; Figure S2). The best fit movement models for the FRDD (n = 31) were OU anisotropic (n = 19), OUF anisotropic (n = 10), and OU (n = 2) (Table S1). We did not exclude female FRDD from further analysis because both female FRDD were well within the range of the male FRDD in their respective categories (farm female FRDD 38: 0.052 $km^2$ and village female FRDD 09: 0.112 $km^2$; Table S1).

### 3.2. Distance moved within an hour

On average, we used 3673 ± 475 SE and 4187 ± 1114 SE successive locations at 60 (±10) minute intervals to calculate mean distance traveled within an hour (mean step length) for farm and village FRDD, respectively (Table S2). The mean step length per hour for farm FRDD (123.22 m ± 11.71 SE, median = 126.82 m) was significantly larger than that of village FRDD (64.76 m ± 9.12 SE, median = 60.84 m; $t = 3.94$, $df = 28.86$, $p = 0.00048$; Table S3). However, the maximum step length reached within an hour was statistically insignificant ($t = 1.16$, $df = 22.49$, $p = 0.26$) between the two categories, farm (mean = 2401.68 m ± 232.87 SE, median = 2348.40 m) and village FRDD (mean = 1973.13 m ± 285.52 SE, median = 2414.54 m; Table S3).

### 3.3. Proportional habitat use during movement

On average, movement paths were created using 4780 ± 658 SE and 6778 ± 1945 SE successive locations that were ≤ 65 min apart. This is 5.0 % and 2.6 % less than the mean number of locations used to calculate home ranges for farm and village FRDD, respectively (Table 1). Village FRDD mostly used the built area (0.68 ± 0.06 SE) during movement compared to other habitat types. In contrast, farm FRDD used a higher proportion of grasslands (0.36 ± 0.04 SE) during movement, followed by agriculture (0.25 ± 0.05 SE), fallow lands (0.23 ± 0.02 SE), and built areas (0.15 ± 0.03 SE). Plantation and water edges were the least proportionately used areas during movement by both categories of FRDD (Fig. 3).

### 3.4. Second-order habitat selection

Habitat selection at the second order (i.e., home range vs. study area) was non-random for both the categories of FRDD (Wilk's lambda Λ 0.109, p = 0.004 by randomization, Table 2). Habitat of village FRDD was ranked as built > >> agriculture > fallow > >> plantation > water edge > grassland (most to least selected; '>>>' indicating a statistically significant difference between the ranks). Meanwhile, habitats for farm FRDD were ranked as built > >> agriculture > fallow > grassland > >> plantation > >> water edge (Table 2). As expected, the village and farm FRDD significantly selected the built habitat more than other habitats present in the study area (Fig. 4). The three top-ranked habitats (i.e., built, agriculture, and fallow) were the same for village and farm FRDD. However, farm FRDD selected grasslands over plantations and water edges in contrast to village FRDD, which selected the grassland the least among all habitat types.

## 4. Discussion

While the negative impacts of domestic dogs on wildlife in India have become increasingly evident (Home et al., 2018), their

**Table 1**
Tracking and home range estimation summary of farm and village free-ranging domestic dogs (FRDD) in Shirsuphal village, Maharashtra, India. wAKDE denotes the weighted Autocorrelated Kernel Density Estimate, MCP denotes the Minimum Convex Polygon, and SE denotes Standard Error.

| FRDD Category | No. of Individuals Tracked | Mean Number of Locations (± SE) | Mean 95 % wAKDE Home Range Size (± SE) ($km^2$) | Median 95 % wAKDE Home Range Size ($km^2$) | Range of 95 % wAKDE Home Range Size ($km^2$) | Mean 95 % MCP Home Range Size (± SE) ($km^2$) |
|---|---|---|---|---|---|---|
| Farm | 20 | 5035 ± 689 | 0.865 ± 0.181 | 0.528 | 0.021 – 2.210 | 1.707 ± 0.445 |
| Village | 11 | 6957 ± 1987 | 0.108 ± 0.036 | 0.069 | 0.004 – 0.444 | 0.128 ± 0.031 |

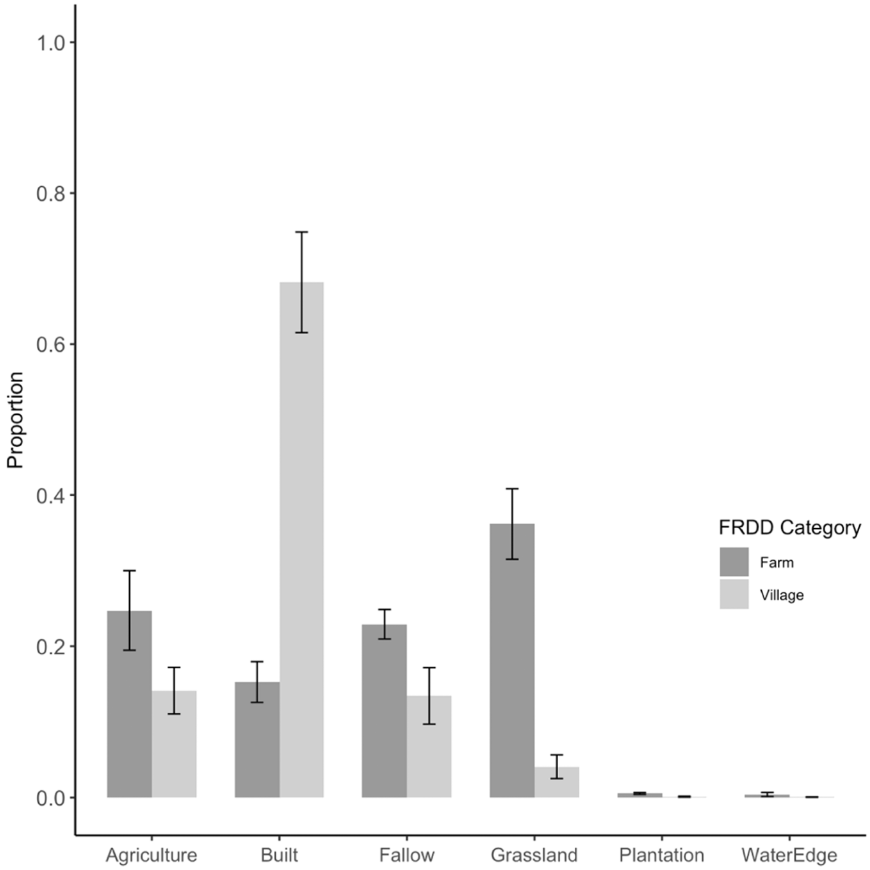


**Fig. 3.** Mean + /- SE proportion of proportionate habitat used by farm and village free-ranging domestic dog (FRDD) while traveling in the study area.

**Table 2**
Ranking matrices derived from compositional analysis of habitat selection at the second order for farm and village free-ranging domestic dogs (FRDD) in Shirsuphal village, Baramati, Maharashtra, India. The resulting ranked variables range from the most selected habitat (5) to the least selected (0) at the second order. A '+ ' symbol indicates that the habitat in the row is selected more than the habitat in the column, relative to their availability in the study area. Conversely, a '−' symbol indicates that the habitat in the row is selected less than the habitat in the column. A triple sign ('+++' or '—') denotes a statistically significant difference in selection at $p < 0.05$.

| | Water Edge | Built | Agriculture | Fallow | Grassland | Plantation | Ranking |
|---|---|---|---|---|---|---|---|
| **Village FRDD*** | | | | | | | |
| Water Edge | 0 | - - - | - - - | - - - | + | - | 1 |
| Built | ++ + | 0 | ++ + | ++ + | ++ + | ++ + | 5 |
| Agriculture | ++ + | - - - | 0 | + | ++ + | ++ + | 4 |
| Fallow | ++ + | - - - | - | 0 | ++ + | ++ + | 3 |
| Grassland | - - - | - - - | - - - | - - - | 0 | - - - | 0 |
| Plantation | + | - - - | - - - | - - - | ++ + | 0 | 2 |
| **Farm FRDD**** | | | | | | | |
| Water Edge | 0 | - - - | - - - | - - - | - - - | - - - | 0 |
| Built | ++ + | 0 | ++ + | ++ + | ++ + | ++ + | 5 |
| Agriculture | ++ + | - - - | 0 | + | + | ++ + | 4 |
| Fallow | ++ + | - - - | - | 0 | + | ++ + | 3 |
| Grassland | ++ + | - - - | - | - | 0 | ++ + | 2 |
| Plantation | ++ + | - - - | - - - | - - - | - - - | 0 | 1 |

* Wilks lambda: weighted mean = 0.0000503; p = 0.004; n = 11; through *randomisation*
** Wilks lambda: weighted mean = 0.1087477; p = 0.002; n = 20; through *randomisation*

movement and habitat use patterns in relation to wildlife habitats are poorly understood in the region. To our knowledge, our study was the first to compare the movement patterns and habitat use of two categories of FRDD that are abundant and ubiquitous in rural areas of India. The results reveal a preliminary but clear distinction between the movement behavior and habitat use of village and

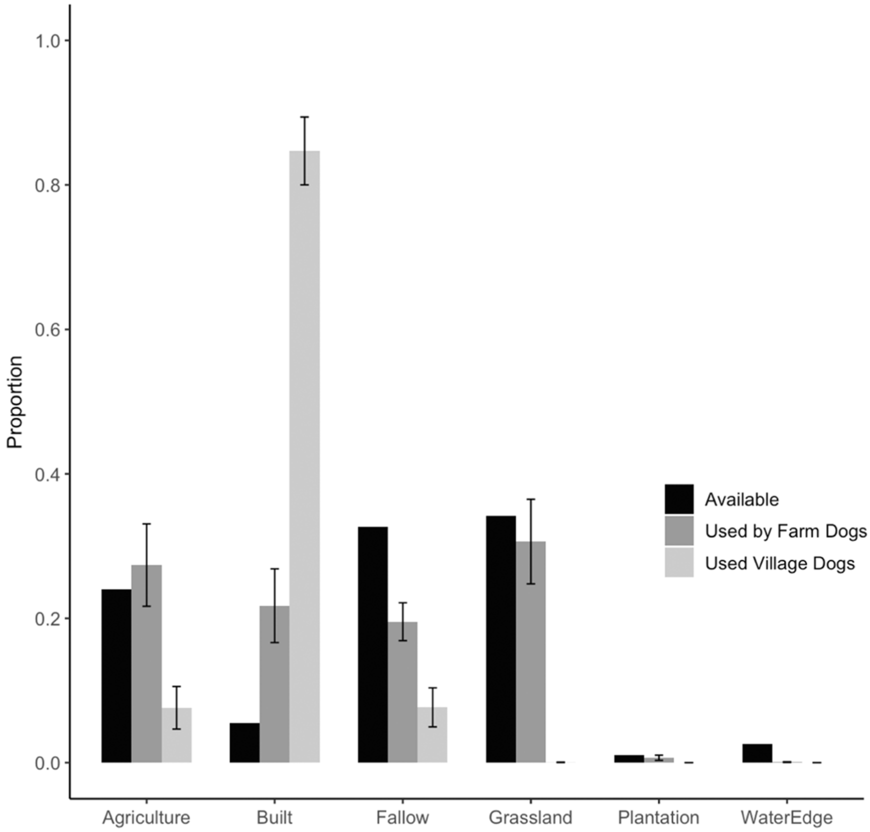


**Fig. 4.** Comparison between utilisation distribution (UD)-weighted mean + /- SE proportions of habitat used by farm and village FRDD and habitat available in the study area.

farm FRDD, which can have consequences for dog-wildlife interactions in rural landscapes. First, farm FRDD are generally more wide-ranging than village FRDD and they are more likely to make large forays during their movements. Second, during movement, farm FRDD mostly used grassland habitats surrounding farmed and fallow areas, whereas village FRDD predominantly used built areas. At the landscape level, both categories of FRDD selected human-modified areas; however, farm FRDD still have a higher selection of grassland habitats than village FRDD. These findings suggest that farm FRDD are more likely to encounter and potentially pose a threat to wildlife inhabiting fragmented natural areas in human-dominated landscapes. These remnant patches serve as essential habitats for various endemic and endangered species in central India, such as the great Indian bustard (*Ardeotis nigriceps*) and the blackbuck antelope (*Sarada superba*), as well as habitat specialists like the Indian fox (Madhusudan and Vanak, 2023; Punjabi et al., 2013).

Farm FRDD had significantly larger home range sizes than village FRDD (Table 1; Figure S2). Median home range size for both categories of FRDD was similar to values previously reported in India (Vanak and Gompper, 2010) and globally (Dürr et al., 2017; Muinde et al., 2021; Schüttler et al., 2022; Wilson-Aggarwal et al., 2021). However, caution should be exercised when making comparisons to other studies due to differences in tracking regimes, sampling effort, the type of FRDD studied, home range estimator used, and the landscape type (Dürr and Ward, 2014; Schüttler et al., 2022). Additionally, on average farm FRDD traveled approximately twice the distance than village FRDD within an hour. However, both the categories had comparable average maximum step lengths travelled within an hour, suggesting village FRDD occasionally make large forays outside the village as well (Table S2; Figure S3). The general difference in ranging behavior between farm and village FRDD may be explained by the Resource Dispersion Hypothesis (Macdonald, 1983), which predicts that home range size for a given species is a function of the dispersion of resource (food) patches. Farm FRDD may need to extend their home ranges due to the poor and/or scattered availability of resources in farmlands, in contrast to village FRDD, which may rarely have to leave the vicinity of the village due to readily available and concentrated human-derived resources (also see Sparkes et al., 2014). In addition, the wide-ranging behavior of farm FRDD may be a result of their role in farm management, especially when their daily activities may involve guarding and/or ranging livestock (Vanak and Gompper, 2009b) or accompanying owners in their activities (dos Santos et al., 2018).

Despite the generally wide-ranging behavior of farm FRDD, we observed a considerable amount of variation in home range size within the population (Table 1; Figure S2). This type of variation has been observed in other studies on FRDD around the world. For example, home ranges varied from 0.016-148.76 $km^2$ in Chile (Schüttler et al., 2022), 0.009–1.31 $km^2$ (Molloy et al., 2017), and 0.01–24.51 $km^2$ in Australia (Meek, 1999), 0.008–5.095 $km^2$ in Cambodia (Ladd et al., 2023), and 0.011–1.03 $km^2$ in Chad

(Warembourg et al., 2021). Generalization is common and key to drawing population-level inferences for wildlife management purposes. However, we recognise that it is challenging when studying FRDD, as some FRDD might display more extreme ranging behavior than others (Meek, 1999; Dürr and Ward, 2014; Schüttler et al., 2022). For example, in our study, 5 of the 20 farm FRDD (25 %) had home ranges exceeding 1.78 $km^2$, which is significantly larger than our reported median of 0.53 $km^2$ (Table 1; Table S1). In addition, a farm FRDD (Dog 21) travelled a maximum distance of 5.15 km within an hour (Table S2; Figure S4). Variability within FRDD populations has been linked to sex and the reproductive status of individuals among other biological factors (Dürr et al., 2017; Sparkes et al., 2014). However, we could not test for the effects of sex and reproductive status on home range sizes due to the very small sample size of female FRDD (n = 2) and limited data on their reproductive status. Additionally, a study highlighted how differences in dog-caregiver bond may influence the ranging behavior of FRDD in rural areas (Saavedra-Aracena et al., 2021). All the farm FRDD in our study were either owned or semi-owned; therefore, understanding how human interaction influences roaming behavior specific to the cultural context of the region is a gap in our understanding of FRDD behavior and merits further investigation.

During movement, we observed that farm FRDD mostly used grasslands, agriculture, and fallow lands, whereas village FRDD primarily used built areas. Open habitats (grasslands and fallow lands) provide little resistance to movement (Sepúlveda et al., 2015) and are a critical link between human settlements and farmlands in the study area (Fig. 1). Moreover, if the farm FRDD's role included protecting livestock and ranging with humans, this could probably explain why they use open habitats, such as grasslands, for movement (Sepúlveda et al., 2015), more so than village FRDD, which rarely foray into grasslands (Vanak and Gompper, 2009b). However, it is important to note that although the village FRDD mostly stayed in the village and used built areas, all of the village FRDD in our study made a few exploratory forays outside of it. For example, village FRDD (Dog 10) travelled a maximum distance of 3.24 km within an hour outside the village (Figure S3).

A different pattern emerged at the second order of selection (home range vs study area), where both categories of FRDD significantly selected built areas, followed by agriculture over other habitat types (Table 2). This finding is consistent with other studies that indicate that FRDD clearly select anthropogenic habitats in heterogeneous rural areas (Cunha Silva et al., 2022; Vanak and Gompper, 2010; Woodroffe and Donnelly, 2011). Selection for built and other human-modified areas is expected as domestic dogs largely depend on human-derived foods and shelter (Cunha Silva et al., 2022; Silva-Rodríguez and Sieving, 2011; Vanak and Gompper, 2009a). For instance, a previous study at a similar site in India reported that the diet of farm FRDD predominantly consisted of human-derived foods, including garbage, direct feeding from humans, crops, and livestock carcasses (Vanak and Gompper, 2009a). Although we observed a higher selection of grasslands by farm FRDD than by village FRDD, grasslands were generally not preferred by both categories of FRDD. A slightly higher selection by farm FRDD may be due to the continuous interface of farmlands and human settlements with grasslands, making them easily accessible to farm FRDD during movement and farm roles discussed earlier. A lower selection of open habitats, such as fields, shrublands, and pastures, has been previously observed at the landscape scale in both farm and village FRDD. However, studies are not concordant in their findings. In rural sub-Antarctic Chile, village FRDD strongly avoided shrublands at the landscape scale (Schüttler et al., 2022). Similarly, farm dogs in central India did not select for grasslands and ploughed lands despite their availability in the study area (Vanak and Gompper, 2010). In contrast, farm FRDD selected pastures in their forays in the rural coastal range of Chile (Sepúlveda et al., 2015). We believe that the differences in habitat use by FRDD areas are context-dependent and affected by a multitude of interacting factors, including where a FRDD lives (or where its owner lives if owned), resource availability and distribution, their utility in the society and/or role in farm management, human-dog relationships and interactions, and landscape composition and arrangement. Our study highlights the differences in habitat use during movement and second-order habitat selection between the two categories of FRDD; however, it does not address the factors that might influence these behaviors. We believe that these predictors should be further investigated as they can provide key insights into creating effective management practices for FRDD in rural areas.

Behavioral motivation, such as foraging and resting, drives the habitats animals select (Beumer et al., 2023; Roever et al., 2014). As a result, not incorporating behavioral states in habitat selection studies can lead to 'inferential pitfalls' as described by Roever et al. (2014). In our study, we used pooled data and did not estimate behavior-specific habitat selection at the second order. Therefore, we acknowledge that this may have consequences for our quantification of habitat selection in FRDD, especially when a particular habitat is selected more during one behavioral state but least selected during another (Roever et al., 2014). Despite this shortcoming, we believe that our findings suggest a general yet important pattern of space-use between the two categories of FRDD that can have management implications. Moreover, a common limitation in wildlife GPS studies, including ours, is the potential bias arising from missing and irregular tracking data (Fleming et al., 2018). We observed some irregularities in our dataset due to changes in the sampling schedule during the observation period, habitat-related collar success rates in terms of GPS location acquisition, and unpredictable collar malfunctions. To account for these tracking-related issues, we used the *ctmm* R package's optimal weighing method to accurately estimate home ranges and reduce error (Fleming et al., 2018). However, it was challenging to account for this bias when estimating the proportionate habitat use during movement with the recreated linear trajectories. In order to minimize the impact of irregularity, we only recreated trajectories of consecutive location points that were less than 65 min apart.

### 4.1. Conservation implications

FRDD are a pervasive threat to biodiversity in developing countries (Gompper, 2014). As human populations expand along with rapid habitat fragmentation in rural areas, understanding the ecology, behavior, and impacts of FRDD on wildlife is of great conservation interest globally where they display free-ranging behavior. While we did not directly investigate the impacts of FRDD on wildlife, our findings reveal how their space-use might lead to various negative interactions with wildlife inhabiting fragmented habitats outside protected areas. For instance, habitat generalists such as golden jackals and jungle cats are known to select human-modified habitats, including agricultural areas, at the second order (Katna et al., 2022 Figure S2), thereby increasing the spatial overlap with farm FRDD. However, this may not be of a special conservation concern given the species are widely distributed, abundant, and are not endangered. Additionally, although farm FRDD did not select grasslands, they are more likely than village FRDD to interact with grassland specialists, such as Indian foxes and great Indian bustards, during their movements within or along the edges of grasslands and in open areas interspersed throughout human-modified areas. A previous study observed spatial niche partitioning between farm FRDD and Indian foxes at the landscape level due to interference competition (Vanak and Gompper, 2010). However, due to the small and fragmented tracts of grassland habitats and the widespread reach of domestic FRDD in our study area (72.5 % of camera traps detected FRDD– Carricondo-Sanchez et al., 2019), we believe that this spatial segregation may not be as achievable as we initially thought. As a result, foxes may rely on avoiding FRDD temporally (Carricondo-Sanchez et al., 2019). This exacerbated interference competition, as suggested by Vanak and Gompper (2010), could lead to lower population sizes and possibly local extirpation of native populations of foxes. Additionally, pathogen spill-over (with foxes– Belsare et al., 2014) and hybridization (with grey wolves– Tyagi et al., 2023) are other major threats to carnivore populations that rely on grassland patches and other open-natural ecosystems in rural human-dominated landscapes. These threats are further exacerbated by the limited representation of such habitats in Indian protected areas and their increased vulnerability to agricultural conversion due to their classification as 'wastelands' (Madhusudan and Vanak, 2023).

### *4.2. Management recommendations*

FRDD management is exceptionally challenging and complex in areas where there is a lack of sustained efforts to control them and a widespread availability of human resources that support these populations. A multi-pronged, targeted, and locally tailored approach is necessary to minimize dog-wildlife interactions in rural areas, especially those that host a diverse range of wildlife (Gompper, 2021). In our study, we determined that not all FRDD are likely to exhibit space-use patterns that can be detrimental to all wildlife. Wide-ranging farm FRDD are more likely to foray into natural areas and present a human-associated edge effect in habitat matrices (Vanak and Gompper, 2009b), thus increasing their likelihood of interacting with wildlife that rely on these patches in an extremely fragmented landscape. Future action plans should be tailored towards owned farm FRDD, rather than implementing a 'one-size-fits-all' strategy for all rural FRDD. For example, this can include a strong emphasis on responsible dog ownership and measures that limit the free-ranging behavior of domestic dogs. Sepúlveda et al. (2015) also suggest using leashes and kennels to restrict free-ranging behavior. However, the measures implemented on owned farm FRDD must be compatible with the owners' needs, capacity, and the cultural context of the region to avoid management complications, especially if the dogs are used for protection towards livestock predation and crop raiding. Although the impact of village FRDD on wildlife is probably low, this might change as the landscape undergoes rapid land-use change, making habitats more fragmented and accessible to village FRDD during their forays as well. Therefore, the management approach should also include the active removal of unowned FRDD (when possible) in areas of conservation concern (for e.g. near protected areas, corridors, etc.), as well as controlling populations through improved waste disposal management, re-homing and stricter pet ownership rules.

## Ethics approval

The study was conducted under the approval of the Animal Ethics Committee of the Ashoka Trust for Research in Ecology and the Environment (ATREE), Bangalore, India, with permit number: AAEC/101/2016. Permission was also obtained from the FRDD owners or the village council before handling the FRDD.

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## CRediT authorship contribution statement

**Abi T. Vanak:** Writing – review & editing, Conceptualization, Funding acquisition, Methodology, Data curation, Supervision. **James D. Murdoch:** Writing – review & editing, Methodology, Supervision. **Abhijeet Kulkarni:** Writing – review & editing, Methodology, Data curation, Project administration. **Soham P. Mehta:** Writing – original draft, Methodology, Formal analysis, Visualization, Validation.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03931.

## Data availability

Data will be made available on request.

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