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Research Article

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Annual, seasonal, and daily space-use of Common Fallow Deer (*Dama dama*) in Australian agricultural landscapes

Sebastien Comte[1,2,*], Andrew J. Bengsen[3], Lee Parker[3], David M. Forsyth[1,2]

[1]Vertebrate Pest Research Unit, NSW Department of Primary Industries and Regional Development, 1447 Forest Road, Orange, NSW 2800, Australia
[2]Evolution & Ecology Research Centre, The University of New South Wales, Biological Sciences North (D26), High Street, Sydney, NSW 2052, Australia
[3]Vertebrate Pest Research Unit, NSW Department of Primary Industries and Regional Development, 4 Marsden Park Road, Calala, NSW 2340, Australia

[*]Corresponding author: Vertebrate Pest Research Unit, NSW Department of Primary Industries and Regional Development, 1447 Forest Road, Orange, NSW 2800, Australia. Email: sebastien.comte@dpird.nsw.gov.au

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Abstract

The Common Fallow Deer (*Dama dama*; hereafter "fallow deer") has been widely translocated from its native Mediterranean range and is now present on all continents except Antarctica. In some countries—such as Australia—introduced populations of fallow deer have increased in range and abundance, negatively affecting agricultural production. However, little is known about how this species uses these agricultural landscapes annually, seasonally, or daily. We used GPS collars to track the hourly movements of 68 adult fallow deer (25 males, 43 females) at 3 sites in mixed pastoral farmland (a mosaic of open eucalypt woodland and pasture) in eastern Australia between 2020 and 2024. We estimated annual and monthly home ranges, daily distance moved, and diel movement cycles. As expected, annual home ranges (using the biased random bridge method) were larger for males (median = 1,848.1 ha, 95% CrI: 929.2 to 3,584.0 ha) than females (median = 646.3 ha, 95% CrI: 368.1 to 1,068.5 ha), and home ranges and core areas were similar across the 3 sites. Both sexes had a strong crepuscular movement pattern that was consistent across sites. Male fallow deer increased their movement rates in April–May (i.e., during the mating season), and their movement patterns were most restricted during summer. Female fallow deer movements were more consistent across the year than those of males, but movement patterns were also most restricted during summer. There was substantial individual variation in daily movement patterns between and within sites, especially during the mating season. Most individuals exhibited strong site fidelity, but some males and females made short excursions (up to a week and 10 km) from their home range. The strong site fidelity of fallow deer suggests that management strategies utilizing repeated culling will be most effective at reducing overabundant fallow deer populations in Australian agricultural landscapes.

Key words: diel movement cycle, home range, invasive species, lek/lekking, movement pattern, spatial ecology, ungulates, utilization distribution

Movement ecology is an individual-based decision process that scales up over time and is influenced by individual factors (e.g., age, sex, health, hormonal stage) and external biotic (e.g., social interactions, competition for resources, predation) and abiotic (e.g., management, landscape, weather, circadian cycle) stressors (Nathan et al. 2008). Understanding how ungulates move in the landscapes that they inhabit is critical for their management (Porter et al. 2004; Meisingset et al. 2018). For non-native ungulates that are considered overabundant, as is the situation for most wild deer in Australasia, understanding where and when deer are most accessible is crucial to maximize the efficiency of control operations (Nugent 1994). For example, knowing how deer use open and wooded areas during the day or night can improve the efficiency of ground-based cullers (Comte et al. 2022). Similarly, the spatial scale of deer movements can be an important determinant of the optimal scale of management operations, as observed in deer culling operations to protect woodlands in the United Kingdom (Fattorini et al. 2020). The degree of site fidelity of a species can be important for understanding and managing disease transmission hazards (Webb et al. 2010) and for predicting how surviving animals move during and after culling operations (Bengsen et al. 2024). This information can then be used to plan repeated operations at the same site if deer display high site fidelity (Brough et al. 2017) or to define the spatial extent over which further control operations need to be conducted if deer have low site fidelity (Wäber et al. 2013). This is particularly important when culling operations are used to prevent or constrain infectious disease outbreaks with potential spillover to livestock and humans (Orange et al. 2021).

Interspecific differences in movement behaviors of ungulates are well documented using both radio and satellite tracking devices (Mysterud et al. 2001; Ofstad et al. 2016). Differences between populations of the same species are less understood (Kie et al. 2002; Morellet et al. 2013), and there can also be substantial variation among individuals within a population (Seigle-Ferrand et al. 2021; Heit et al. 2023). Two of the main systemic questions in movement ecology are: (i) how to extrapolate individual tracking data to robust population patterns and (ii) how to generalize those patterns between populations, especially for species introduced into novel environments (Girard et al. 2002; Latham et al. 2015). One way to improve the robustness of

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population inferences is to increase the sample size. Some studies have tracked many hundreds of deer (Mysterud et al. 2017; van de Kerk et al. 2021), but the costs of tracking devices and the challenge of capturing wild deer in some habitats mean that many studies rely on small sample sizes—sometimes <10 individuals (e.g., Amos et al. 2022). Replication of tracking across multiple populations is therefore needed to provide robust knowledge about deer movement ecology on which to base effective management strategies.

Regarded as a valuable game and farming resource, the Common Fallow Deer (*Dama dama*; hereafter "fallow deer") has been translocated across Europe since the Neolithic period (Baker et al. 2024). Consequently, fallow deer have been extensively introduced into new habitats around the world and are now present in ~38 countries and on all continents except Antarctica (Long 2003; Nugent et al. 2025). Originally introduced to Australia for sport hunting in the 1800s (Bentley 1978), fallow deer were commonly farmed in the 1980s and 1990s (Mulley et al. 2000), and many populations have since established from escaped or deliberately released captive animals (Moriarty 2004). Wild fallow deer are present in all Australian states and the Australian Capital Territory (Mulley 2023) and are increasing in distribution and abundance (Cunningham et al. 2022; NSW DPIRD 2023). Fallow deer have reached densities of ~37 per km^2 in some agricultural areas, leading to competition with domestic livestock for food (Davis et al. 2023). Fallow deer are also potential hosts and reservoirs for diseases (e.g., bovine tuberculosis, foot and mouth disease), which could have dire consequences for Australia's livestock industries (Cripps et al. 2019; Huaman et al. 2023). Current management strategies focus on reducing deer densities through culling (Bengsen et al. 2023) or excluding deer from local assets with fences (Forsyth et al. 2023). Understanding daily, seasonal, and annual movements of fallow deer can help target culling efforts at the most efficient time and at the most relevant spatial scale to maximize the management outcome. This information is also crucial for understanding risks of disease transmission among deer populations and to livestock (Cripps et al. 2019).

Previous studies on fallow deer movements are scarce (Table 1). Pre-2000s, 4 studies used VHF tracking on single populations in Europe and Australasia, all with tracking frequency <12 locations per deer per month (Nugent 1994; Statham and Statham 1996; Ciuti et al. 2003; Davini et al. 2004). More recently, GPS collars were used for introduced fallow deer on Little St. Simons Island (United States; Morse et al. 2009), but only 4 individuals had tracking data for a full year. In Europe, 1 study used GPS collars to study fallow deer reintroduced in Dilek Peninsula National Park (Turkey), with only 6 individuals continuously tracked for ≥12 months (Durmuş 2019). In Australia, (McCarthy et al. 2025) recorded hourly locations of 12 fallow deer for at least 12 months in the Australian Alps.

Most studies conducted to date (based on VHF or GPS; Table 1) show that male fallow deer have larger annual home ranges than females. However, differences in habitat, management, and the technology used resulted in annual home range sizes (based on the same minimum convex polygon method) varying from a minimum of 206 and 99 ha to a maximum of 7,820 and 5,020 ha for males and females, respectively (Table 1). Males also increase their movements during the autumn mating season due to lekking behavior (Table 1). Lekking occurs when several male fallow deer congregate and

Table 1. Common Fallow Deer (Dama dama) home ranges from tracking data collected around the world.

Data collection	Country	Deer per km^2	Main habitat	Method	Duration (month)	Collared deer	Location frequency	Sample size (>12 month)	Annual MCP (ha)	Seasonal min	Seasonal max	Source
1985 to 1988	New Zealand	22	Deciduous and pine forests	VHF	2 to 30	M=33 F=26	10 to 12 locations per month	M=19 F=19	206 99	Summer Summer	Autumn Spring	Nugent 1994
1994 to 1995	Australia	NA	Open eucalypt woodlands and pastures	VHF	2 to 14	M=9 F=11	Weekly	M=1 F=7	2950 740	NA NA	NA NA	Statham and Statham 1996
1996 to 2000	Italy	26	Deciduous and pine forests	VHF	Up to 36	M=14 F=13	12 locations per month	M=33 F=23	461 583	Winter Summer	Autumn Autumn	Ciuti et al. 2003; Davini et al. 2004
1999 to 2000	Poland	3	Deciduous and pine forests	VHF	12	M=3 F=5	Few per month	M=3 F=5	975 206	Winter Winter	Autumn Spring	Borkowski and Pudełko 2007
2005 to 2006	USA	13 to 22	Salt marshes and forests	GPS	6 to 16	M=5 F=2	Every 3 hours	M=2 F=2	654 233	No seasonal variation No seasonal variation		Morse et al. 2009
2011 to 2013	Turkey	NA	Deciduous and pine forests with shrublands	GPS	1 to 26	M=5 F=10	Every 2 hours	M=4 F=2	525 388	NA NA	NA NA	Durmuş 2019
2021 to 2023	Australia	12 to 26	Eucalypt forests and pastures	GPS	1 to 31	M=11 F=9	Every hour	M=5 F=7	7820 5020	Summer Winter	Autumn Spring	McCarthy et al. 2025
2020 to 2024	Australia	8 to 37	Open eucalypt woodlands and pastures	GPS	1 to 33	M=27 F=43	Every hour	M=10 F=31	1885 502	Summer Summer	Autumn Winter	Comte et al. (*This study*)

M, male; F, female; NA, not available.

compete to defend 1 or multiple mating grounds (or leks) to secure mating opportunities (Apollonio 1989). This high variability in space use among populations suggests strong plasticity in movement behaviors, making it difficult to generalize from existing studies. Management actions that do not account for local movement and habitat use patterns are unlikely to be effective. In this study, we use GPS collars to track the movements of adult fallow deer at 3 pastoral sites in New South Wales, eastern Australia, where deer are managed by ground-based and helicopter-based shooting to minimize their undesirable agricultural impacts. We use the tracking data to estimate annual and monthly home ranges and characterize seasonal changes in daily movement patterns. At each spatio-temporal scale, we test hypotheses based on fallow deer ecology, focusing on sex- and site-specific patterns of movements. Finally, we discuss the implications of our results for the management of non-native fallow deer in Australia.

Methods

Study area.

The 3 study sites (Fig. 1) were characterized by a mosaic of open pasture for livestock (sheep and beef cattle) production and patches of predominantly eucalypt woodland. Tree cover typically increased into continuous woodlands and open forest on steeper slopes, with trees up to 20 m tall. Site A was slightly higher in elevation than Sites B and C, but the local climatic conditions were similar (Table 2). Site B was more topographically diverse than Sites A and C and had greater woodland and forest cover. Rain fell in all seasons, but precipitation was generally greatest during the warmer summer months (the Australian Government Bureau of Meteorology; http://www.bom.gov.au).

Fallow deer densities at all 3 sites were considered relatively high by New South Wales standards (NSW DPIRD 2023; Fig. 1). Deer density at Sites A and C were 8.1 (95% CI: 5.2 to 12.6; September 2020) and 37.5 (95% CI: 25.3 to 55.8; February 2023) deer per km^2, respectively, as estimated using helicopter mark–recapture distance sampling during the course of other studies (Bengsen et al. 2023; Forsyth 2025). Small numbers of Red Deer (*Cervus elaphus*) were observed at both sites—Chital Deer (*Axis axis*) and Rusa Deer (*C. timorensis*) were also present in very low numbers at Site C where deer had been actively managed as a game resource for over 20 years on 1 prominent property. No estimate of deer density was available for Site B.

There are no restrictions on the hunting of any deer species on private land in New South Wales, other than the need to have the permission of the landowner. In our 3 study areas, ground-based shooting of deer occurred during both day and night. Helicopter-based shooting of deer and feral pigs (*Sus scrofa*) was also conducted no more than once a year, as described previously (Bengsen et al. 2023, 2024). Comparison of the movement rates, activity range areas, and daily activity patterns of 48 GPS-collared fallow deer for 1 month before and after helicopter-based shooting revealed that this disturbance caused only minor and temporary increases in daily and hourly distance travelled, activity range areas of female deer, and increased nocturnal activity in female and male deer during shooting (Bengsen et al. 2024).

Deer capture and GPS tracking collar attachment.

We used aerial net-gunning (Bengsen et al. 2021) to capture adult fallow deer at the 3 sites. At Site A, deer were captured during 30 June to 2 July, 14 to 16 September 2020, and 15 to 16 June 2021. At Sites B and C, deer were captured during 5 to 8 October 2021 and 4 to 6 April 2022, respectively. We fitted captured deer with 1 of 2 types of GPS tracking collars, either G5-2D (Advanced Telemetry Systems Inc., Isanti MN, USA) or LiteTrack Iridium 420 (Lotek Wireless Inc., Newmarket, ON, Canada). All GPS units were programmed to record locations hourly and to transmit locations to satellites at least daily.

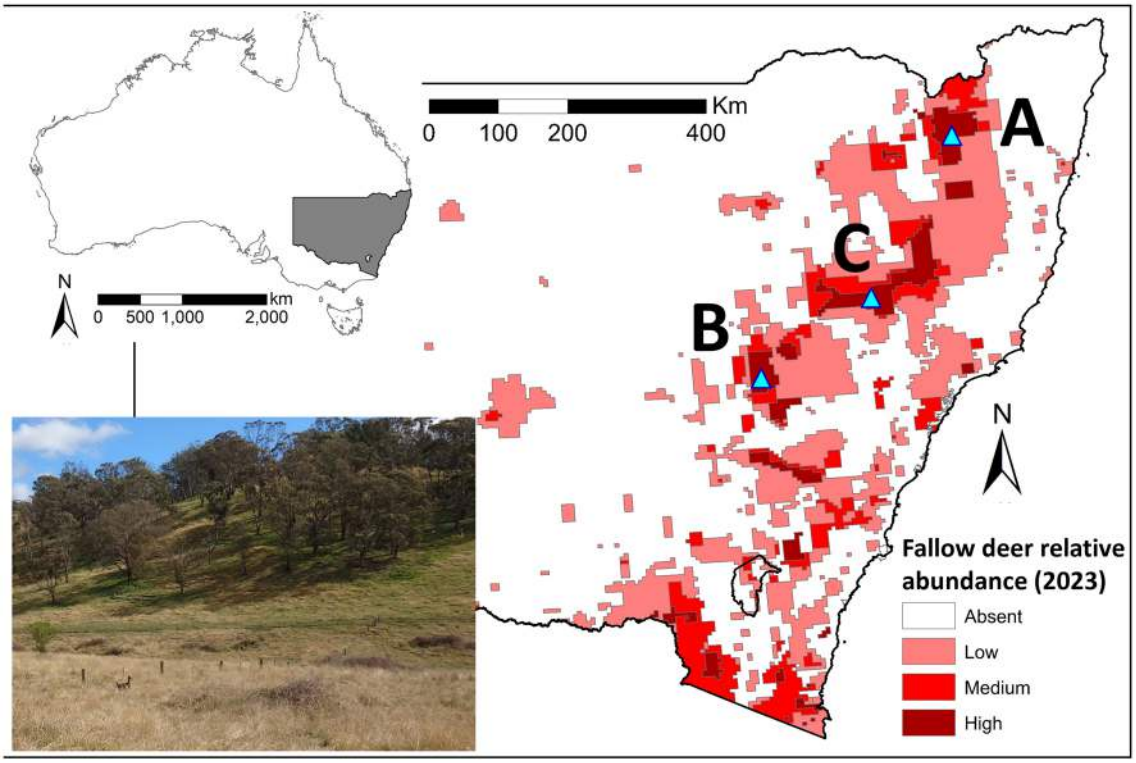

Fig. 1. Location of the 3 study sites (triangles) in pastoral New South Wales, Australia (2020 to 2024). Shading indicates the reported relative abundance of Common Fallow Deer (*Dama dama*) in 2023 (NSW DPIRD 2023). Inset shows New South Wales in Australia. The photograph shows an adult female fallow deer equipped with a GPS collar in habitat typical of the 3 sites.

Table 2. Geographical location, approximate size (area covered by the tracking data), range of elevation, and monthly climate (averaged 2020 to 2024) for the 3 study sites in pastoral New South Wales, Australia, 2020 to 2024.

Site[a]	Longitude, latitude	Approximate size (km²)	Elevation (m.a.s.l)	Monthly max daily temperature (°C)	Monthly rainfall (mm)
A	151.73°E, 29.74°S	200	970 to 1430	13.4 to 26.7	47.7 to 118.1
B	149.14°E, 32.72°S	250	360 to 815	15.3 to 33.0	45.5 to 71.1
C	150.56°E, 31.78°S	500	480 to 1140	12.6 to 28.5	32.4 to 85.2

Data collected from the Australian Government Bureau of Meteorology (http://www.bom.gov.au).
[a]See Fig. 1 for locations of the 3 sites within New South Wales.

Protocols for animal capture and collaring were approved by the NSW Department of Primary Industries and Regional Development's Orange Animal Ethics Committee (ORA 20-23-003, ORA 21-24-013).

Data cleaning.

We removed the first 2 weeks of data from all individuals so as to avoid including any post-release movements in subsequent analyses (Bengsen et al. 2021). We then removed stationary locations following the activation of a mortality signal (i.e., after 24 h of inactivity) or after an animal was known to have died. We discarded any GPS location with a horizontal dilution of precision >5 (Bjørneraas et al. 2010). Finally, we screened the remaining tracking data to remove any unrealistic movement spikes, defined as 2 consecutive hourly steps with a speed of more than 15 km h^{-1} and a turning angle between 150° and 210° (Gupte et al. 2022). All timestamps were rounded to the hour (variance <10 min). We calculated the stationary error (i.e., pseudo-movement observed between 2 successive locations of a stationary collar) for 3 of each GPS collar model, using tracking data collected after the known death of the animal. Following Theuerkauf et al. (2023), we then subtracted the mean stationary error from all hourly step lengths prior to analyses.

Annual ranges.

Animal space use is inherently dependent on the time window over which it is measured. For species such as fallow deer that can live for many years, adult space use is commonly considered as an annual cycle based on climate and ecological seasons. Therefore, the fundamental metric of space use is the annual home range, which, according to most definitions, represents the area used by an animal to fulfill all individual and social requirements (Burt 1943; Powell and Mitchell 2012). We therefore split the individual tracking data into 365-day periods (max 2 successive periods) starting from the first day (i.e., 14 days after capture). With a high frequency (hourly) of locations recorded by the GPS collars, we used the biased random bridges (BRB; Benhamou 2011) method, which combines an advection component (i.e., directional drift) with a diffusion coefficient to model the uncertainty of the animal trajectory between 2 successive known locations. This method is particularly suited to estimate home ranges from autocorrelated tracking data and can accommodate missing locations (Benhamou 2011). We considered 2 levels of utilization distribution, hereafter referred to as the annual core area (BRB50%) and the annual home range (BRB99%). To allow direct comparison with previous studies, we also estimated the annual home range based on the classical 95% minimum convex polygon (MCP95%) method (Mohr 1947).

We hypothesized that male fallow deer would have larger home ranges over a given time period than females, as has been typically reported for this species (Table 1). Our 3 study sites were similar in terms of landscape and climate, and hence we hypothesized that home range sizes would not vary among the sites. We tested these 2 hypotheses by fitting Gamma Bayesian regressions on the annual home range (BRB99%) and core area (BRB50%) sizes with sex (males and females) and site (A, B, and C) as fixed effects. Due to the limited sample size, we did not include interaction between the fixed effects. As some deer had sufficient tracking data to estimate 2 successive annual home ranges, we included animal ID as a random effect. For those deer with 2 annual home ranges, we also calculated the inter-annual overlap as a measure of site fidelity (Webb et al. 2007). All home range analyses were performed in R v4.4.1 (R Core Team 2024) with the R package "adehabitatHR" v0.4.21 (Calenge 2006). We fitted the models using the R package "brms" v2.20.4 (Bürkner 2017) with diffuse normal priors $N(0,10)$ for all model parameters. We ran 3 MCMC chains of 20,000 iterations (5,000 burn-in runs and 15,000 sampling runs) for an effective sample size >1,000 for the posterior distributions of the parameters. We assessed the mixing of the MCMC chains visually and with the Gelman–Rubin diagnostic (Brooks and Gelman 1998).

Monthly ranges and movements.

With limited knowledge on fallow deer seasonal ranging behaviors in Australia, and to limit preconceived bias, we calculated the area used by each deer for each calendar month. We selected all individual months with at least 20 consecutive days of tracking data and used the BRB method to calculate the monthly ranging areas (BRB99%). We also calculated the overlap between successive monthly ranges of the same animal as a measure of site fidelity. We hypothesized that males would increase their ranging behavior (hence reducing their site fidelity) during the mating season (March to May; Mulley 2023) and that females would have less variable space use and higher site fidelity during the year (Nugent 1994; Davini et al. 2004). As we expected non-linear cyclic responses, we tested our hypotheses by fitting a Gamma general additive mixed model (GAMM) on the monthly ranging area with sex-site-specific fixed effects ($n=6$; means and smooth terms). We included year and animal ID as random effects (means and smooth terms). We used the same model structure for the monthly overlap, but with a Beta GAMM due to the overlap being constrained between 0 and 1.

Quantifying the changes in total daily distance moved provides an additional layer of information to the monthly ranging behaviors previously described (Pépin et al. 2009). For each animal in our study, we therefore calculated the daily distance moved as the sum (km) of all linear distances between consecutive GPS locations (corrected for stationary error) for each calendar day. As for the monthly range areas, we fitted a Gamma GAMM on the daily distance moved with sex-site-specific means and smooth terms ($n=6$). We included year and animal ID as random effects (means and smooth terms). We fitted the GAMMs using the package "mgcv" v1.8-42 (Wood 2011) and visually checked for an absence of pattern in the model residuals and a k-index close to 1 with an effective degree of freedom below the maximum degree of freedom (Wood 2017).

Diel movement cycles.

As with many ungulates, fallow deer movements are strongly influenced by the circadian cycle (Ager et al. 2003; Comte et al. 2022). Fallow deer are commonly considered crepuscular but have been observed shifting toward diurnal activity in response to the presence of a predator (Rossa et al. 2021) and to nocturnal activity in response to daytime culling (Zanni et al. 2021). Given the absence of predators in our study areas, but with hunting occurring day and night, we expected to find 2 peaks of longer movements around sunrise and sunset. To test this hypothesis, we first filtered the tracking data to

keep only the linear distances moved during 1-h steps, corrected for stationary error. To reliably compare the diel movement cycle between sites and across the seasons, we transformed time into suntime (i.e., midnight = 0 am, sunrise = 6 am, midday = 12 pm, and sunset = 6 pm) using the central geographic coordinates of each site and the function "sunTime" of the R package "overlap" v0.3.4 (Nouvellet et al. 2012). We divided the year into 4 seasons: summer (December to February), autumn (March to May), winter (June to August), and spring (September to November). We fitted Gamma GAMMs to the hourly distance, independently for each sex, with season-site-specific means and smooth terms ($n = 12$). We included year and animal ID as random effects (means and smooth terms). We checked the goodness of fit of the models as previously described.

Results

Data scope.

Between July 2020 and April 2022, we captured and collared 43 fallow deer on Site A, 14 on Site B, and 14 on Site C for a total of 71 adult deer (27 males and 44 females). Data collection ceased on 10 April 2024, when only 6 of the 71 collars were still providing location data (see online supplementary material SD1). Due to collar failure, no locational data were collected for 2 males on Site A and 1 female on Site B. We therefore collected hourly GPS locations for 68 fallow deer with a median of 319 days (range 19 to 1,002), totaling 584,020 location fixes. The LiteTrack Iridium 420 (Lotek) collars had a mean success rate of 81.3% (SE = 4.0%) and a mean stationary error of 7.91 m (SE = 0.41 m). The G5-2D collars (ATS) had a mean success rate of 94.4% (SE = 1.8%) and a stationary error of 6.40 m (SE = 0.21 m; see online supplementary material SD2 for details).

Annual ranges.

A total of 32 fallow deer (10 males and 22 females) from the 3 sites (Site A = 10, Site B = 11, and Site C = 11) had >350 days of tracking from which to estimate annual home ranges. Nine females (3 in Site A and 6 in Site C) had enough tracking data (>710 days) to estimate successive annual home ranges. Fallow deer annual space use differed by sex but not between sites, although individual variability meant that 95% credible intervals overlapped (Fig. 2), particularly apparent for males. For example, 1 male at Site B had an annual home range less than half the size of all others (online supplementary material SD3). Annual home ranges (BRB99%) of male fallow deer (median = 1,848.1 ha, 95% CrI: 929.2 to 3,584.0 ha) were 2.9 times larger than those of females (median = 646.3 ha, 95% CrI: 368.1 to 1,068.5 ha). Similarly, the size of the male annual core areas (BRB50%; median = 159.7 ha, 95% CrI: 66.4 to 349.4 ha) was 2.3 times larger than for females (median = 68.9 ha, 95% CrI: 30.9 to 132.4 ha). Fallow deer showed concentrated space use within their annual home ranges, with core areas representing only 8.7% (95% CrI: 4.8% to 15.1%) and 10.7% (95% CrI: 6.1% to 17.3%) of the annual home ranges for males and females, respectively. Compared to the BRB99%, the median annual home ranges based on the MCP95% were 10% larger for males (median = 2,053.3 ha; 95% CrI: 541.1 to 6,716.6 ha) and 10% smaller for females (median = 594.1 ha; 95% CrI: 168.4 to 1,626.8 ha). The 9 females with successive annual home ranges showed a median overlap of 75.2% (range: 36.4% to 90.9%) and a median core area overlap of 31.1% (range: 8.5% to 69.3%). For 8 of these 9 females, there was limited change in home range area between years (median = −0.2%, range −33.3% to 49.4%).

Visual inspection of the 41 annual home ranges showed that 31 (76%) were unimodal (i.e., GPS locations were concentrated in a single spatial cluster used all year round; Fig. 3A), 9 (4 males and 5 females) were bimodal (2 spatially separated clusters; Fig. 3B), and 1 male was trimodal. Fallow deer in Site B were more likely to have multimodal home ranges ($n = 6$, 55%) than those in Sites A ($n = 1$, 8%) and C ($n = 3$, 18%). For all males and 2 females with multimodal home ranges, the use of seasonal clusters coincided with mating season (March to May), with the duration of use varying from 2 weeks to almost 3 months. This was particularly evident in Site B, where 3 males and 2 females converged during the mating season (Fig. 3C). Short excursions (up to 1 week) outside the annual home range were also observed during mating season for 2 males and 2 females with unimodal home ranges (Fig. 3A). Similar excursions were also observed for 3 out of 5 males in Site A with tracking data that included mating season but were too short to be included for the annual home ranges. Seasonality was also observed for a third of the fallow deer with unimodal annual home ranges (6 males and 4 females), with parts of their range used more intensely during March to April and other parts during October to January.

Monthly ranges and movements.

Male fallow deer monthly ranges ($n = 262$) were on average 1.7 times larger than those of females ($n = 574$), but variance was larger than the effect size (i.e., overlapping 95% confidence intervals; Fig. 4). At

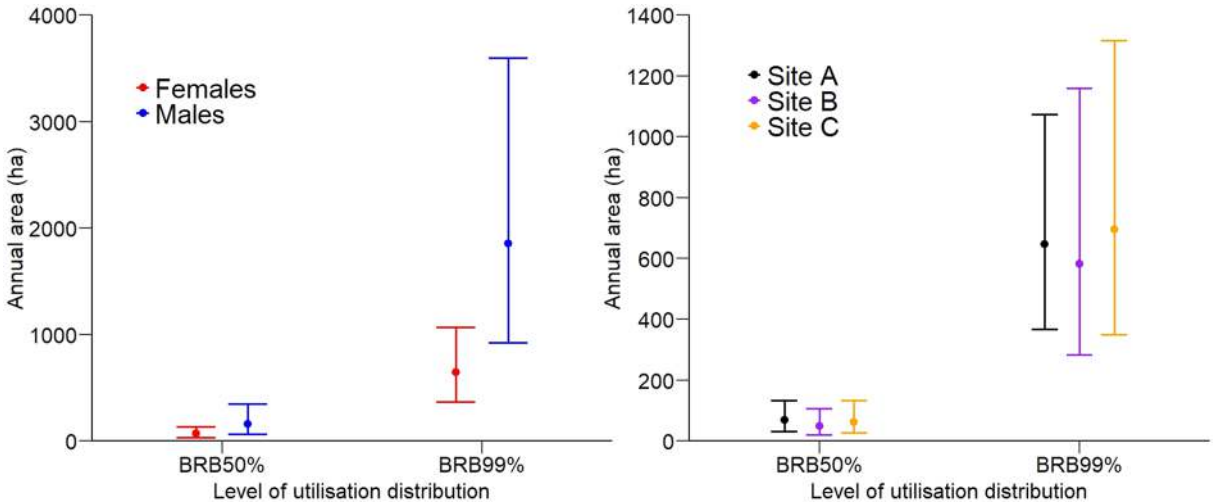

Fig. 2. Predicted mean (and 95% credible intervals) annual core area (BRB50%) and home range (BRB99%) sizes for male and female Common Fallow Deer (*Dama dama*; left) in 3 sites (right, see Fig. 1 for site locations) in pastoral New South Wales, Australia, 2020 to 2024. Utilization distribution estimated by biased random bridges (BRB).

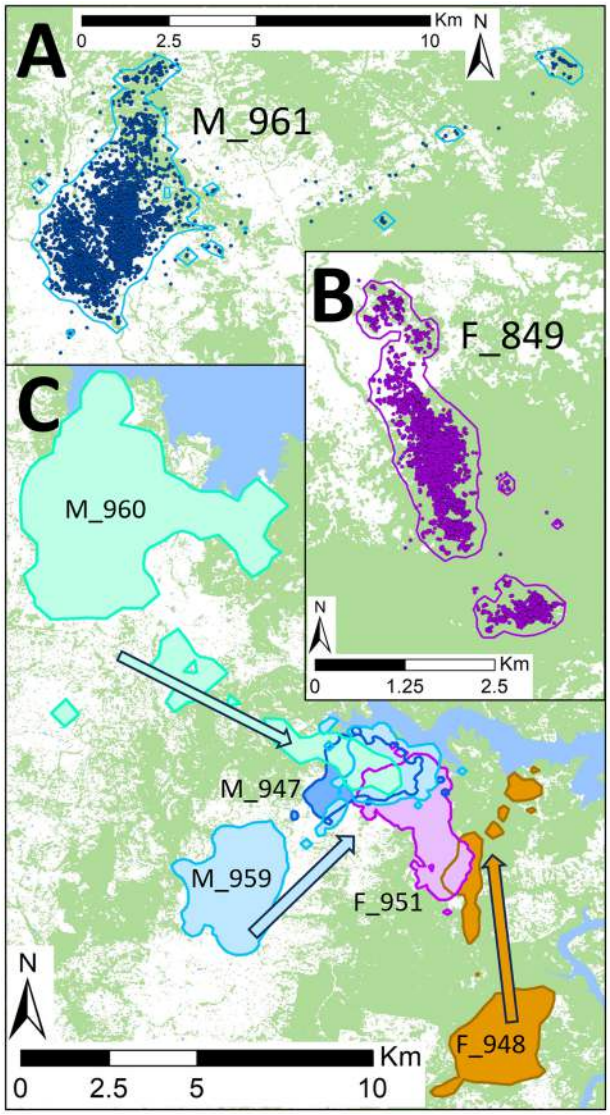

Fig. 3. Visual representation of annual home range (BRB99%) of Common Fallow Deer (*Dama dama*) in pastoral New South Wales, Australia, 2020 to 2024. A) Unimodal home range of a male in Site C showing an excursion east during the mating season. B) Bimodal home range of a female in site C with southern cluster used between November and January. C) Probable lekking behavior observed in Site B, with 3 males and 2 females converging during the mating season (arrows indicate directional movement at start of mating season).

all 3 sites, male monthly range areas were smallest in summer (minimum Site A = 198 ha, Site B = 226 ha, Site C = 270 ha), followed by a sharp increase and a peak during the April–May mating season (Site A = 647 ha, Site B = 914 ha, Site C = 653 ha; Fig. 4). The pattern during the second half of the year varied between sites: at Site A, male ranges remained large until October; at Site B, male range sizes decreased immediately after the mating season and then steadily decreased further until summer; at Site C, male range sizes decreased slightly after the mating season but remained large until August. Range sizes then increased to a second higher peak in September–October (maximum 839 ha) before decreasing in summer. At all 3 sites, female monthly range sizes were more consistent during the year, with smaller ranges in summer (minimum Site A = 165 ha, Site B = 167 ha, Site C = 249 ha; Fig. 4) and larger ranges in winter at Sites A and C (maximum Site A = 281 ha and Site C = 374 ha), and spring at Site B (maximum = 303 ha). Compared to males (mean monthly overlap = 63.6%; 95% CI: 59.5% to 67.4%), females showed greater and more stable site fidelity (mean monthly overlap = 72.6%; 95% CI: 67.9% to 76.8%; Fig. 5) throughout the year. Male site fidelity mostly reflected changes in monthly range sizes (Fig. 4), with the largest ranges in autumn resulting in the lowest range overlap in Sites A and B. At Site C, male site fidelity remained low between autumn and spring, matching the large monthly range sizes.

The mean daily distances moved were similar between male (mean = 2.5 km; 95% CI: 2.1 to 3.1 km) and female (mean = 2.3 km; 95% CI: 1.8 to 2.9 km) fallow deer, but their annual trend differed by sex and site (Fig. 6). As for the monthly range areas, male daily movements were lowest in February before increasing rapidly to a peak in April–May (mating season). The daily distance rapidly decreased in Sites A and B in winter (Fig. 6) but remained high in Site C, with a second peak at the latter site in October (similar to the trend observed for monthly range). Female movements remained much more stable throughout the year. For both sexes, there were still important individual variations in daily distance moved during the year (Fig. 6), with our model explaining 27.1% of the deviance compared to 72.3% for the monthly range model.

Diel movement cycles.

As expected, both male and female fallow deer showed strong crepuscular movement cycles characterized by larger distances moved around sunrise and sunset (Figs 7 and 8). The observed increase in male daily distance moved during mating season (March to May) was the result of ~40% longer movements around sunrise and sunset and ~80% longer nocturnal movements compared to December to February (Fig. 7). The greater stability in female daily distance moved during the year was also apparent for their diel movement cycles. The exception was at Site B, where female movements in spring and summer

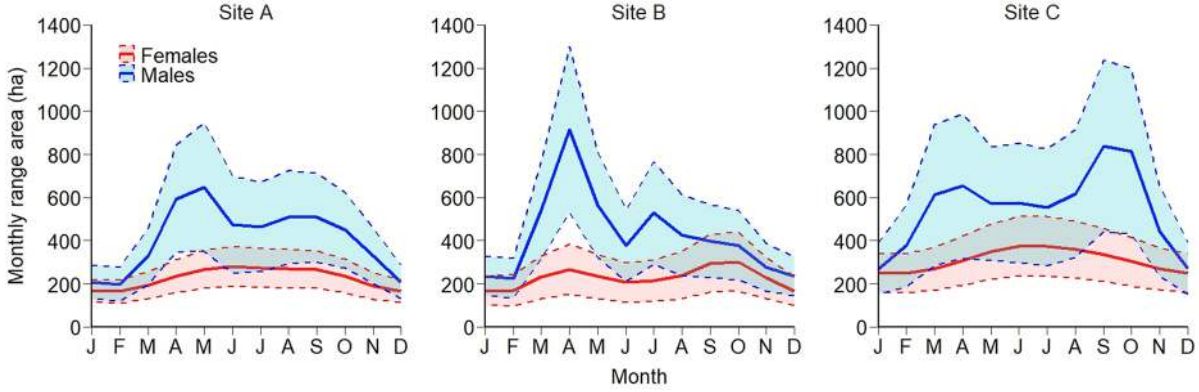

Fig. 4. Predicted monthly range areas (BRB99%, mean and 95% confidence intervals) for male (blue) and female (red) Common Fallow Deer (*Dama dama*) in 3 sites in pastoral New South Wales, Australia, 2020 to 2024.

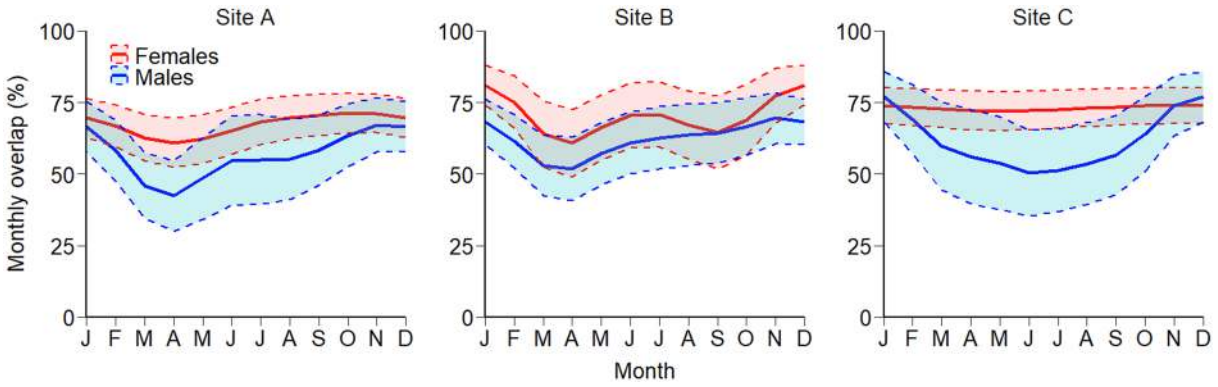

Fig. 5. Predicted monthly range overlap (BRB99%, mean and 95% confidence intervals) for male (blue) and female (red) Common Fallow Deer (*Dama dama*) in 3 sites in pastoral New South Wales, Australia, 2020 to 2024.

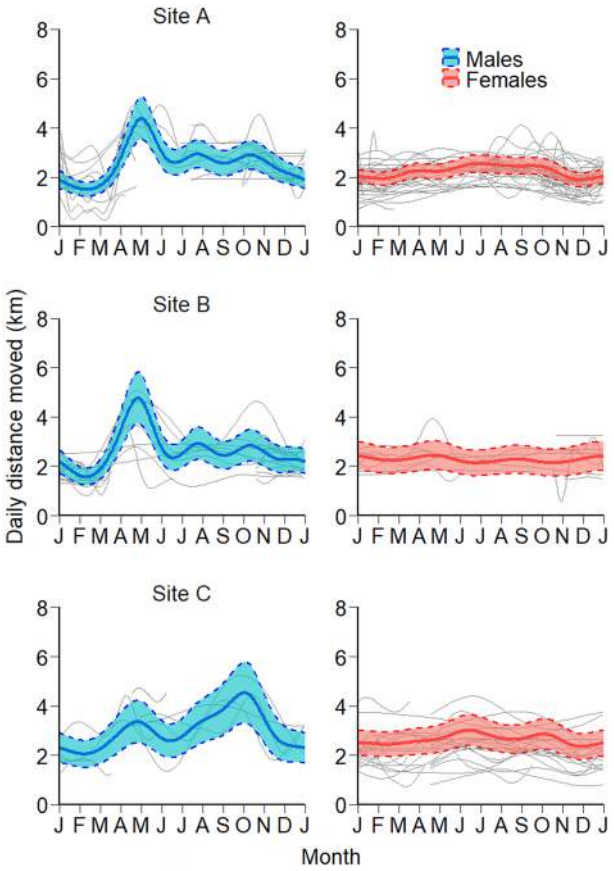

Fig. 6. Predicted daily distance moved (mean and 95% confidence intervals) for male (blue) and female (red) Common Fallow Deer (*Dama dama*) in 3 sites in pastoral New South Wales, Australia, 2020 to 2024. Light gray lines show the observed data for individual deer.

peaked around sunset and in winter peaked during the first half of the night in autumn and winter (Fig. 8). At the hourly scale, our model revealed a greater individual variance than at the daily scale, explaining 4.8% and 5.7% of deviance for males and females, respectively.

Discussion

Despite having a long association with humans and a wide global distribution, there have been few studies of the spatial ecology of fallow deer in either their native or non-native ranges (Table 1). Our study, using hourly GPS locations from 68 adult fallow deer at 3 independent sites in eastern Australia, is the most comprehensive in terms of sample size to date. We found that the size of the annual home ranges and core areas were similar at the 3 sites, with males using larger areas than females. At all 3 sites, male monthly ranges and daily distance moved increased during the autumn mating season, whereas female movements were more consistent throughout the year. Fallow deer at the 3 sites showed strong site fidelity throughout the year and between successive years for females. Both sexes showed strong crepuscular movement activity at all sites. Our results also highlighted inter- and intra-site variability in individual movement behaviors. Fallow deer at Site B showed stronger seasonality, with more individuals having multimodal home ranges, and movements of males at Site C peaked during spring (October–November); these patterns were not observed at the other sites. Individual variability in movements increased with shorter temporal resolution (i.e., the deviance explained by our models: hourly < daily < monthly < annually).

Common limitations of animal tracking studies are the small number of animals tracked and limited site replication, both of which could result in over-interpreted ecological conclusions (Steidl et al. 1997). Although our study provides, to our knowledge, the largest tracking dataset of fallow deer, it only covered a small fraction of individuals present at the 3 sites. Given the density of 8.1 deer per km^2 in Site A and the ca. 200 km^2 covered by the 43 collared deer, our sample size represented 2.7% of the estimated population, whereas in Site C, our 14 collared deer represented <0.001% (37.5 deer per km^2 over ca. 500 km^2). Site A was similar to the study in Italy (Ciuti et al. 2003; Davini et al. 2004), where 2.2% (n=27) of the estimated population was tracked, but much lower than the 59% (n=59) achieved in New Zealand (Nugent 1994). By replicating the tracking of fallow deer at 3 sites with similar habitat and management, we identified commonalities in deer movements beyond the noise of individual variability. Our study, therefore, provides robust estimates of annual home range sizes and movement activity for adult fallow deer in their preferred mixed grassland–woodland habitat (Chapman and Chapman 1997), but additional studies are still needed for populations living in different habitats (e.g., periurban and arid landscapes).

In our study, male fallow deer monthly home ranges increased during the autumn mating season, a pattern consistently described in other studies (Table 1), with the exception of one island-based study that was hampered by small sample size (n=7 deer; Morse et al. 2009). The increased monthly range during mating season was associated with lower site fidelity (i.e., monthly range overlap), longer daily distances moved, and longer step lengths at dawn and dusk. These results are consistent with male fallow deer moving to and defending leks during mating season (Davini et al. 2004; Ciuti et al. 2011). However, a third of the males in our study showed no such movements outside their annual home range, but rather increased their movements within their home range. This pattern could have

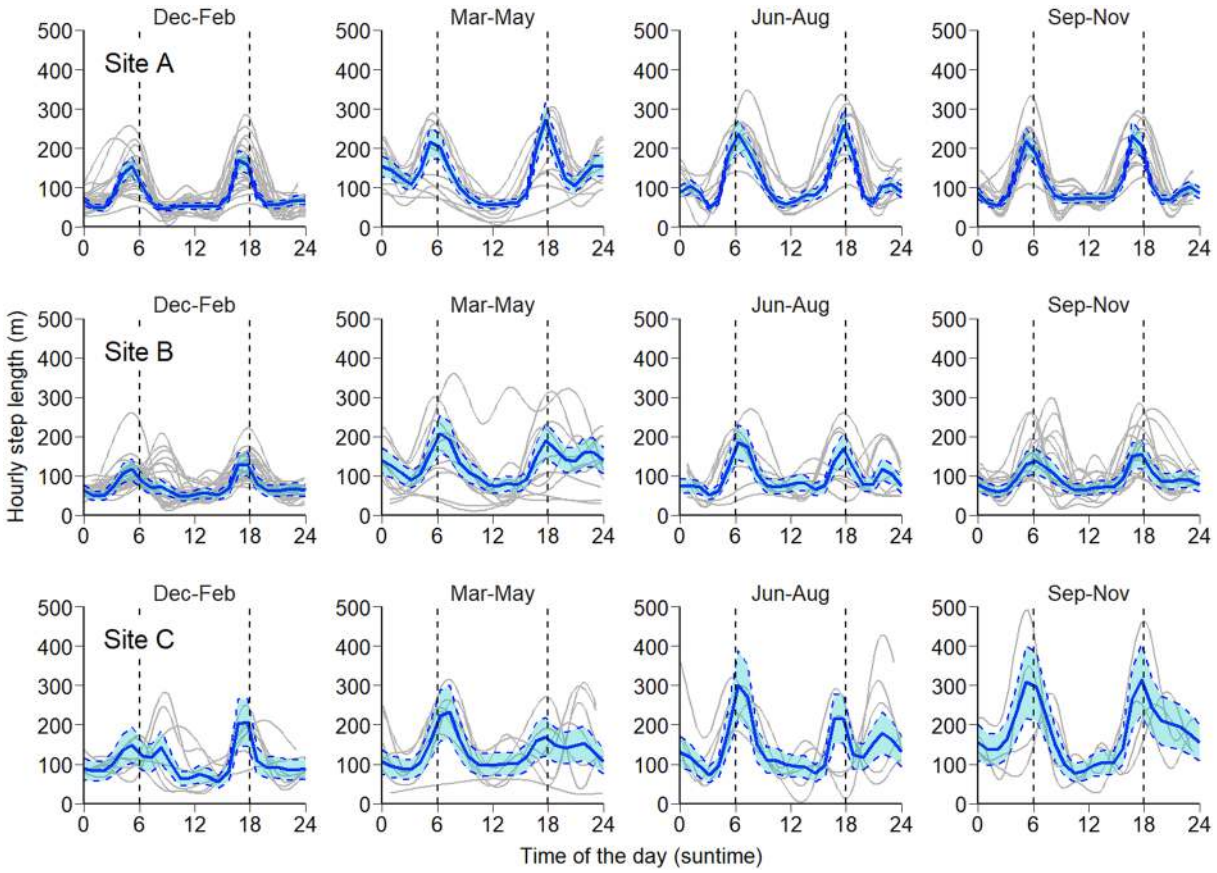

Fig. 7. Predicted diel movement cycles for male Common Fallow Deer (*Dama dama*) in 3 sites in pastoral New South Wales, Australia, 2020 to 2024. Panels represent 4 seasons (horizontally) for each site (vertically) showing mean hourly step length (solid line) and 95% confidence intervals (shaded areas). Time of day is standardized to suntime with vertical dashed lines showing sunrise (6 h) and sunset (18 h). Light gray lines show the observed data for individual deer.

occurred if their home range already included 1 or several leks or if some males followed a different mating strategy, such as defending single territories away from established leks (Clutton-Brock et al. 1988; Apollonio et al. 1992). Age, antler size, and body condition can influence the mating strategy and success of males at leks (Clutton-Brock et al. 1988; Apollonio et al. 1992), but without regular visual observation of tracked animals and of other males without collars, we were unable to further characterize individual behaviors during mating season. We observed the smallest movement activity of males during the summer months prior to the intense activity of the mating season. In Italy, males that concentrated their activity in highly productive habitats prior to the mating season had a higher success defending a lek (Ciuti et al. 2011). By reducing their movements around optimal food resources, males can increase their body mass and accumulate the energy needed to defend leks or territories against other males during mating season.

Compared to males, female deer space use is generally more influenced by resource distribution and reproductive status (Saïd et al. 2009). In our 3 sites in New South Wales, female fallow deer had lower seasonal variability in movement behavior than males, but like males, their smallest monthly ranges were in summer. Fallow deer give birth during late spring or early summer, and females must restrict their movements to maintain proximity to dependent calves (Chapman and Chapman 1997; Ciuti et al. 2006). The frequent short excursions followed by a shift in space use observed in late winter and spring in our study could therefore indicate an effort by females to find optimal habitat to settle in for the summer. In Italy, visual observation of females during mating season showed that they maintained their ranging activity around the best food resources and only visited leks for short periods (mean = 20.46 h, SE = 2.76 h) when in estrus (Imperio et al. 2020). This behavior is consistent with the short excursions made mid-April by a female in Site A (observed for 2 consecutive mating seasons) and 2 females in Site B outside their annual home ranges. Most females in our study, however, had unimodal annual home ranges with no seasonality and no short excursions, suggesting that some mating grounds were also used during the rest of the year.

Most populations of fallow deer are actively managed for conservation in their native range (Arslangündoğdu et al. 2010), as an economic resource (hunting and farming) in many introduced populations (Kudrnáčová et al. 2018), or as an invasive species in South America and Australasia (Nugent 1988; Barrios-Garcia et al. 2012; Davis et al. 2023). Where deer populations are managed as a game resource or as an overabundant invasive, home range size estimates can help to determine minimal viable areas for effective management (e.g., Webb et al. 2010; Fattorini et al. 2020; Jarnemo et al. 2023). Our results showed that fallow deer living in pasture–woodland mosaics in eastern Australia occupied relatively large annual home ranges compared to previous estimates from other landscapes (Table 1). Given that mosaic habitat is the preferred habitat of the Common Fallow Deer across its global distribution (Chapman and Chapman 1997; Lethbridge et al. 2024), our results have widespread significance. In Australia, these pasture–woodland mosaic habitats commonly occur on private land that has been partially cleared for livestock production, and it is here that fallow deer compete with livestock for food (Davis et al. 2023). By using relatively large home ranges, most fallow deer crossed multiple property boundaries annually, highlighting the importance of coordinating management actions among neighboring landholders (Webb et al. 2007). Culling operations

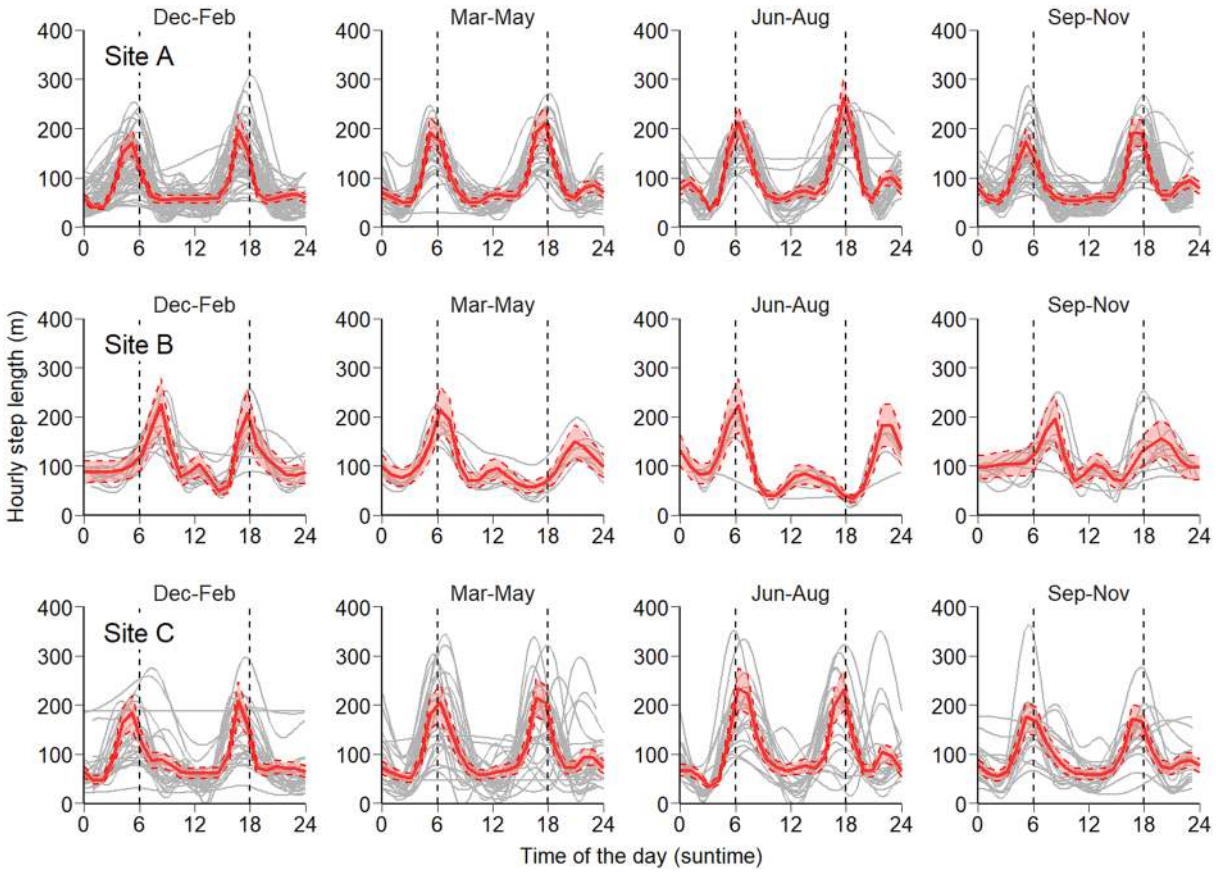

Fig. 8. Predicted diel cycles for female Common Fallow Deer (*Dama dama*) in 3 sites in pastoral New South Wales, Australia, 2020 to 2024. Panels represent 4 seasons (horizontally) for each site (vertically) showing mean hourly step length (solid line) and 95% confidence intervals (shaded areas). Time of day is standardized to suntime with vertical dashed lines showing sunrise (6 h) and sunset (18 h). Light gray lines show the observed data for individual deer.

conducted on scales of tens rather than hundreds of square kilometers are unlikely to provide enduring reductions of overabundant fallow deer populations in Australia. Failure to manage populations at spatial scales informed by animal range size, and to coordinate management actions across neighboring properties, has been identified as some of the greatest impediments to effective ungulate management in Europe (Apollonio et al. 2010).

The presence of fallow deer in pasture–woodland mosaic habitats highlights their potential role as sylvatic hosts for pathogens that can infect livestock (Huaman et al. 2023). The larger range size of adult male deer suggests that they may pose a greater risk for disease dispersion compared to females. Deer with larger ranges are likely to carry pathogens farther from their infection source than those with smaller ranges (Cripps et al. 2019). Additionally, larger ranges may increase the likelihood of deer contacting different groups, as observed in male feral pigs (Proboste et al. 2025). This is particularly significant during the rut, when males actively seek or attract females. Therefore, culling operations aimed at reducing the geographical spread of diseases in fallow deer populations might be more effective if they preferentially target males over females when a choice must be made between sexes.

Annual home ranges for most individuals in our study were unimodal with a small core area, demonstrating high site fidelity among fallow deer. This pattern was supported by the absence of long-distance movement from the home range (even after aerial shooting operations) and the high overlapping of successive monthly ranges. This pattern was also evident in the large overlap of successive annual home ranges for 8 of 9 females. We only tracked adult deer in our study, so we could not infer site fidelity for immature deer. However, dispersal is expected to occur primarily in yearling males (Webb et al. 2010; Ducros et al. 2020), which typically comprise only a small proportion of fallow deer populations at any time (Dzięciołowski 1979). High site fidelity means that repeated control operations, such as helicopter-based shooting, can be successfully used to reduce local densities (Bengsen et al. 2023) because individuals that are not killed in an initial operation are likely to be present in subsequent operations. The potentially rapid decline in deer density and the low risk of surviving individuals dispersing into new areas suggest that helicopter-based shooting is appropriate to manage infectious disease outbreaks in wild fallow deer populations (Bengsen et al. 2024).

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Author contributions

S. Comte (Conceptualization, Data curation, Formal analysis, Methodology, Visualization, Writing—original draft, Writing—review &

editing), A.J. Bengsen (Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Resources, Validation, Writing—review & editing), L. Parker (Data curation, Investigation, Validation, Writing—review & editing), and D.M. Forsyth (Conceptualization, Funding acquisition, Project administration, Resources, Validation, Writing—review & editing)

Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

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Conflict of interest

None declared.

Data availability

To preserve the privacy of the landholders, the data used in this study are only available by direct request to the corresponding author.

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