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The first evidence of the monogamous golden jackal's adaptive response to partner loss

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ABSTRACT

The range of the golden jackal (*Canis aureus*) has expanded rapidly in Europe in recent decades. The lack of comprehensive behavioral data limits our understanding of their role in the ecosystem. Flexibility in social behavior, including the features of the mating system and the presence of helpers, may have contributed to the successful expansion. In areas of high jackal density, non-breeding individuals face options such as dispersion or, on conversely, waiting for the possibility of vacancies. Following the behavior of 91 GPS-collared golden jackals in Hungary, we detected a unique interaction between an alpha pair (F1 female and M1 male) with offspring and a neighboring female (F2 female). F1 and M1 have reared at least three pups, and the alphas' home ranges and core areas also overlapped significantly. The unmated F2, had been living separately in the immediate vicinity of the alpha pair as part of a family group, rapidly entered the former alpha pair's home range within a day after F1's death. F2 did not return to the previous home range and remained close to the alpha male, remaining in its new home range even after M1 died. We documented that an unrelated, non-reproductive female replaced a deceased alpha female outside the breeding season. This previously undocumented pair bond formation in golden jackal suggests an evolutionarily beneficial strategy. The expansion may have implications for wildlife management, grazing-based animal husbandry, competition with other carnivores and ecosystem services. Rapid mate replacement may also contribute to our understanding of the reasons for the rapid population expansion.

1. Introduction

Cooperative helper-based complex group structures are found in several mammalian and bird species (Mumme et al., 2000; Macdonald et al., 2019). While this is an adaptive strategy in terms of both the fitness of the breeding pair and the preparation of the helpers for independent life, it is also usually associated with constraints (Macdonald, 1979, 1983; Moehlman, 1979, 1987). Such constraints include the need to hunt large prey in gray wolves (*Canis lupus*) (Macdonald, 1983; Mech and Boitani, 2003), the lack of a suitable reproductive partner, or the lack of free territory in many species (e.g., Mumme et al., 2000; Morin and Kelly, 2017; Macdonald et al., 2019). How can a sexually mature, non-reproductive individual become a reproductive alpha? In a saturated area, such an individual would most likely either disperse to a new habitat or stay and wait for vacancies regarding either territory or mate (Moehlman, 1987; Mech and Boitani, 2003; Glen et al., 2007; Sparkman et al., 2011; Morin and Kelly, 2017).

The flexibility of the social system (Macdonald, 1979; Moehlman, 1979, 1987; Macdonald et al., 2019) may play an essential role in the success of mesocarnivores expanding rapidly on a continental scale (Gehrt et al., 2009; Rutkowski et al., 2015). In the case of the golden jackal (*Canis aureus*), the drivers of the recent success remained to be determined, while the species has also appeared beyond the Arctic Circle in Norway and close to the Atlantic Ocean coast in France (Ranc et al.,

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2022). This expansion may have implications for wildlife management (Trouwborst et al., 2015), livestock production based on grazing (Yom-Tov et al., 1995), competition with other carnivores (Crooks and Souleé, 1999; Glen et al., 2007), ecosystem services (pest, e.g., microtine voles' control, carcass removal; Lanszki and Heltai, 2010; Ćirović et al., 2016), in general, terrestrial ecosystems and wetlands. Nevertheless, their rapid expansion in Europe may indicate a tendency to disperse (Rutkowski et al., 2015; Stronen et al., 2021), or these previously populated areas may have become saturated (Rotem et al., 2011; Morin and Kelly, 2017).

In golden jackals, as in many social canids, the basis of the group (or pack) is the breeding (alpha) pair, in which females and males share equal roles in pup-rearing and resource-defense, and they are usually monogamous (Macdonald, 1979, 1983; Moehlman, 1987; Mech and Boitani, 2003). They typically mate for lifetime unless one of them dies. In addition to the alpha pair, the family group also includes additional subordinate nonbreeding adults (Macdonald et al., 2019). In cooperative-breeding groups, these so-called helpers are offspring from the previous litter, helping their parents (alphas) to raise the next litter (Moehlman, 1979, 1983; Macdonald et al., 2019). Mate-seeking occurs between November and March in Europe (Castelló, 2018; Lanszki et al., 2018b; Stronen et al., 2021). According to the authors' observations in Hungary, the mating season lasts from January to March, and the pupping begins in April. Compared to better-studied social canids, e.g., gray wolf, black-backed jackal (*Canis mesomelas*), and coyote (*Canis latrans*) (Moehlman, 1979; Gese et al., 1996; Mech and Boitani, 2003; Morin and Kelly, 2017; Kamler et al., 2019), the mate-seeking behavior of the golden jackal is still poorly studied (Pecorella et al., 2023).

Resource depletion (Kapota et al., 2016) and strong social pressures (Gese et al., 1996), absence of reproductive opportunities in the natal pack (Sparkman et al., 2011), are associated with high population density (Lanszki et al., 2018b), may be an important factor in the dispersal or home range shift of social canids. Young and unpaired adults (low-rank in their respective groups) may disperse from their natal home range (Moehlman, 1987, Gese et al., 1996; Mech and Boitani, 2003; Lanszki et al., 2018b; Macdonald et al., 2019). Dispersal distances can be short depending on available habitat and conspecific density (Kapota et al., 2016). It may be possible to acquire a territory between established home ranges (Mech and Boitani, 2003) or have a long dispersal (Mech and Boitani, 2003; Kapota et al., 2016; Stronen et al., 2021) depending on multiple and mostly unknown factors (Lanszki et al., 2018b). Understanding how a dead alpha individual is replaced (Moehlman, 1987) and how harmful levels of inbreeding might be avoided (Pemberton, 2008) may help to reveal the adaptability of golden jackal social dynamics. Although in all canids, from foxes to wolves, the home ranges of residents are expectedly to be re-occupied by juveniles or transients following the death of a resident (e.g., Moehlman, 1989; Morin and Kelly, 2017), the pair replacement has not been well documented with data in most species. We assumed that filling vacancies as soon as possible for non-reproducing jackals is an absolute fitness-enhancing necessity (Moehlman, 1989; Sparkman et al., 2011; Morin and Kelly, 2017). We can also assume that in the case of high jackal densities, a beneficial strategy for an unpaired adult jackal would be to replace a deceased alpha individual, even if the alphas were rearing offspring.

In recent decades, the golden jackal has become one of the most abundant (Ranc et al., 2022) and important medium-sized carnivore species in Central Eastern Europe. A more thorough knowledge of its social structure is essential for the management of its population (Trouwborst et al., 2015). Exploring the social system of jackals in a dense vegetation-covered area is best facilitated by continuous and real-time GPS tracking, especially the parallel tracking of several individuals (Kernohan et al., 2001; Kays et al., 2015). To investigate the movement ecology and social structure of golden jackals in a high population density area, we tagged 91 individuals with GPS collars between 2020 and 2023 (see Supplementary material, Table S1, Fig. S1) and collected hourly data. In the case of only these three adult individuals, we observed a particular type of social interaction previously unknown to the golden jackal. Our aim was to demonstrate the phenomenon that an unrelated adult female can immediately replace the deceased alpha female of another group even outside the breeding season, and to investigate the possible drivers of this rapid mate replacement.

2. Material and methods

2.1. Study area and investigated species

The GPS-collaring of golden jackals was carried out in southwestern Hungary, Somogy County, within an area of 600 km^2, mainly in the Boronka Landscape Protection Area. The study area consists mainly of natural forest dominated habitats, that are part of the ecological network between Lake Balaton and the Dráva River (Lanszki et al., 2007). The habitat distribution of the area (45 km^2) used by the three studied golden jackals (Fig. 1) is as follows: broad-leaved forest 50.6% (hornbeam and oak *Fraxino pannonicae-Carpinetum* with island-like formations of beech *Leucojo verno-Fagetum* and Austrian oak *Quercetum petraeae-cerris*), coniferous forest 4.8% (Scots pine *Pinus sylvestris*), mixed forest 24.8%, transitional woodland-shrub 3.8%, non-irrigated arable land 12.3%, pastures 0.8%, and water and wetlands 2.9%. The lowland beech forest in the central part of the area is a strictly protected forest reserve where neither hunting nor forestry are practiced. Six dammed valley eutrophic fishponds are adjacent to this forest reserve, forming a natural boundary between the jackal groups studied. The ponds are surrounded by willow swamps (*Calamagrosti-Salicetum cinereae*) and alder swamps (*Dryopteridi-Alnetum*). More than a quarter of the ponds are covered with reeds (*Scirpo-Phragmitetum*). In some ponds, the fish were removed (harvested) in summer due to dry weather in 2021. Field cultivation is less intensive on the sandy soils of the plains, and sheep flocks graze on the dry grasslands. Human population density is low ($<$ 10 persons per km^2). The populations of red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*) are high in this region, and their hunting is also intensive (Csányi et al., 2022). Highly abundant and energetically profitable discarded viscera and hunted ungulate carcasses are one of the main foods of jackals here (Lanszki et al., 2018a). The climate is continental with sub-Mediterranean features, such as moderately humid, mild winters, with an annual mean temperature of 10.3 °C and annual precipitation of 700–750 mm, with warm and dry weather in 2021 (11.1 °C and 441 mm, respectively; Hungarian Meteorological Service).

The golden jackal is the largest predatory mammal in the study area, and its population has increased significantly in the last two decades. The jackal population density here and in this county, based on hunting statistics and acoustic survey data, can be considered high in Hungary (hunting bag, Somogy County: 0.45 individuals/km^2, Hungary, county mean $\pm$ SE: 0.13 $\pm$ 0.03 individuals/km^2; Csányi et al., 2022) or Central European context (overview: Krofel et al., 2023). In the 600 km^2 study area in 2021, an estimate of a minimum of 515 jackals ($\geq$ 10-month-old individuals) were estimated based on an acoustic population survey (Giannatos et al., 2005) performed during the late winter period, and due to limitations of acoustic survey (Jaeger et al., 1996), more, that is 649 jackals (1.1 jackals per km^2) were shot. Jackal hunting is currently allowed throughout the year in Hungary without quotas. The anthropogenic impacts on the golden jackal population in the region is significant regarding food availability and hunting.

2.2. Capture, data collection, and data processing

Golden jackals were captured using baited box traps. Control poles and muzzles were used to immobilize the captured animals without chemical anesthesia. The animals' heads were covered with a soft blanket during the handling. Based on body dimensions, fur coloration,

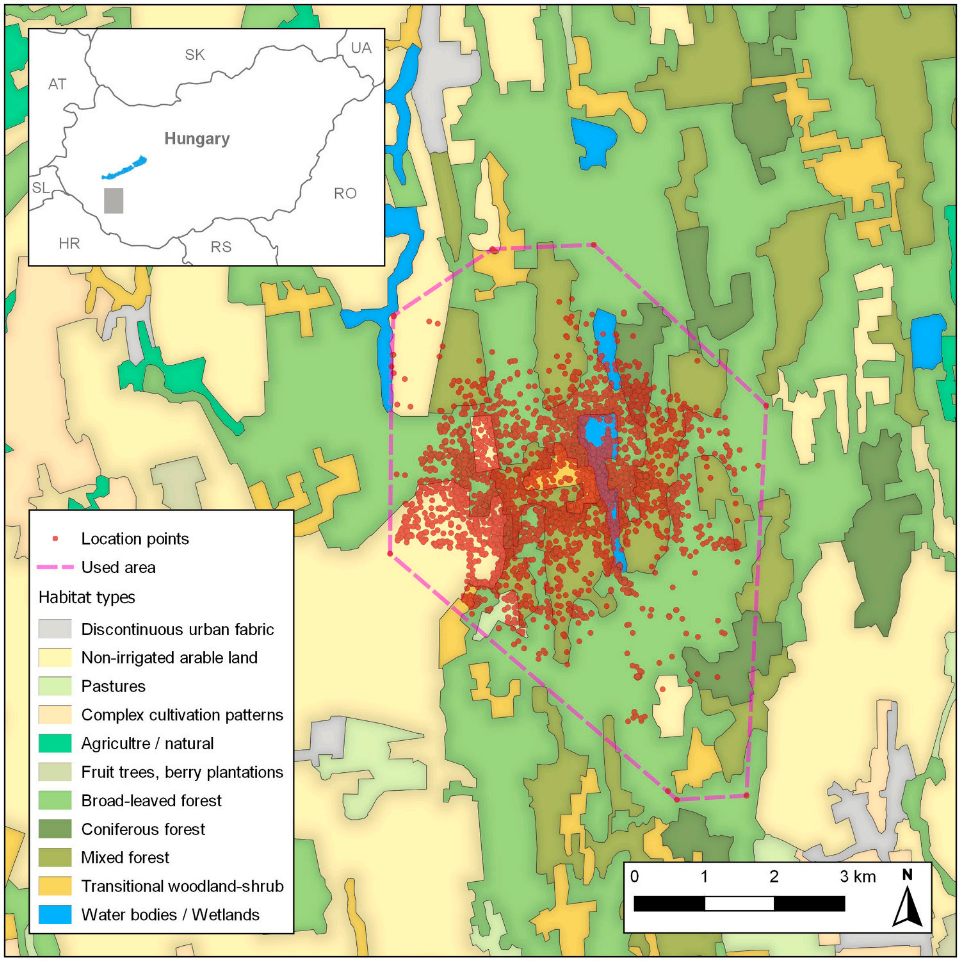

Fig. 1. The habitats of the study area, the localization points of the three GPS-collared golden jackals (red dots) and the area they use (delimited by a pink line) in southwestern Hungary.

and dentition characteristics (Lanszki et al., 2018a; Kamler et al., 2021), the three examined jackals (F1 female, M1 male, and F2 female) were over one year old (adults) at the time of tagging. F1 weighed 11.9 kg at the time of capture (May 13, 2021) and was lactating. M1 weighed 12.7 kg (May 19, 2021) and F2 9.9 kg (April 28, 2021, non-lactating, non-pregnant reproductive status). The relatedness examination is described in detail in Supplementary material, Panel A1. Vertex Lite 1 C Iridium GPS satellite collars (Vectronic Aerospace GmbH) were fitted on the golden jackals (collar weight 270 g, reliability ± 1 m). Coordinates from the GPS collars (24 fixes/day) were downloaded via the Vectronic INVENTA wildlife monitoring web service or directly from the collars. The battery of F1's tag was depleted on August 3, 2021, before the individual was shot on August 21, 2021; image recordings confirmed its presence in its home range. F1 was shot during a legal hunting event at the neighboring hunting unit, and the hunter immediately informed the head of this research project. The location of death was 200 m outside the known home range. Captures were performed according to the Hungarian legislation on hunting and with relevant authorization (permission No. SO/FM/02856–1/2020). No animals were killed for the purpose of this study.

2.3. Data analysis

We used the 95% and 50% kernel density estimation (kernel home range; KHR95, KHR50) methods (e.g., Gehrt et al., 2009; Kamler et al., 2021), with an ad hoc smoothing parameter to determine the home range and core area (i.e., the area of most intensive use; Fenton et al., 2021) sizes. Home range overlap of the golden jackal individuals was measured using percent overlap (the proportion of animal *i*'s home range that is overlapped by animal *j*'s home range; Kernohan et al., 2001; Kamler et al., 2021) and Utilization Distribution Overlap Index (UDOI; Fieberg and Kochanny, 2005), to detect differences in the movement ecology between the two periods (before and after the death of the F1 female). The distances between the hourly localization points of M1 and F2 were measured in QGIS and compared between the periods before and after the death of F1. Analyses were performed in R (v 4.2.2; R Core Development Team 2022) with the *amt* package (Signer et al., 2019).

3. Results

The three adult jackals (F1 female, M1 male, and F2 female) were unrelated (Supplementary material, Panel A1). The spatial and temporal characteristics of the home ranges suggest that all three individuals were residents using well-defined areas on a regular basis. F1 and M1 used the same area between May and August 2021 until the death of F1 (Fig. 2a). The home ranges of F1 and M1 were both 6–7 km^2 (Table 1), with almost complete overlap (Table 2). F1 was lactating at the time of tagging, and the rearing of three pups was observed (one seen in Fig. 2b, Fig. S2), but the presence of additional individuals moving in cover was also likely. A video film record (Video 1) shows the parental relationship between the 4–5- months-old pup and the alpha pair.

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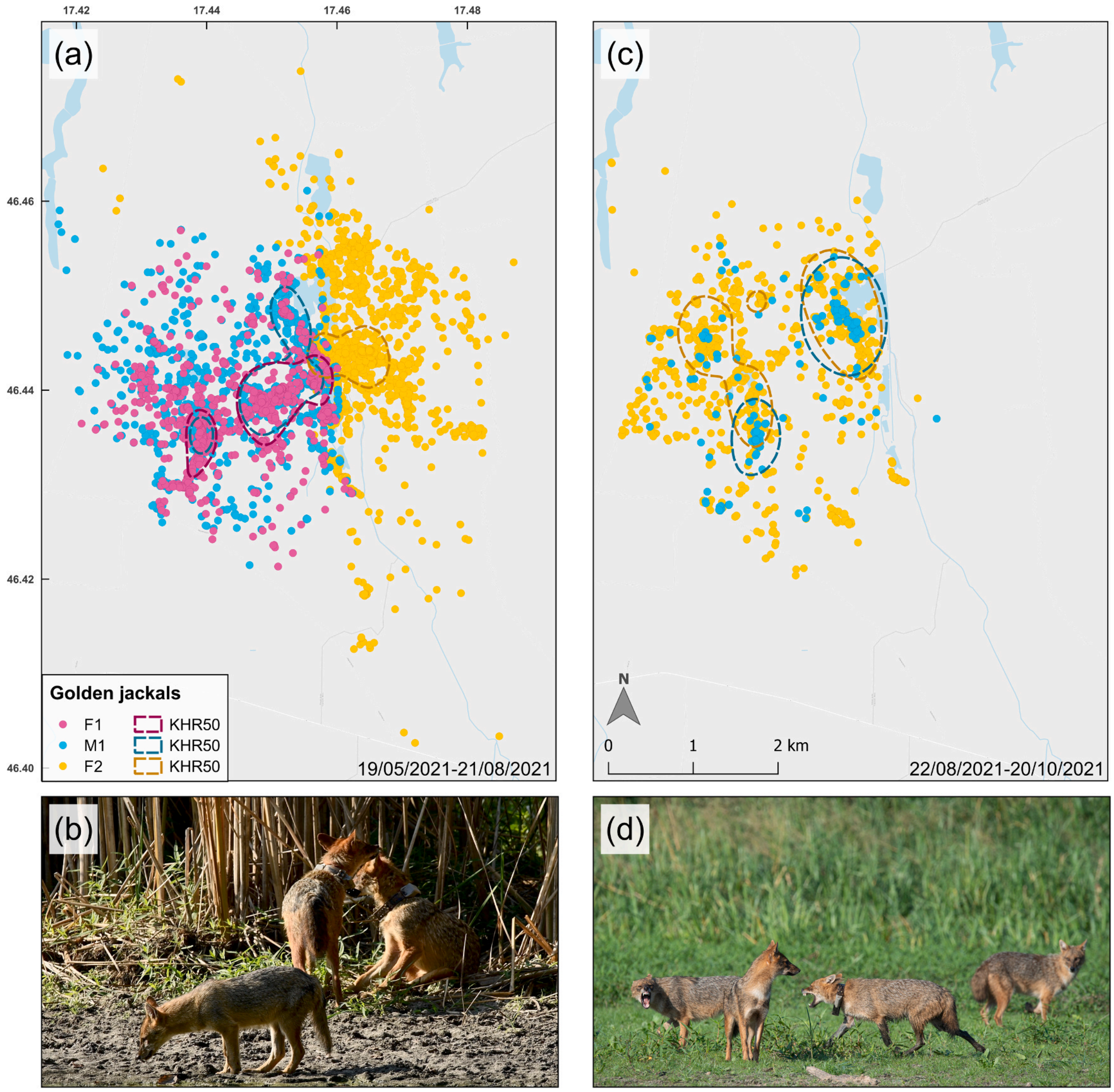

Fig. 2. GPS locations within the home range of a golden jackal pair (F1 female: pink, M1 male: blue) and a neighbor, the F2 female (orange), before (a) and after (c) the death of the F1 female (August 21, 2021) in southwestern Hungary. Core areas (KHR50) are marked with dashed lines. b – F1 and M1 with their young offspring (August 13, 2021), d – F2 in her family group (August 14, 2021) (photos by Márk Gschwindt).

Table 1
Home range sizes of GPS-tracked golden jackals (*Canis aureus*) in southwestern Hungary.

ID	Period	Home range (km^2)		No.
		KHR95	KHR50	fixes
F1	May 19 – Aug 21, 2021	6.3	1.0	1232
M1	May 19 – Aug 21, 2021	6.7	1.0	2229
F2	May 19 – Aug 21, 2021	5.8	0.5	2273
M1	Aug 22 – Oct 20, 2021	8.6	1.5	236
F2	Aug 22 – Oct 20, 2021	10.2	2.0	1434

Notes:
ID – golden jackal individuals: F1 female, M1 male and F2 female.
Periods (interindividual overlapping periods) – before and after the death of the F1 female (August 21, 2021).
KHR95, KHR50 – 95% and 50% kernel density estimation.

Table 2
Percentage home range overlaps of GPS-tracked golden jackals (*Canis aureus*) in southwestern Hungary.

ID	Period	HR overlap (%)		UDOI	
		KHR95	KHR50	KHR95	KHR50
F1 – M1	May 19 – Aug 21, 2021	92.6	71.0	2.3	0.8
F2 – M1	May 19 – Aug 21, 2021	20.2	3.4	0.05	0.0001
F1 – F2	May 19 – Aug 21, 2021	16.7	5.5	0.06	0.003
F2 – M1	Aug 22 – Oct 20, 2021	76.5	56.7	1.7	0.7

Notes:
ID – golden jackal individuals: F1 female, M1 male and F2 female.
Periods – before and after the death of the F1 female (August 21, 2021).
KHR95, KHR50 – 95% and 50% kernel density estimation.
The percentage home range overlap values are derived from 95% and 50% kernel density estimates. UDOI values range from 0 (no overlap) to 1 (uniformly distributed and have 100% overlap), but can be >1 if both home ranges are non-uniformly distributed, and have a high degree of overlap.

F2 also used an area of 6 km^2 in the immediate vicinity of the alpha pair until the death of F1 (Table 1), and F2 lived in a family group of at least four individuals, with additional adults (Fig. 2d, Fig. S3). The home ranges of the alpha pair and F2 were separated (Fig. 2a, Table 2).

F1 was shot on the evening (21 h) of August 21, 2021. F2 shifted her movement pattern, entered the home range of the former M1–F1 pair, 6 hours later circled the site where F1 was shot, and occupied F1's home range within a day (Fig. 2c, Video 2). The hourly localizations of F2 before the death of F1 fell between 107–5789 m away from the localizations recorded at the same time for M1 (mean ± SD = 1554 ± 953 m, median = 1432 m); after the death of F1, these distances decreased to 1–3050 m (943 ± 920 m, median = 622 m), which were very similar to the 'former' distances between M1 and F1 (range = 0–3820 m, 677 ± 637 m, median = 613 m).

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F2 did not return to her previous home range, closely associated with M1, and used the same home range as previously F1-M1 until M1's death (Fig. 2c, shooting date: October 20, 2021) and after. Staying in the new area indicates that F2 may have replaced a deceased alpha female. The F2 female's behavior changed significantly during the home range shift. F2's home range size increased nearly double, and her core area has increased fourfold (Table 1). The F2's home range size overlap with M1 has increased remarkably (Table 2). F2 was later shot (December 28, 2021), thus completing the tracking of the group.

4. Discussion

We first demonstrated the pair replacement in golden jackal using GPS telemetry data from a large sample size dataset from a densely vegetated area of Central-Europe. Although the pair replacement is known in carnivores, the study of this phenomenon provided new insight in several respects. Previous studies on pair replacement in golden jackals or close relatives were limited to observations and lacked knowledge of the timing of replacement. Unlike direct mammal observations (Sanderson, 1966) or indoor observations (Scheinin et al., 2006), our study was conducted in a densely forested area where free roaming golden jackals show primarily nocturnal or crepuscular activity (Fenton et al., 2021), and they avoid humans. Direct day and night observation in these conditions would require significant human resources (Dodge et al., 2013; Williams et al., 2020), and it could disturb or alter the natural behavior of the animals, leading to biased results (Cagnacci et al., 2010). Direct observations in open field conditions or other suitable daytime environments provide information on the interactions between individuals (Lawick-Goodall and Lawick-Goodall 1970; Macdonald, 1979; Moehlman, 1987), which was limited in the case of our GPS telemetry tracking.

The lack of close relatedness supports the assumption that the individuals that make up the pair (Moehlman, 1989; Mech and Boitani, 2003), in the case of the monogamous jackal, represent different bloodlines, even in areas of high population density. The proximity of unrelated adults also suggests that mature offspring can also disperse widely after becoming independent (Rutkowski et al., 2015; Lanszki et al., 2018b; Kamler et al., 2019; Stronen et al., 2021). Presumably, dispersal and different genetic backgrounds also contribute to rapid partner replacement in the event of loss of an alpha individual. However, inbreeding does occur in wolves in saturated environments (Mech and Boitani, 2003).

The reproductive relationship between the F1 and M1 individuals was proven by GPS tracking, as was found in Serbia (Fenton et al., 2021), and by direct photography and video recordings of the pair with the pup (s). M1 remained in place, and his home range did not change. Indirect and direct evidence supports that F1 and M1 had alpha status and formed a pair.

Short-distance (1–2 km) movements (F2 female, Fig. 2a) from more frequently used parts of the home range are known to occur in adult subordinate or territorial alpha females in winter (Lanszki et al., 2018b). In areas with high jackal densities, unpaired individuals, males or females, demonstrate long-distance dispersal even at high mortality risk (Kapota et al., 2016), allowing them to quickly occupy vacant space in adjacent areas (Mech and Boitani, 2003; Morin and Kelly, 2017; Lanszki et al., 2018b; Stronen et al., 2021) or become urbanized (Gehrt et al., 2009; Rotem et al., 2011).

Typically, in August and for months thereafter, the alpha pair, helpers, and the young offspring of that year live in family groups. In the African wolf (*Canis lupaster*), a close relative to the golden jackal (Krofel et al., 2022), the first 14 weeks are critical for survival (Moehlman, 1987). In our study, the 4–5-month-old offspring were still dependent on their parents, although they could already search for food. In social canids (e.g., Moehlman, 1987; Gese et al., 1996; Sillero-Zubiri et al., 1996), the unrelated female is kept away by the alpha female, as might have been the case between F1 and F2. Replacement of a member of the alpha pair in the summer is rare (Mech and Boitani, 2003). The role of F2 in rearing the offspring of F1 and M1 remained unclear. Given that the alpha male survived, the survival probability of the offspring may have been more favorable than that observed Moehlman (1987) in the case of the African wolf. After the death of the alpha male, a new alpha pair entering his territory killed the pups and fatally wounded the alpha female. According to direct observations in our study area, the 4–5 months-old pups were already searching for food together with the adults in August (before the death of their mother, F1). Unrelated male gray wolves can replace an alpha male, and subsequently help rear a litter that is not their own (SunderRaj et al., 2022). In golden jackal, allonursing has been documented (Pecorella et al., 2023). The observed shift in home range usage, coupled with F2's entry and cohabitation with M1, strongly suggests the possibility of a new pairing between F2 and M1. We have shown that subordinate adult individuals can replace lost alphas not only during the winter breeding season but also during the summer pup-rearing season. Further field data collection, genetic studies and observations in captivity would be required to explore the variability of pair-bonding strategies in golden jackals (Ah-King and Gowaty 2016; Macdonald et al., 2019; Pecorella et al., 2023).

The intense hunting pressure on the golden jackal population is evidenced by the high jackal hunting bag data and the mortality events of GPS-collared specimens (23 were shot, and four were lost from 91 marked individuals in the neighboring game management units, independently of the research). Intensive hunting may affect the group and population structure of the golden jackal, as it may accelerate dispersal and shorten the generation interval (e.g., Glen et al., 2007). It does not necessarily reduce the population size, although it may affect trophic interactions, e.g., lone jackals may shift their diet towards consuming animals that are easy to prey on (Glen et al., 2007; Rotem et al., 2011; Kapota et al., 2016; Lanszki et al., 2018a).

The rapid pair replacement suggests that the family structure damaged by hunting or other reasons can regenerate quickly. This further strengthens the social competitive advantage of the jackal over, for example, the partial competitor red fox (*Vulpes vulpes*) (Lanszki and Heltai, 2010). The developed parental care, the stable family structure, and its rapid restoration among others, are predicted to result in higher reproductive output (review: Macdonald et al., 2019).

5. Conclusion

Our study provides new insights into the behavioral ecology of monogamous golden jackals. The revealed behavioral pattern, proved mostly indirectly by GPS telemetry data, is a new result related to the territoriality, social dynamics, and mate selection of golden jackals, which were previously only known from direct observations in closely relative species. By tracking three genetically unrelated golden jackals with GPS collars in an area of high jackal density, we found that 1) the deceased alpha female was quickly replaced by a neighboring adult female and invaded the former F1 home range within a day. The distances between F2 and M1 were reduced to an extent similar to that between F1 and M1, presumably for a fitness advantage, for example helping behavior. 2) The male remained in the same area as before. 3) The non-reproducing mature female, living nearby may have waited for an established breeding position, a strategy not yet demonstrated among golden jackals. (4) Partner replacement can occur during the pup-rearing season, indicating that the search for new territory is not restricted to the breeding or natal dispersal period. (5) Pair replacement occurred between unrelated individuals. The detected phenomenon, the rapid regeneration of the broken family structure, provides evidence for an evolutionarily beneficial strategy. Studying it may help us to better understand the social flexibility and the reasons for the rapid spread of golden jackals across Europe.

CRediT authorship contribution statement

Erika Csányi: Conceptualization (equal), Data curation (lead), Methodology (equal), Writing – original draft (lead), Writing – review & editing (equal). **József Lanszki**: Conceptualization (supporting), Methodology (equal), Formal analysis (equal), Writing – original draft (supporting), Writing – review & editing (equal). **Miklós Heltai**: Conceptualization (supporting), Methodology (supporting), Writing – review & editing (supporting). **Máté Pölös**: Conceptualization (supporting), Methodology (supporting), Formal analysis (equal), Writing – review & editing (supporting). **Gergely Schally**: Conceptualization (supporting), Methodology (supporting), Formal analysis (equal), Writing – review & editing (supporting). **Gyula Sándor**: Conceptualization (equal), Methodology (supporting), Writing – review & editing (supporting).

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.

Data availability

The data sets generated during the current study are available in the Supplementary materials. Datasets are the following: All_HR_locs_before_22_aug CSV file: Localization points of three GPS-collared golden jackals (Canis aureus) before 22 August 2021; All_HR_locs_after_22_aug CSV file: Localization points of three GPS-collared golden jackals (Canis aureus) after 22 August 2021; Overlap 230707 TXT file: R script for the home range size and HR overlap calculation of three golden jackal (Canis aureus) individuals examined in Hungary.

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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.applanim.2023.106095.

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