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Research Article

Age ratio in groups of a social ungulate affects epizoochorous dispersal and diaspore exchanges

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Animal-mediated seed dispersal is a key process in plant population dynamics, species distribution and ecosystem functioning. As long-distance dispersal agents, ungulates help to maintain native plant populations facing abiotic changes in their habitat and habitat fragmentation or habitat loss. However, they also contribute to the spread of exotic species. Most ungulates live in groups, whose dynamics depend on the social status, personality, sex, age and body size of its different members. But how ungulate sociality affects zoochory remains largely unknown. We designed our experiment with sheep to test the effect of age composition on epizoochorous dispersal. Ewe lambs have stronger social links and respond more strongly to stress than adult ewes, therefore showing higher group cohesion. First, we expected that the more frequent interactions among ewe–lambs would shorten diaspore retention times and dispersal distances as ewe–lamb proportion increases. Second, diaspore exchange should be higher with increasing ewe–lamb proportion. We monitored groups of six domestic sheep *Ovis aries* (Romane breed) individuals with different age ratios, replicated four times: respectively, 0/6, 2/4, 4/2 and 6/0 adult ewes to ewe lambs. We attached five cocklebur *Xanthium strumarium* diaspores, colour-coded for each animal, to the fur on each individual flank, 10 in total. We traced each diaspore fate during six-hour sessions where we recorded movements, physical interactions among individuals and individual behaviour resulting in diaspore detachment or exchange. As expected, we found shorter retention times and dispersal distances and more diaspore exchanges as the proportion of ewe–lamb increases in the groups. Shaking, then scratching were the main behaviours leading to diaspore loss. Non-intentional contacts between individuals were the most frequent interactions associated with diaspore exchange. We encourage further research on the effect of group living, be it group size or composition, on the different phases of epizoochorous dispersal.

Keywords: group composition, living in groups, sociality, inter-individual interactions, seed dispersal, plant-animal interactions

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Introduction

Seed dispersal is a key ecological and evolutionary process that influences species distribution, plant population dynamics, gene flow and the functioning of the plant community (Schupp et al. 2010, Beckman and Sullivan 2023).

Vertebrates are among the primary vectors of seed dispersal, being responsible for the dispersal of approximately 64% of gymnosperm and 27% of angiosperm species (Herrera 1989). They are capable of dispersing seeds over long distances (Bullock et al. 2011, Liehrmann et al. 2018), often in a directed manner with a high probability of seed survival (Wenny 2001). Animals play a crucial role in maintaining connectivity between populations in agricultural landscapes (Graae 2002, Panter and Dolman 2012), conserving regional species pools (Cain et al. 2000) and facilitating adaptation or migration in response to climate change (Thurman et al. 2020).

In Europe, ungulates are responsible for the dispersal of approximately 44% of plant species (Albert et al. 2015). Over the past several decades, wild ungulate populations have significantly increased (Milner et al. 2006, Bijl and Csányi 2022), now occupying around 90% of the European continent (Linnell et al. 2020). Additionally to seed dispersal, ungulates shape forest ecosystems through herbivory, soil disturbance, nutrient fluxes and dispersal processes (Boulanger et al. 2011, 2018). Domestic ungulates have contributed to the conservation of meadow ecosystems for centuries, following the decline of large wild herbivores (Pärtel et al. 2005). Rotational shepherding practice supports genetic and demographic exchange between meadows and adjacent ecosystems such as agricultural fields and moorlands (Poschlod et al. 1998). Additionally, Manzano and Malo (2006) documented long-distance dispersal during transhumant sheep migrations spanning several hundred kilometers in Spain.

Endozoochory and epizoochory by ungulates have been extensively studied (Albert et al. 2015, Baltzinger et al. 2019, Petersen and Bruun 2019), primarily through the lens of functional traits of plants, seeds and animals (Tackenberg et al. 2006, Klinger et al. 2021, Sato et al. 2023). In contrast, the effect of individual behaviours and social interactions within group-living species on seed dispersal remains poorly understood. Baltzinger et al. (2019) emphasize the need to incorporate these behavioural dimensions into future research. The sex- and age-composition of an animal group may influence the three steps of zoochory, seed load, transfer and release. Venkataraman et al. (2022) showed in a group of geladas *Theropithecus gelada* that physical differences between the different age and sex categories in the group lead to different amounts of seeds transported in their fur by each individual. They showed that males have a larger contact surface and own a cape which increases the probability of attachment for seeds unlike the juveniles which have smaller body size than male and female adults.

According to Karubian and Durães (2009), the number of individuals in a group may influence seed deposition pattern. Indeed, a larger group size increases the probability of seed accumulation, as all members move together in time and space. Conversely, it may also lead to greater dispersal distances due to food depletion, which forces the group to explore further to find sufficient resources for all group members. In addition to the structure, the social organization within the group may have consequences on seed dispersal. Indeed, as highlighted by Jadeja et al. (2013) and Tsuji et al. (2020), the social status of an individual may affect its quality as a seed disperser because of the access to resources. In a context where fruits are the preferred food item, dominant individuals defend this resource and have a greater access to them than subordinates (Tsuji et al. 2020). They can thus consume a greater number of fruits and so, a greater number of seeds and then disperse more seeds in the landscape (Jadeja et al. 2013, Tsuji et al. 2020).

Group formation entails both benefits and costs for individual fitness, and group cohesion depends on the balance between these factors. Among the benefits are reduced predation risk (Pays et al. 2007), increased foraging efficiency, and opportunity for mutual care (Green et al. 1989, Cameron et al. 2009). Conversely, group living can increase competition for food and mates, facilitate the spread of parasites and diseases (Rowcliffe et al. 2004, Sansom et al. 2008, Fortin and Fortin 2009), and require additional time and energy to synchronize and maintain cohesion (Conradt and Roper 2000, Pays et al. 2012). Indeed, activity patterns and energy requirements often differ among individuals based on sex, body size, mass and age (Gompper 1996). In ungulate groups, the balance of these costs and benefits is dynamic and can lead to group fission of fusion events (Conradt and Roper 2000, Pays et al. 2007).

Ungulates express a variety of social behaviours such as play, allogrooming and antagonistic interactions that can increase the likelihood of diaspore early detachment (Liehrmann et al. 2018, Baltzinger et al. 2019). Early detachment may also result from specific movements – such as jumping, shifting position or sudden changes in direction – or from autogrooming behaviours (Heinken et al. 2006, Baltzinger et al. 2019). Using tri-axial accelerometers, Abecia et al. (2024) found that lambs exhibited 42% more movements than adult ewes. In relation to autogrooming, Liehrmann et al. (2018) observed a decrease in grooming frequency with increasing body mass across three ungulate species. They suggested cocklebur *Xanthium strumarium* may cause more irritation in smaller-bodied species, potentially leading to earlier diaspore removal.

In addition to early diaspore detachment, Liehrmann et al. (2018) identified social interactions as a source of secondary diaspore dispersal, with diaspores exchanged during inter-individual contacts. Previous studies on sheep sociality showed that spatial proximity tends to occur between individuals that formed social bonds through prior management (Ozella et al. 2020), among juvenile ewes (Lawrence 1990), and between adults of similar age (Doyle 2016, Ozella et al. 2020). These associations are dynamic and influenced by biological cycles, weather or management practices (Ozella et al. 2020, 2022). Moreover, social relationships can

evolve throughout an individual's lifespan, influenced by changes in physical and physiological conditions, cognition, social selectivity, and kinship dynamics, with these effects being species-specific (Siracusa et al. 2022a). For example, Siracusa et al. (2022b) showed that the oldest female rhesus macaques *Macaca mulatta* reduced their social networks, expressing increased selectivity and a preference for stable, well-connected partners.

In this study, we manipulated the ewe–lamb ratio in groups of six domestic sheep *Ovis aries* (Romane breed), each animal equipped with cocklebur epizoochorous diaspores dyed in a unique colour to track diaspore trajectory and fate. We examined activity differences in relation to age and group composition, and then assessed diaspore retention time, dispersal distance and diaspore exchange dynamics as a function of ewe–lamb ratios within flocks (Bullock et al. 2011). We hypothesize that both retention time (H1a) and dispersal distance (H1b) will vary with group composition, both expected to decrease with increasing ewe–lamb proportion in the group. We hypothesize (H2) that diaspore exchange dynamics is influenced by age composition within the group. Specifically, we predict that diaspore exchanges should increase with a higher proportion of ewe–lambs, due to their greater mobility, greater responsiveness to stimuli response, higher exposition to repeated social contacts in nursery and greater age similarity.

Material and methods

Study site, animals and diaspores

The experimentation took place from 12 March to 5 April 2024 at INRAE Experimental Unit UE P3R (EU0023 with valid approval number G1817401), Osmoy (47°03′34.0″N, 02°30′30.9″E, Cher, France). The experimental plot measured 0.8 ha, consisting of a meadow and lawn vegetation (see the Supporting information for vegetation details) and was fenced with electric and non-electric wire. We conducted our observations from a hut located 5 m outside the plot and 1.5 m above ground level for better visibility.

The weather conditions were 8.8°C ± 3.3°C, with 24 ± 50 mm of daily rainfall accumulation. We calculated the wind chill index (WCI) following Tucker et al. (2007) for each day, as wind and temperature might influence grouping behaviour (Ozella et al. 2020). $WCI = 13.12 + 0.62 \times T - 13.17 \times V^{0.16} + 0.40 \times T \times V^{0.16}$ where T represents air temperature (°C) and V represents wind speed (km h^{-1}). WCI showed a significant decrease over the course of the experimentation (estimate = −0.43, SE = 0.05, $p < 0.001$), potentially reducing grouping of individuals.

Our out-of-scope experimentation used eight adult ewes and eight lambs of the Romane breed, randomly selected from the INRAE herd. Animal restraint was swift and controlled by trained staff. The adults were 36.6 ± 13.0 month old (on average 3 year-old) with an average body mass of 66.1 ± 14.9 kg and lambs were 6.0 ± 0.1 month old with an average body mass of 32.5 ± 2.2 kg. Age ($t_7 = -6.679$, $p < 0.001$, Mann–Whitney test) and body mass ($W = 0$, $p < 0.001$, Welch test) significantly differed between ewes and ewe–lambs.

Since wool thickness and length may influence diaspore retention (Liehrmann et al. 2018), these parameters were measured weekly on three random spots along the flanks of each animal. During the experiment, average wool thickness was 20.6 ± 5.6 mm for ewes and 21.5 ± 4.3 mm for ewe–lambs. We observed a significant increase in wool thickness (estimate = 2.750, SE = 0.622, t = 4.421, $p < 0.001$) and in fur length (estimate = 5.323, SE = 0.700, t = 7.610, $p < 0.001$) over the experiment. Thickness and length did not differ between age classes across time.

We used *Xanthium strumarium* epizoochory-adapted diaspores. Their numerous hooks and diaspore releasing height matching ewe body size made them well suited for attachment and epizoochory transport on sheep flanks. Furthermore, the size of the diaspores made them easier to track by observers. We collected the diaspores along the Loire River in Briare (Loiret, France) during the diaspore shedding period, autumn 2023. The diaspores measured 28.6 ± 1.8 mm in length and weighed 433 ± 34 mg. As diaspore mass can affect retention time (Wessels et al. 2008), we checked there were no significant differences among the daily sets of diaspores attached to each animal ($F = 0.941$, $p = 0.527$). Diaspores were sprayed with different colours to facilitate remote observation and follow their trajectories (Fig. 1). Half the surface in contact with animal fur was kept natural (i.e. unsprayed) to prevent attachment alteration.

Experimental design

We evaluated the effect of sociality on the external diaspore dispersal process according to the proportion of ewe–lambs in the group. We tested four types of groups, with a fixed group size of six individuals and zero, two, four or six ewe–lambs per group. We replicated each group type four times. Assignment of individuals and groups' planification were organised to minimise confounding effects such as social bonds (Nituch et al. 2008, Ozella et al. 2022), habituation to experimental conditions (Ozella et al. 2022) or to other individuals (Keller et al. 2011), wool traits and wool change over time, weather conditions or individual personality (Michelena et al. 2009, Keshavarzi et al. 2022). To achieve this, 1) we changed type of group daily; we used equally 2) each animal across the experimentation and in all group types and 3) pairing between individuals of the same age. We detailed the experimental organisation in the Supporting information. Non-selected animals for a day were housed in a distant building to avoid interactions with the ones that were selected. At the end of the day, we grouped all animals in the same pasture.

During six hours per day and sixteen days (four times each of the four group types), three observers monitored individuals (ewes and/or ewe–lambs) and their diaspores to evaluate external retention time and dispersal distance, dynamics and causes of diaspore exchange. At the start of each day, ten coloured diaspores were placed on each individual, five per



Figure 1. Standing ewes grazing, the individual in the background carrying blue and orange diaspores.

flank. Each individual was assigned a unique colour to be able to track diaspore transfers between individuals. A single operator conducted this procedure next to the experimental plot to reduce bias in diaspore attachment among individuals involved.

Behaviours and diaspore exchange

We adapted the ethogram used by Liehrmann et al. (2018) to address our research questions and match with sheep behaviours. This ethogram (Supporting information) includes individual and social behaviours likely to cause diaspore detachment, and animal's posture (standing, generally feeding individual, or lying down, resting/ruminating individual). We continuously recorded behaviours during the six-hour sessions using the Animal Behaviour Pro ver. 1.7.1 application. Additionally, whenever possible, we live recorded diaspore detachment and exchange caused by specific behaviours, and individuals involved. Most of the time, we discovered a diaspore had been lost or exchanged a posteriori, during the next systematic check (every 10 min). This could be due to the distance of observation, the fact that we could generally only see one flank of each individual at a time or that individuals were grouped.

External retention time and dispersal distance

We evaluated retention time by checking the number and colour of remaining diaspores by systematic check, every ten min during 6 h, for each monitored individual. We measured dispersal distance using Garmin GPS collars: two TT15Fmini, two DC50 and two DC40. These collars transmitted location data every five seconds with a minimum accuracy of 8 m. We tested the accuracy of each collar type at different locations within the pasture over a two-day period. We considered as outliers any data location outside an 8 m buffer or corresponding to speeds exceeding 12 m s^{-1} (maximal recorded speed for sheep). Additionally, we excluded three days from the dispersal distance analysis due to partially or completely defective collars.

Data analyses

We analysed the change in wool growth using a linear mixed-effect model, with length and thickness as response variables. Week and age were included as fixed effects, and individual identity as a random effect.

We used Wilcoxon rank-sum tests to assess differences between age classes in the number of autogrooming, number of remaining diaspores at the end of the experiment and number of diaspores exchanged. Since normality and homoscedasticity were met, we used a Student's t-test to compare the number of interactions. We fitted generalized linear models (GLM) using a Gaussian distribution to test the effect of the ewe–lamb ratio on the net balance between diaspores gained and lost. We used GLM with quasi-Poisson distribution to account for data overdispersion for all other investigations concerning interactions, diaspore exchanges, diaspores remaining at the end of each monotoring session or WCI according to ewe–lamb ratio.

To assess retention time and dispersal distance, we tested non-linear functions proposed by Bullock et al. (2011) presented in the Supporting information and selected the simple exponential function ($y = a \times e^{-bx}$) as it provided the best fit to our data based on the Akaike information criterion (AIC), in agreement with these authors for short monitoring periods (< 48 h). We applied the simple exponential function using 'nls.multstart' R package ver. 1.3.0 (Padfield et al. 2025) where parameter 'b' represents the fall rate of the simple exponential function, parameter 'a' was set to ten (i.e. initial number of diaspores attached). We plotted the number of remaining diaspores on the individual on the y-axis, the time elapsed or distance covered during that time on the x-axis. We excluded exchanged diaspores from this analysis. Subsequently, we tested the effect of ewe–lamb proportion on 'b' by using weighted linear regression, with weights based on the inverse of the variance. For each statistical analysis, we assessed the assumptions of normality and homoscedasticity.

Results

Behaviours and movements

We compiled behaviours and their frequency (Supporting information). Over the course of the 96-h experiment, ewe–lambs exhibited 43% more interactions than adult ewes ($t_{14} = 3.256$, $p = 0.006$, Fig. 2). Agonistic interactions were the only type more frequently exhibited by adults, primarily directed toward lambs. Unintentional contact was the interaction most often associated with diaspore detachment. At the end of the experiment, diaspore exchange between individuals was observed in 4.1% of interactions (59/1425), whereas diaspore loss was recorded in 0.1% of interactions (2/1425). The daily number of social interactions had a significant positive effect on diaspore exchanges (estimate = 0.020,

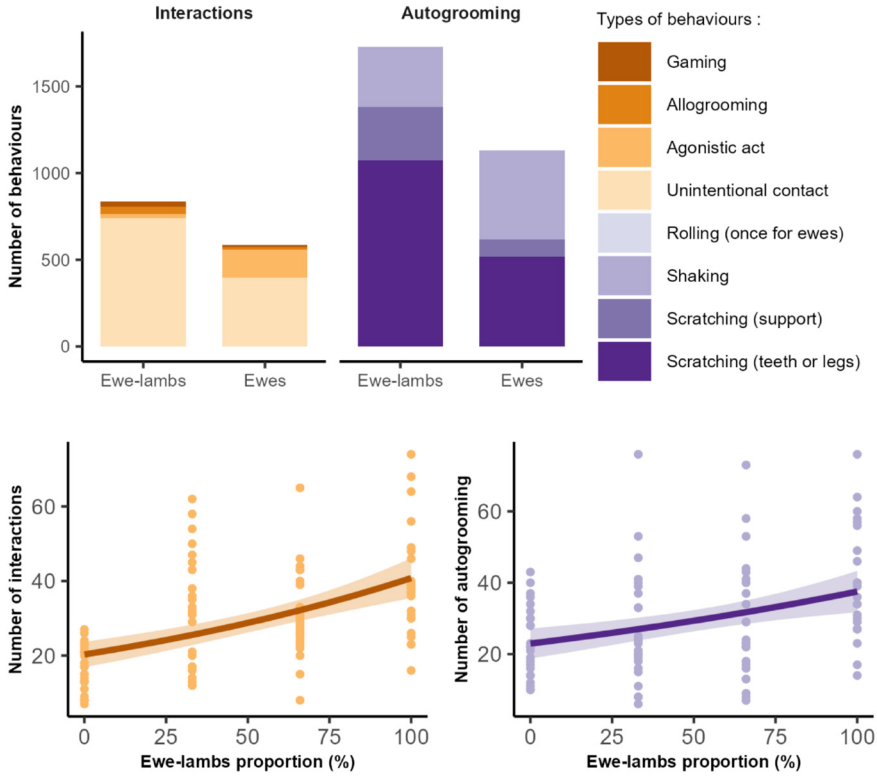


Figure 2. Description and number of all recorded types of interactions and autogrooming events between individuals per ewe–lambs and ewes (top row). Average number of interactions and autogrooming events by individual according to ewe–lambs proportion in the group (from 0 to 100%, bottom row). Shaded areas represent 95% confidence intervals.

SE = 0.005, t = 3.675, $p < 0.001$, Supporting information) and a significant negative effect of remaining initial diaspores (estimate = −0.015, SE = 0.005, t = −2.853, p = 0.005, Supporting information). Similarly, the daily number of autogrooming behaviours had a significant negative effect on the number of remaining initial diaspores (estimate = −0.011, SE = 0.004, t = −2.618, p = 0.010, Supporting information). WCI had a significant negative effect on the daily number of interactions (estimate = −0.085, SE = 0.019, t = −4.572, $p < 0.001$, Supporting information) but no effect on diaspore exchanges.

With regard to autogrooming behaviour, ewe–lambs performed 52.7% more grooming actions than did adults (W = 9, p = 0.015, Fig. 2). Adults engaged more in shaking, whereas ewe–lambs exhibited more scratching with teeth or legs or against the wire fence or a wooden stake. Overall, 1.7% of these autogrooming behaviours resulted in diaspore detachment (one or two diaspores). We gave more details about numbers and gains and losses probability in the Supporting information.

The ewe–lamb proportion within groups had a significant positive effect on both interaction (estimate = 0.007, SE = 0.001, t = 5.709, $p < 0.001$, Fig. 1c) and autogrooming numbers (estimate = 0.005, SE = 0.001, t = 3.557, $p < 0.001$, Fig. 2).

In total, we directly observed only 117 of 811 diaspore losses (14.4%), among which 467 were exchanges (57.6%). We witnessed 64 of these diaspore exchanges (13.7%) over the course of the experiment.

Animals spent approximately 26% of their time lying down (roughly 1.5 h), with variation from no resting time on rainy days to up to 3 and a half h. We found no significant differences in lying time between age classes or group compositions. However, ewe–lambs performed 83.4% more transitions from lying to standing than did adults. Lying posture accounted for 14.9% of diaspore detachments. Walking time represented 36.3% of the experiment and 44.5% of diaspore loss occurred during movements. The daily distance travelled during the 6-h observation period did not significantly differ between age classes or group compositions. The average distance per individual was 2.37 ± 0.20 km for ewe–lambs and 2.37 ± 0.22 km for adults.

Diaspore retention time and dispersal distance

The four group compositions exhibited a decreasing falling speed per unit of time or dispersal distance (Fig. 3) throughout the day. Half of the initial diaspores had detached after 293, 206, 153, 128 min, 1603, 1566, 1184 and 717 m for groups with 0%, 33%, 66% and 100% ewe–lamb proportions, respectively. The falling rate for retention time significantly increased with ewe–lamb proportion (estimate = 3.708×10^{-5}, SE = $9.053.10^{-6}$, t = 4.096, p = 0.001, Supporting information). Similarly, the falling rate for dispersal distance significantly increased with ewe–lamb

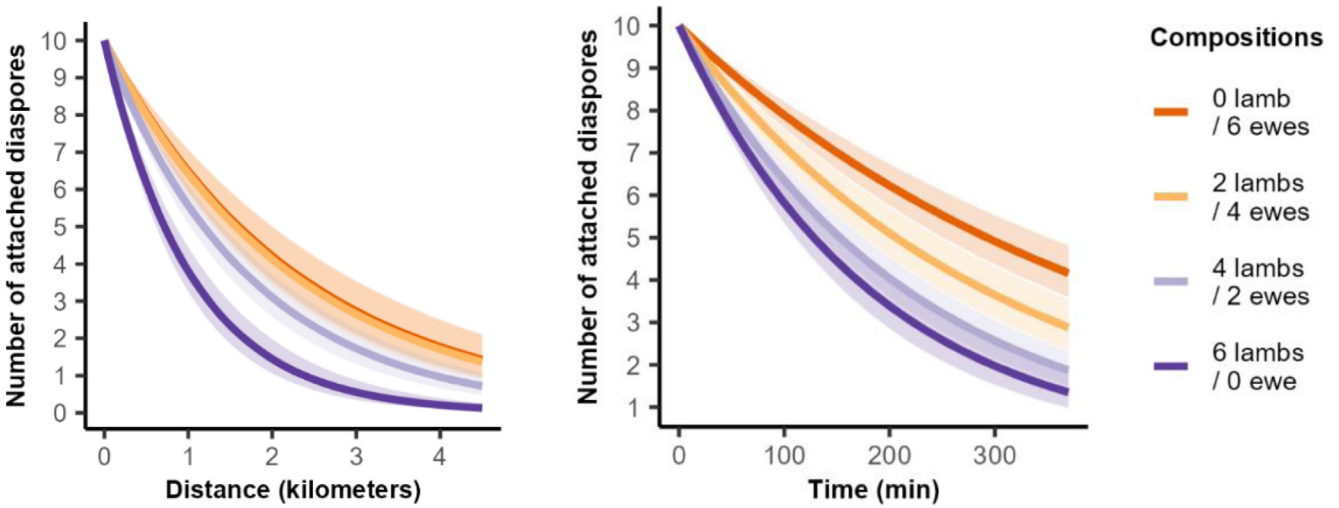


Figure 3. Predicted dispersal distance (left) and retention time (right) of initially attached diaspores according to the ewe–lambs proportion in the group. Shaded areas represent 95% confidence intervals.

proportion (estimate = $3.769.10^{-6}$, SE = $1.702.10^{-6}$, t = 2.215, p = 0.049, Supporting information).

At the end of the day, the mean numbers of initial diaspores retained per individual was 5.7, 5.0, 4.1 and 2.6 for groups with 0%, 33%, 66% and 100% of ewe–lamb proportions, respectively. This number was significantly higher in adults than ewe–lambs (W = 1916.5, $p < 0.001$).

Diaspore exchanges

The mean number of diaspores exchanges per individual was 3.0, 4.4, 4.6 and 7.5 for groups including 0%, 33%, 66% and 100% of ewe–lambs respectively. An increasing ewe–lamb proportion in the group (Fig. 4) had a significant positive effect on the number of diaspore exchanges (estimate = 0.008, SE = 0.002, t = 3.900, $p < 0.001$), whereas age class had no significant effect (W = 976.5, p = 0.197).

Taking diaspore exchanges into account, the mean number of remaining diaspores per individual at the end of the day was 7.4, 7.0, 5.8 and 5.4 for groups with 0%, 33%, 66% and 100% ewe–lambs, respectively. Overall, the net daily gain–loss balance (Fig. 4) decreased significantly with increasing ewe–lamb proportion (estimate = −0.022, SE = 0.010, t = −2.187, p = 0.031).

Discussion

In this study, we tested one group composition characteristic, age ratio on epizoochorous dispersal. We implemented a controlled experimental design for group composition and individual selection to mitigate intrinsic and extrinsic factors, including wool changes, weather variability, inter-individual trait differences and social bonds. We confirmed all our predictions: diaspore retention time and dispersal distance decreased (H1a, H1b), while the number of diaspore exchanges increased (H2) with a higher proportion of ewe–lambs in the group.

Behaviours and activities

We observed an increase in the frequency of autogrooming behaviour with a higher proportion of ewe–lambs in the group, consistent with Liehrmann et al. (2018), who suggested that smaller body size might enhance grooming activity. However, while ewe–lambs engaged more frequently in scratching, adult ewes exhibited more shaking, which appeared the most effective behaviour to detach diaspores. Although autogrooming did not appear specifically directed towards diaspore removal, the daily grooming frequency significantly influenced the number of diaspores retained by the end of the day. This result aligns with Sorensen (1986) and Kiviniemi and Telenius (1998), who reported that allogrooming reduced diaspore retention time. In our study, the probability of diaspore removal associated with specific grooming behaviours was low and notably lower than reported by Liehrmann et al. (2018) for dwarf goats, donkeys or red deer. Diaspore detachment frequently occurred near structural elements such as fences or wooden stakes used for scratching, echoing Heinken et al. (2006), who observed similar diaspore accumulation nearby trees rubbed by wild boar.

Similar to grooming behaviours, the frequency of social interactions increased with the proportion of ewe–lambs in the group. We confirmed the significant effect of interactions on diaspore exchange previously reported by Liehrmann et al. (2018).

Although lying behaviour accounted for only 14.9% of diaspore losses, these losses were spatially concentrated in small areas also subject to trampling and nutrient deposition. In our study, lying areas were typically located close to human observers and enclosure exits. We postulate that under natural or warmer conditions, resting areas would more likely be situated in shaded or sheltered locations.

We likely underestimated diaspore losses and exchanges due to behavioural processes. First, our experimental design tracked colour-coded diaspore groups rather than individual

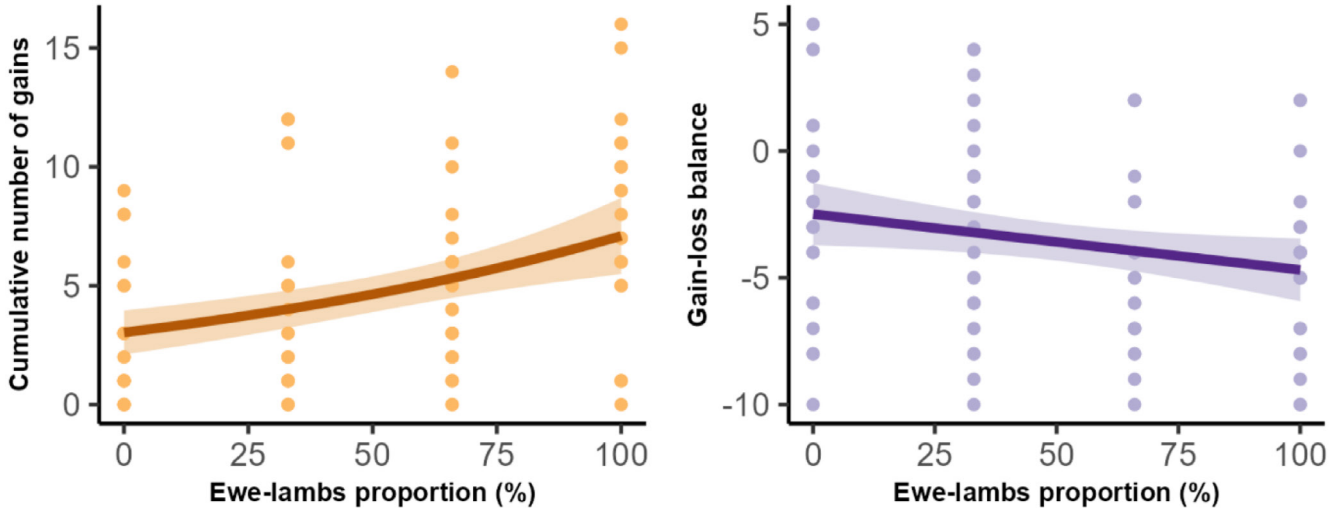


Figure 4. Diaspore exchange dynamics according to ewe–lambs proportion in the group shown as the cumulative number of diaspore gains (left) and the balance between gained and lost diaspores (right) per individual during the monitoring. Shaded areas represent 95% confidence intervals.

diaspores. Identical diaspore counts across 10-min intervals may obscure movements of individual diaspores. Second, detection limitations constrained our observations. For instance, we directly observed only 13.7% of diaspore exchanges, despite most being socially mediated. Similarly, only 14.4% of diaspore losses were directly observed. While we cannot precisely quantify how many losses were behaviourally induced, detection rates were likely as low for diaspore losses and exchanges.

Weather conditions also influenced movement, activity, and group dynamics. In our study, a decrease in WCI over time coincided with increased daily social interactions, consistent with Ozella et al. (2020). Although WCI did not significantly affect diaspore exchange or loss, our results highlight the importance of alternating group composition in long-term experiments.

Retention time and dispersal distance

Supporting observations of Bullock et al. (2011), the simple exponential function best fitted our data. However, this function predicts complete diaspore detachment within 7 to 16 h depending on group composition, whereas, in practice, some individuals retained tightly encrusted diaspores at the end of the day. To better capture such long-term retention, the power exponential function (Liehrmann et al. 2018) may offer a more realistic representation of long-distance diaspore dispersal.

We based our analysis of external diaspore retention time and dispersal distance on initial diaspores only, excluding those acquired through exchange. The four group compositions exhibited a similar retention pattern, marked by a rapid initial loss followed by a slower rate of diaspore detachment, in agreement with De Pablos and Pecos (2007), who used a dummy sheep model. As expected, we confirmed our first hypothesis with diaspore retention time and dispersal distance decreasing as the proportion of ewe–lambs increased. Although the enclosure design limited our ability to measure real dispersal distances between the mother plant and the releasing site, the data remain ecologically relevant. With an average of 2.8 retained diaspores for ewe–lambs and 5.9 for adult ewes, and an average 6-h movement of 2.3 km, we confirmed sheep as effective long-distance seed dispersers (Manzano and Malo 2006, Wessels et al. 2008).

Diaspore retention depends on a wide range of plant and animal traits. Our regular measurements revealed a steady increase in both wool thickness and length, consistent across age classes, throughout the experiment. Several studies (Wessels et al. 2008, Liehrmann et al. 2018, Sato et al. 2023) identified wool properties as key factors influencing diaspore retention time, which militates for monitoring sheep wool changes in studies exceeding a single week. Autogrooming daily frequency remained stable over time, indicating that wool had no effect on grooming behaviour.

In our study, both age classes displayed similar wool characteristics, distances covered and temporal activity patterns. We therefore attribute the observed differences in diaspore retention time and dispersal distance across groups to varying ewe–lamb proportions and primarily age-specific behaviours (i.e. grooming, social interactions and mobility).

Diaspore exchanges

Interactions significantly drove diaspore exchanges, although rarely directly witnessed. Individuals sometimes collected diaspores lying on the ground while resting. Overall, diaspore exchanges increased with the proportion of ewe–lambs in the group and the higher number of interactions they accidentally or voluntarily initiated, supporting H2. However, diaspore exchanges did not differ significantly between age classes, suggesting that diaspore exchange is only partially understood.

Accounting for diaspore losses, the diaspore gain-loss balance over the 6-h session decreased with increasing ewe–lamb proportion, indicating that gains from exchanges did not compensate for overall losses. Including diaspore exchanges in the analysis, the average number of diaspores remaining per individual differed significantly between age classes, with ewe–lambs retaining less diaspores (4.8) than adult ewes (8.1). We further showed that roughly one-third of the diaspores remaining on an individual resulted from exchanges. Our experimental design did not allow us to determine whether diaspore exchanges extended retention time or increased dispersal distance. Whether an individual engaged in social interactions acted as a longer distance disperser than one moving alone remains to be tested. While interactions clearly promoted diaspore exchanges, we were unable to assess whether the different types of contact between individuals reinforced or weakened diaspore attachment to its original vector, or how securely it attached to the recipient when transferred.

Previous studies reported increased diaspore dispersal success related to exchanges (Chambers and MacMahon 1994, Kiviniemi and Telenius 1998). In our study, we solely focused on the transfer phase of the dispersal process. We hypothesize that diaspore exchanges between sheep of different age classes may also modulate diaspore dispersal trajectories, alter retention time, dispersal distances, spatial deposition patterns and seed dispersal effectiveness as a whole.

Perspectives

Given the significant influence of behaviour and activity patterns on diaspore loss and exchange, future research should integrate their spatial and temporal dynamics to improve predictions of diaspore shadows. In our study, group size was relatively small, and activities such as resting and walking were largely time-dependent and synchronized across age classes. In contrast, Doyle et al. (2016) observed that in larger groups of ewes, daily contact time varied with age differences, suggesting a desynchronization of activities. Similarly, Conradt and Roper (2000) demonstrated that activity desynchronization can drive sexual segregation within red deer groups. Furthermore, in fusion–fission societies, Pays et al. (2012) found that group size affected diffusion rate of herds in the landscape, which may in turn led to individuals leaving the group, especially individuals with bold personality (Michelena et al. 2009).

Therefore, accounting for sociality in zoochory, be it group size or age/sex group composition, during seasonal groupings or along migration routes for instance, thus deserves further investigation.

This line of research could be extended to other ungulate species with differing social structures, functional traits, and patterns of spatio-temporal habitat use. Moreover, our study focused on large diaspores of *Xanthium strumarium*, characterized by long hooks. However, the dynamics of diaspore exchange are likely influenced by seed traits, as highlighted in studies reporting variations in seed loss (Couvreur et al. 2004, Manzano and Malo 2006, Bullock et al. 2011).

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Author contributions

Antoine Roux: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Cloé Balson**: Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Morgane Audiguier**: Conceptualization (equal); Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Marie Battista**: Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Didier Marcon**: Conceptualization (equal); Investigation (equal); Writing – review and editing (equal). **Olivier Pays**: Conceptualization (equal); Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Christophe Baltzinger**: Conceptualization (equal); Funding acquisition (lead); Investigation (equal); Methodology (equal); Project administration (lead); Supervision (lead); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.brv15dvpx (Roux et al. 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

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