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Can physical closeness measure variation and change in pair association strength in captive geckos?

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Abstract

Pair bonding is a key social behaviour but remains understudied in reptiles despite a growing body of evidence suggesting that some species exhibit complex sociality. The lack of evidence regarding the expression of pair association in social lizards species hampers our understanding of its effects on captive welfare. As a first step towards a better understanding of pair related social behaviour in lizards, we investigated if physical closeness, a measure often used to qualify pair bonding in mammals and birds, can be used to assess pair association strength in captive tokay geckos (*Gekko gecko*). We analysed how physical closeness is related to measures of spatial behaviour collected through scan sampling across two sampling years. Physical closeness was not related to movement but to hiding and basking behaviour, albeit not consistently across years. We also show that although on average our measure of pair association strength did not change across the experimental period, individuals that were paired with new individuals in 2024 exhibit a change. If differences in pair association also occur in the wild and if they confer different fitness outcomes is unknown. However, our results have implications for captive welfare and we propose to monitor socially housed individuals closely to avoid unnecessary socially induced stress.

Keywords: pair bond, reptile, social behaviour, Squamata, welfare

Introduction

Pair bonding, defined as an intra-specific, selective aggregation of two adult individuals (Whiting & While, 2017), is an important social behaviour demonstrated by many social animals. Four main behaviours are described as defining a pair bond: shared territory, joint displays and types of affiliation and proximity (Bales et al., 2021). The strength of a pair bond can be measured by the time individuals in a pair spend in close proximity (Kleinman, 1977; 1981). Importantly, it has been suggested that such associations confer benefits in the wild such as better territory and predator defence, maximizing reproductive success, higher male investment in offspring, and it might be more cost efficient to stay with the same mate than finding a new mate (Bull, 2000; Clutton-Brock, 1991; Freed, 1987; Schuiling, 2003). Despite its' importance in the wild and prevalence across vertebrates (Bales et al., 2021), how pair bonding contributes to animal welfare in captivity is understudied.

Good welfare is determined by many different aspects of the environment. However, the social environment is of particular importance for social animals (Bracke & Hopster, 2006; Rault, 2012). In many social species, isolation from conspecifics leads to stress and depression (McKinney & Bunney, 1969; Morgan & Tromborg, 2007). In dogs, for example, social isolation increases abnormal behaviours, in piglets social isolation increases escape behaviour and decreases paly behaviour, and in ewes social isolation leads to increased signs of distress (Carbajal & Orihuela, 2001; Herskin & Jensen, 2000; Hubrecht et al., 1992). Housing animals in suboptimal social environments is, therefore, disregarding not only their freedom to express normal behaviour and the provision of conspecific company, but also the freedom of fear and distress (Farm Animal Welfare Council, 1993; Mellor, 2016). Consequently, a stronger focus on better understanding the sociobiology of different species is required to improve the social aspect of captive welfare (Asher et al., 2009; Warwick et al., 2023).

Even though pair bonding and it's fitness benefits are widely studied in mammals and birds (Bales et al., 2021) they are rarely considered in reptiles, possibly due the prevailing misconception that reptiles are asocial creatures which only socialize to reproduce (Doody et al., 2013; 2021). Empirical evidence is accumulating which shows that many reptiles species have a secret social live expressing family group living and long-term monogamy (Whiting & While, 2017) and that some individuals can become more social if the population density increases (Doody et al., 2013; 2021). To this day we understand very little about what it means to be social in reptiles, and therefore, should assume that the social environment is as important for social reptiles as it is in social non-reptile species (Hurst et al., 1997, 1998; Meehan et al., 2003; Visser et al., 2008; Williams et al., 2017). The impact of the social environment on the welfare of reptiles in captivity is still poorly understood (Tetzlaff et al., 2022). Therefore, we need more research on the influence of social housing on captive reptile welfare, with a special focus on reptiles in which anecdotal and empirical evidence suggests family group living.

The aim of this study was to understand whether measures of physical closeness between Tokay geckos (*Gekko gecko*) housed together in a pair can capture variation in pair association strength or whether it captures random spatial behaviour within enclosures. Tokay geckos are a social lizard species that have been reported to form pairs in the wild (personal communication) as well as in captivity (Grossmann, 2007). However, if these associations between males and females differ in quality is unexplored. Therefore, we collected data on physical closeness as well as movement, hiding and basking behaviour in captivity to provide a measure of pair association strength for captive Tokay geckos which can be used in the future to explore how such differences might influence behaviour as well as welfare in captive individuals. To the best of our knowledge, no measure for pair bonding has been proposed for reptiles that can capture variation in pair associations necessary in order to uncover the benefits and costs of these associations in the wild as well as their potential importance in captive animal welfare.

Methods

Study animals and husbandry

We collected data from 25 adult tokay geckos (*Gekko gecko*) which were bred in captivity, 13 females and 12 males (Table 1). We collected data from nine pairs in 2021 and an additional 12 pairs in 2024 (new pairs partly made up of the same individuals used in 2021; Table 1). Animals were between 2-9 years old and originated from different breeders (N = 11 females and 10 males) or were the offspring of our original stock (N = 2 females and 2 males). The presence (male) or absence (female) of femoral pores was used to identify sex (Grossmann, 2007).

Geckos were housed in rigid foam terraria (90L x 45B x 100H cm; only suitable for scientific purposes) with glass front sliding doors and a mesh top. Enclosure furnishings include a compressed cork back wall, cork branches, cork branches cut in half as shelters hanging on the back wall and life plants. The ground is composed of two layers, organic rainforest soil (Dragon BIO-Ground) as the top and expanded clay as the bottom layer separated by a mosquito mesh. Additionally, we spread autoclaved red oak leaves and sphagnum moss on the soil. To break down the faecal matter of the lizards our terraria include isopods and earth worms. Each terraria is equipped with a heat mat (Tropic Shop) on the right outside wall, which locally increases the temperature up to 10°C and a UVB light (Exo Terra Reptile UVB 100, 25 W) which provides UVB during the light phase. Geckos are nocturnal and we keep them under a reversed 12h:12h photo period (light: 6 pm to 6 am, dark: 6 am to 6 pm) to be able to work with them during their natural active period. We use a red light (PHILIPS TL-D 36 W/15 RED) invisible to the geckos (Loew, 1994) during the night phase to provide minimal light conditions for husbandry purposes. The light cycle includes a simulated sunrise and sunset which are accompanied by a gradual change in temperature from 31°C during the day and 25°C during the night simulating natural conditions. Humidity is set to 50% but is increased to 100% for a short period of time by rainfall twice a day (reverse osmosis water, 30s every 12 h at 5 pm and 4 am each day). The lizards are kept across two rooms, on shelves.

Geckos are fed on Mondays, Wednesdays and Fridays with 25 cm long forceps which allows to monitor their food intake. They are fed with 3-5 adult house crickets (*Acheta domesticus*) or cockroaches (*Nauphoeta cinerea*). To provide optimal nutrition to our geckos, insects are fed with cricket mix (reptile planet LDT, which provides Vitamin D and calcium), dry cat food (various brands) and fresh apples and carrots. Geckos have access to water *ad libitum* from water bowls within their enclosures. To track the condition of animals, lizard's snout vent length (SVL) is measured every two to three month and their weight is taken once a month.

Table 1. Individual specific information for the 25 geckos that participated in the study. Information given are the individual identity (ID) of the vocal individual, the sex (F – female, M – male) of the focal individual and their origin. Because some individuals were samples in both sampling years the table also includes the individual identity of the mate for both sampling years as well as the snout vent length (SVL, in cm) for each focal individual each year. – did not participate in that sampling year.

			2021		2024	
Vocal ID	Sex	Origin	Mate ID	SVL	Mate ID	SVL
G001	F	External	-	-	G006	14.91
G002	F	External	G006	13.07	G024	13.71
G003	M	External	-	-	G015	15.69
G004	M	External	G015	14.60	G008	15.05
G005	F	External	G014	13.54	G018	14.09
G006	M	External	G002	13.69	G001	15.46
G007	F	External	G018	12.09	G009	13.00
G008	F	External	-	-	G004	13.73
G009	M	External	G012	13.65	G007	15.00
G010	F	External	G017	12.60	G011	13.35
G011	M	External	G020	12.82	G010	14.03
G012	F	External	G009	11.93	G013	13.52
G013	M	External	G016	13.66	G012	15.09
G014	M	External	G005	13.49	G021	14.82
G015	F	External	G004	12.21	G003	13.21
G016	F	External	G013	11.27	-	-
G017	M	External	G010	14.39	G020	15.24
G018	M	External	G007	13.68	G005	15.79
G020	F	External	G011	13.80	G017	13.90
G021	M	External	G022	12.23	G014	12.77

G022	F	External	G021	12.54	G043	14.29
G024	M	Own breeding	-	-	G002	14.29
G032	F	Own breeding	-	-	G037	14.42
G037	M	Own breeding	-	-	G032	13.97
G043	F	Own breeding	-	-	G022	13.13

Set-up and procedure

We collected data from the 22nd of September to the 3rd of December 2021 and from the 9th of January to the 7th of March in 2024. Before the start of the experiment, animals had been housed in pairs for about 2 weeks to ensure that they had gotten used to the new housing conditions.

We used scan sampling to record gecko behaviour. On two days per week (Monday to Friday) we entered the rooms every 15 minutes for a total of 12 sampling points. Only one room was sampled at a time resulting in two sampling periods per day: either in the morning between 8:00 and 10:45 or in the afternoon between 11:30 (2021) or 12:00 (2024) and 14:15 (2021) or 14:45 (2024). During each sampling lizards behaviour was sampled in a random order to account for order effects. On feeding days (Monday, Wednesday, Friday), we sampled one room before and the other after feeding and we sampled the rooms an equal number of times on feeding and non-feeding days (Tuesday, Thursday). Furthermore, we distributed the sampling periods an equal number of times across weekday and rooms. Sampling was done for 12 weeks in 2021 and for 10 weeks in 2024. Consequently, we collected 288 data points (5184 data points for the whole group) per individual in 2021 and 240 data points per individual in 2024 (5760 data points for the whole group).

During each sampling event we entered the room form the same door and as quiet as possible. First, we tried to record a lizards location from a distance (1.5 m) so as to not disturb natural behaviour. If this was not possible, we used a dim white light (LED, SPYLUX® LEDVANCE 3000 K, 0.3 W, 17 lm) and carefully moved closer to an enclosure. In case the lizard could still not be found we opened the terraria door and took a mirror to check behind shelters or branches. Each sampling event took between 2-4 minutes.

Data collection

To measure variation in pair association, we collected data on the physical proximity of geckos during each sampling event. We recorded the distance between individuals of a pair as (1) more than two snout vent length (SVL) apart, (2) within two SVL, (3) within one SVL or (4) touching. To record movement data, we first split the enclosure into 8 sections: (1) top, left, front; (2) top, right, front; (3) bottom, left, front; (4) bottom, right, front; (5) top, left, back; (6) top, right, back; (7) bottom, left, back; (8) bottom, right, back and recorded the location in a coordinate system (Szabo, 2024). If a lizard moved between section from one sampling event to the next, we recorded movement as 1. If the lizard stayed in the same section between sampling points, movement was recorded as 0. Additionally, we recorded if a lizard was found on the heat mat or behind a shelter. These data were recorded as presence (1) or absence (0) and were mutually exclusive (a lizard could not be on the heat mat and under a refuge at the same time). Finally, to be able to account for behavioural changes based on temperature, our system automatically recorded the temperature inside the terraria every 15 minutes.

Statistical analyses

All analyses were run in R version 4.2.2 (R Core Team, 2022). First, we were interested if our measure of physical closeness between individuals in a pair (from here on "pair association strength") changed over time and differed, on average, across sampling years (2021 and 2024). To this end, we ran a Gaussian Bayesian generalised linear mixed model (GLMM, package *brms*, Bürkner, 2017; 2018; 2021) with the average pair association strength per session as the response variable and session (sampling day) and sampling year as fixed effects. We included a random effect of animal identity as well as pair partner identity. This accounted for repeated measures and that some individuals participated in both sampling years but with a different mating partner

Next, we were interested in understanding if movement was related to pair association strength. To this end, we used movement between sections (1 = moved, 0 = did not move) as the response variable in a Bayesian generalised linear mixed model with Bernoulli family. Pair association strength in interaction with sampling year as well as temperature (covariate) were included as fixed effects and animal identity as well as pair partner identity were included as random effects.

Next, we wanted to understand how hiding and basking behaviour were associated with pair association strength. To this end, we used shelter usage (1 = behind a shelter, 0 = not behind a shelter) and heat mat usage (1 = on the heat mat, 0 = not on the heat mat) as the response variable each in a GLMM with Bernoulli family. Pair association in interaction with sampling year as well as temperature (covariate) were included as fixed effects and animal identity as well as pair partner identity were included as random effects.

For all models, we used a generic weakly informative normal prior with a mean of 0 and a standard deviation of 1 and ran 4 chains per model of 5000 iterations each and a thinning interval of 1 (default settings). We made sure that model Rhat was 1, that the ESS was above 2000 and checked the density plots and correlation plots to ensure that the models had sampled appropriately. We provide Bayes factors (BF) to evaluate the results by determining Bayes Factors from marginal likelihoods using the package *brms*. Bayes factors below 1 indicate no difference/ effect while above 1, BF indicate support for a difference/ effect (Schmalz et al., 2023). In case an interaction was significant, we applied estimated marginal means (EMM) *post hoc* tests using the function emtrends from the package *emmeans* (Lenth, 2023).

Ethical note

Our scan samples of animal behaviour were strictly non-invasive and followed the guidelines provided by the Association for the Study of Animal Behaviour/ Animal Behaviour Society for the treatment of animals in behavioural research and Teaching (ASAB Ethical Committee and ABS Animal Care Committee, 2023) as well as the Guidelines for the ethical use of animals in applied animal behaviour research by the International Society for Applied Ethology (Sherwin et al., 2003). Experiments were approved by the Suisse Federal Food Safety and Veterinary Office (National No. 33232, Cantonal No. BE144/2020, BE9/2024). Captive conditions were approved by the Suisse Federal Food Safety and Veterinary Office (Laboratory animal husbandry license: No. BE4/11). During pair formation, we monitored adults closely for 12h to prevent harm. If any aggression occurred within the first 24 hours of pairing, we immediately separated the male and female to avoid injury. Therefore, all pairs used in this study could be considered as stable pairs with a good enough bond to not show any aggression.

Results

We found no evidence that pair association strength changed over time (GLMM, estimate = -0.009, CI_{low} = -0.014, CI_{up} = -0.003, BF = 0.431, Appendix Table A1) or differed, on average across sampling years (GLMM, estimate = -0.002, CI_{low} = -0.083, CI_{up} = 0.079, BF = 0.042, Appendix Table A1). However, all geckos demonstrated a change in pair association strength from 2021 to 2024 when paired with a new individual (Figure 1).

We found no evidence that the probability to move was influenced by an interactive effect of pair association strength and sampling year (GLMM, estimate = -0.068, CI_{low} = -0.200, CI_{up} = 0.065, BF = 0.002, Appendix Table A2). Therefore, we removed the interaction to simplify our model. We found no evidence that the probability to move was associated with pair association strength (GLMM, estimate = -0.001, CI_{low} = -0.239, CI_{up} = 0.229, BF = 0.621, Appendix Table A3).

We found evidence that the probability to be found behind a shelter was influenced by an interactive effect of closeness and sampling year (GLMM, estimate = 0.624, CI_{low} = 0.431, CI_{up} = 0.819, BF = $8.2*10^7$, Appendix Table A4). In 2021, pair association strength was negatively associated with the probability to be found behind a shelter (EMM, estimate = -0.217, CI_{low} = -0.476, CI_{up} = -0.157), while in 2024 the relationship was positive (EMM, estimate = 0.307, CI_{low} = 0.195, CI_{up} = 0.418).

Finally, we found evidence that the probability to be found on the heat mat was influenced by an interactive effect of pair association strength and sampling year (GLMM, estimate = -0.450, CI_{low} = -0.706, CI_{up} = -0.198, BF = 9802, Appendix Table A5). In 2021, there was no association between pair association strength and the probability to be found on the heat mat (EMM, estimate = -0.022, CI_{low} = -0.180, CI_{up} = 0.122), while the relationship was negative in 2024 (EMM, estimate = -0.468, CI_{low} = -0.676, CI_{up} = -0.262).

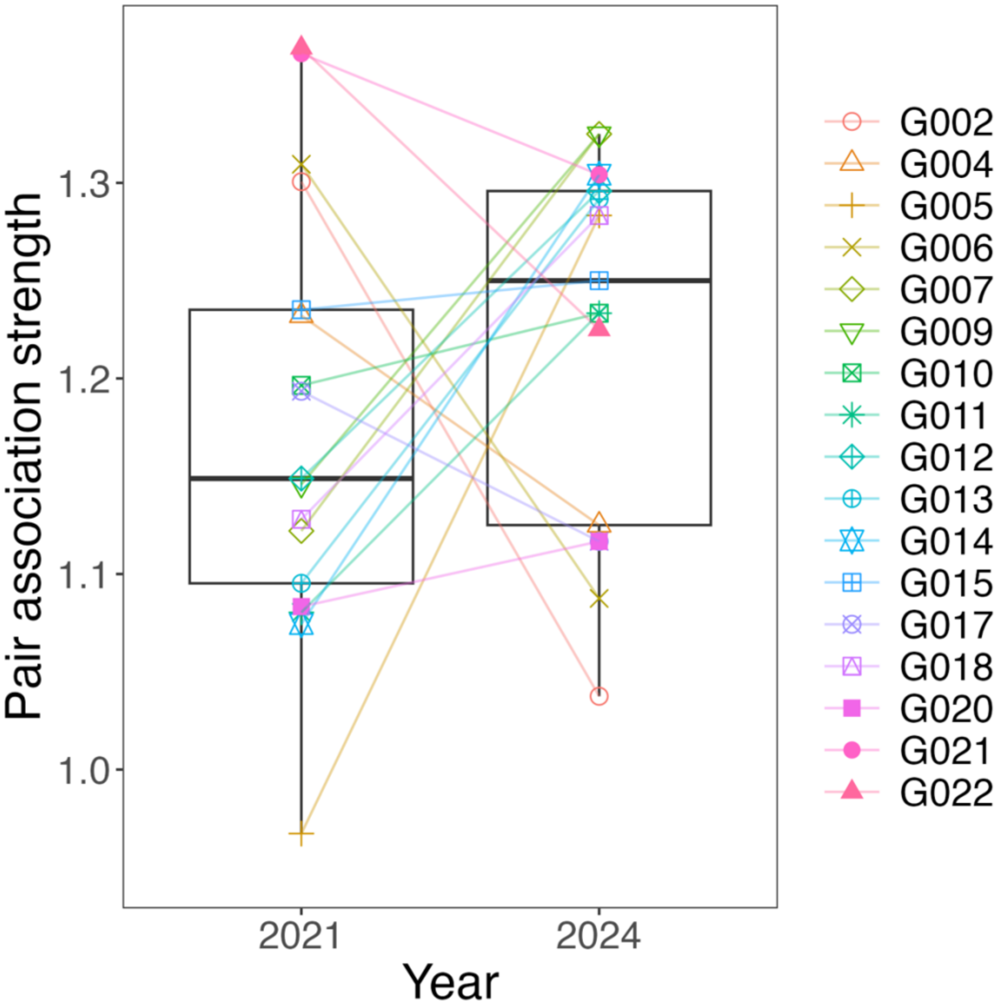

Figure 1. Boxplots showing the distribution of measures of pair association strength across sampling years. The bold line within boxes shows the median, the upper box edges show the upper quartile, the lower edges the lower quartile, the top whisker ends show the maximum and the bottom ends the minimum. The plot only includes data from the 17 individuals that

participated in both sampling years. Individual data points are depicted by different symbols and colours. Lines between points indicate the change in pair association related to a change in mating partner across sampling years.

Discussion

In this study, we investigated if physical closeness can be used as a measure of pair association strength in captive tokay geckos. We find that physical closeness is not associated with movement within the enclosure and associations with basking and hiding change over the two sampling years, but not consistently. Furthermore, pair association strength varies across pairs and changed in individuals that were paired with different partners across years. Together, these results indicate that physical closeness can be used to capture variation and change in pair association strength in these geckos but further studies are needed.

First, we only tested a change in physical closeness across two years in which we paired individuals with different partners. If our measure of pair association strength is indeed qualifying the relationship between individuals in a mated pair, then pairing males and females with the same partner repeatedly should result in similar measures of pair association strength. We have already shown that tokay geckos can chemically recognize their familiar partner and distinguish them from an unfamiliar new mate. However, this previous study also showed that after about six weeks with no contact, geckos are unable to discriminate the odour of a familiar from an unfamiliar individual (Verger et al., 2024). It would, therefore, be informative to understand if lizards still react similarly to the same partner even though they might not recognise it as an individual that they have previously mated with.

Secondly, we only focused on physical closeness and did not observe any other behaviour between mated pairs. Tokay geckos are nocturnal and difficult to observe. In other animals, pair bonds are characterised not only by proximity but also by specific affiliative behaviour such as allo-preening in birds or allo-grooming in primates (Morales Picard et al., 2020). If geckos show behaviours that play a role in maintaining affiliative relationships is unclear. In the future, the use of night vision cameras to record natural behaviour within enclosures could be a powerful method to investigate the occurrence of social behaviour in tokay geckos.

Even though physical closeness was not associated with movement, we found associations with hiding behaviour and basking across years. In 2021, individuals with a lower pair association strength hid more while in 2024, they hid less and were found on the heat mat more often. As our measure relied on the male and female within an enclosure to be close, it is not surprising that differences in space use are related to pair association strength. If one individual in a pair hides more or spends more time on the heat mat then this naturally will increase the distance between them. Therefore, to some extent, physical closeness is dependent on how similar individuals are in their hiding and basking behaviour. Importantly, hiding and basking behaviour was not consistently related to pair association strength, and therefore, likely rather captures social tolerance or attraction between the two individuals in a pair.

In our study, we ensured that all pairs were stable before starting behavioural observations. After moving a female into the enclosure of a male, we monitored their behaviour closely and if aggression (e.g. biting) occurred, they were separated immediately. Consequently, all pairs that participated in the data collection can be considered “good” pairs for which no aggression occurred during the study period. Nevertheless, we find variation in our measure of pair association strength across individuals that did not change across sampling weeks. Furthermore, we can rule out experience as a factor because the direction of the changes in pair association strength across years were not uniform, some individuals associated more with the new partner, some less. In most cases, it became clear within a few hours if a male and female accepted or rejected the provided mating partner. In a few cases, we observed immediate rejection by either the male or the female. It is not clear yet, what lizards base these decisions on. It is likely, that chemicals play a role because previous work in other species has shown that chemical secretions can provide crucial information such as age (e.g. López et al., 2003), kinship (e.g. Bull et al., 2001; Lena & de Fraipont, 1998; O'Connor & Shine, 2006), reproductive status (e.g. Cooper & Pèrez-Mellado, 2002), dominance status (e.g. Martín et al., 2007) and even individual identity (e.g. Bull et al., 1999; Carazo et al., 2008; Mangiacotti et al., 2019). Importantly, as our study was conducted in captivity, differences in health and diet can be ruled out as factors influencing choice. Why some partners are rejected and what leads to differences in how much individuals in a pair associate with each other needs further investigation.

As our study was conducted in captivity, it remains to be shown if the observed variation also occurs in the wild when individuals have free choice of mating partners. It is yet unclear, if tokay geckos mate with the same partner across breeding season in the wild. If variation also occurs in the wild, then it would be interesting to investigate if it is associated with fitness consequences. It has been suggested, that pair bonding facilitates parental care and we would expect pairs with a stronger bond to have better reproductive susses (Bull, 2000; Clutton-Brock, 1991; Rasmussen, 1981; Schuiling, 2003). Tokay geckos perform biparental care and defend their offspring both while still in the egg and after hatching within their territory (Grossmann, 2007). Together, the results of our study as well as what is known about the social behaviour of these geckos already provides a firm foundation to further investigate if pair bonding occurs in these lizards that is similar to mammals and birds.

Nonetheless, our results and observations have implications for the welfare of captive tokay geckos. Our experience demonstrates that careful selection is necessary when housing a potential mating pair to avoid aggression and injury. Additionally, our results show that even in pairs that show no aggression there is variation in how much time they spend close to each other. Less time in physical closeness could be a sign of avoidance or exclusion of one individual by the other. Both are indicative that individuals do not get along which could translate into heightened stress for one individual. If this stress becomes chronic it can impact health and consequently welfare (Warwick et al., 2023). Therefore, we suggest closely monitoring the behaviour of newly paired individuals at the beginning to identify signs of aggression. Importantly, continuous monitoring of behaviour in relation to the mating partner is advisable to recognise issues and separate individuals if needed.

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Conflict of interest statement

We declare no conflict of interest.

Data availability statement

The data generated in this study are available on the Open Science Framework (OSF, link for review purposes: https://osf.io/8h7wy/?view_only=1c74a7ad9e2248eaaf4b2c3f605ca39f)

Code availability statement

The code used to analyse the data generated in this study are available on the Open Science Framework (OSF, link for review purposes: https://osf.io/8h7wy/?view_only=1c74a7ad9e2248eaaf4b2c3f605ca39f)

Author contribution statement

BS - Conceptualization; AK, BS - Data curation; AK, BS - Formal analysis; BS - Funding acquisition; AK, BS - Investigation; BS - Methodology; BS - Project administration; BS - Resources; BS - Validation; BS - Visualization; AK, BS - Roles/Writing - original draft; AK, BS - Writing - review & editing.

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Appendix

Table A1. Estimates and test statistics from the Bayesian model (with Gaussian distribution) investigating the change in pair association strength across sampling years (2021, 2024) and time (session). Both animal identity and mate identity were included as random effects. CI – confidence interval.

Parameter	Estimate	Estimated error	Lower 95% CI	Upper 95% CI
Intercept	1.301	0.052	1.199	1.401
Session	-0.009	0.003	-0.014	-0.003
Sampling year 2024	-0.002	0.041	-0.083	0.079

Table A2. Estimates and test statistics from the Bayesian model investigating the relationship between movement and physical closeness including the interactions between closeness and sampling year. Both animal identity nested in session and mate identity were included as random effects. CI – confidence interval.

Parameter	Estimate	Estimated error	Lower 95% CI	Upper 95% CI
Intercept	0.465	1.225	-2.008	2.816
Closeness	0.147	0.050	0.048	0.244
Sampling year 2024	0.144	0.152	-0.155	0.433
Temperature	-0.035	0.049	-0.130	0.065
Interaction: Closeness - Sampling year	-0.057	0.071	-0.195	0.080

Table A3. Estimates and test statistics from the Bayesian model investigating the relationship between movement and physical closeness without the interactions between closeness and sampling year. Both animal identity nested in session and mate identity were included as random effects. CI – confidence interval.

Parameter	Estimate	Estimated error	Lower 95% confidence interval	Upper 95% confidence interval
Intercept	-0.404	1.187	-2.778	1.906
Closeness	0.119	0.034	0.052	0.185
Sampling year 2024	-0.001	0.117	-0.239	0.229
Temperature	0.001	0.048	-0.092	0.097

Table A4. Estimates and test statistics from the Bayesian model investigating the relationship between shelter usage and physical closeness including the interactions between closeness and sampling year. Both animal identity nested in session and mate identity were included as random effects. CI – confidence interval.

Parameter	Estimate	Estimated error	Lower 95% CI	Upper 95% CI
Intercept	1.200	1.889	-2.444	4.910
Closeness	-0.318	0.082	-0.479	-0.159
Sampling year 2024	0.653	0.249	0.167	1.133
Temperature	-0.127	0.076	-0.275	0.020
Interaction: Closeness - Sampling year	0.624	0.100	0.431	0.819

Table A5. Estimates and test statistics from the Bayesian model investigating the relationship between heat mat usage and physical closeness including the interactions between closeness and sampling year. Both animal identity nested in session and mate identity were included as random effects. CI – confidence interval.

Parameter	Estimate	Estimated error	Lower 95% CI	Upper 95% CI
Intercept	-4.173	2.495	-9.092	0.676
Closeness	-0.022	0.080	-0.179	0.134
Sampling year 2024	0.030	0.309	-0.578	0.644
Temperature	0.048	0.099	-0.144	0.242
Interaction: Closeness - Sampling year	-0.447	0.132	-0.710	-0.195