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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 behavior 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 lizard species hampers our understanding of its effects on captive welfare. As a first step towards a better understanding of pair-related social behavior 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 25 captive tokay geckos (*Gekko gecko*). We analyzed how physical closeness is related to measures of spatial behavior collected through scan sampling across two sampling years. Physical closeness was not related to movement but to hiding and basking behavior, albeit not consistently across years (e.g., negative in one year and positive in the other). 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 exhibited a change (increase or decrease). It is unknown if differences occur in the wild and if they confer different fitness outcomes. 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 Behavior, Squamata, Welfare, *Gekko gecko*

Pair bonding, defined as an intra-specific, selective aggregation of two adult individuals (Whiting & While, 2017), is an important social behavior demonstrated by many social animals. Four main behaviors are described as defining a pair bond: shared territory, joint displays, 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 (Kleiman, 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 impacted by many different aspects of the environment. However, the social environment is of particular importance for animals (Bracke & Hopster, 2006; Rault, 2012). Housing animals in suboptimal social environments is disregarding not only their freedom to express normal behavior and the provision of conspecific company, but also the freedom of fear and distress (Farm Animal Welfare Council, 1993; Mellor, 2016). In many social mammals, isolation from conspecifics leads to stress and depression (McKinney & Bunney, 1969; Morgan & Tromborg, 2007). In dogs (*Canis lupus familiaris*), for example, social isolation increases abnormal behaviors. In piglets (*Sus scrofa*), social isolation increases escape behavior and decreases paly behavior, and in ewes (*Ovis aries*) social isolation leads to increased signs of distress (Carbajal & Orihuela, 2001; Herskin & Jensen, 2000; Hubrecht et al., 1992). 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 its fitness benefits are widely studied in mammals and birds (Bales et al., 2021), they are rarely considered in reptiles, possibly due to 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 social lives, 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. Therefore, we should assume that the social environment is as important for social reptiles as it is in social non-reptile species (e.g., Hurst et al., 1997, 1998; Meehan et al., 2003; Visser et al., 2008; Williams et al., 2017) and aim to better understand the impact of the social environment on reptile welfare (Doody, 2023; Tetzlaff et al., 2022). Therefore, we need more research on the influence of social housing on captive reptile welfare, with a special focus on the species in which anecdotal and empirical evidence suggests family group living.

The aim of this study was to understand whether measures of physical closeness between pair-housed Tokay geckos (*Gekko gecko*) can describe variation in pair association strength or whether physical closeness captures random spatial behavior within enclosures. Tokay geckos are a social lizard species that have been reported to form pairs in the wild (personal email communication with Thomas Fieldsend) as well as in captivity (Grossmann, 2007). Furthermore, they show biparental care (e.g., protection) towards both eggs and offspring after hatching with which they form family groups for up to 12 months (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 behavior (i.e., as proxies of random spatial behavior) 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 behavior 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. This is 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

Ethics Statement

Our scan samples of animal behavior 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 behavioral 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 behavior research by the International Society for Applied Ethology (Sherwin et al., 2003). Experiments were approved by the Swiss Federal Food Safety and Veterinary Office (National No. 33232, Cantonal No. BE144/2020, BE9/2024). Captive conditions were approved by the Swiss Federal Food Safety and Veterinary Office (Laboratory animal husbandry license: No. BE4/11). During pair formation, we monitored adults closely for 12 hours 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.

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 male-female pairs in 2021 and an additional 12 male-female 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 (90 L x 45 W x 100 H cm; enclosure size only meet the minimum requirements and are only suitable for scientific purposes) with glass front sliding doors and a mesh top. Enclosure furnishings included a compressed cork back wall, cork branches, cork branches cut in half as shelters hanging on the back wall and live plants. The ground was 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 included isopods and earth worms. All terraria were equipped with a heat mat (Tropic Shop) on the right outside wall, which locally increased the temperature up to 10°C and a UVB light (Exo Terra Reptile UVB 100, 25 W) which provided UVB during the light phase. Geckos are nocturnal and we kept 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 used a red light (PHILIPS TL-D 36 W/15 RED; 60 lumen, 4-5 lux depending on room size which could have had a small effect on the circadian rhythms of the animals) invisible to the geckos (Loew, 1994) during the night phase to provide minimal light conditions for husbandry purposes. The light cycle included a simulated sunrise and sunset which were accompanied by a gradual change in temperature from 31°C during the day and 25°C during the night simulating natural conditions. Humidity was set to 50% but was increased to 100% for a short period of time by rainfall twice a day (reverse osmosis water, 30 s every 12 h at 5 pm and 4 am each day). The lizards were kept across two rooms, on shelves.

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

Set-Up and Procedure

We collected data from the 22nd of September to the 3rd of December 2021 (66 h of sampling time) and from the 9th of January to the 7th of March in 2024 (55 h of sampling time). 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 behavior. On two days per week (between Monday and Friday) we entered the rooms every 15 min for a total of 12 sampling points. Only one room was sampled at a time resulting in two sampling periods per day (Table 2): either in the morning between 8:00-10:45 (12 sampling points) or in the afternoon between 11:30-14:15 (2021) or 12:00-14:45 (2024) (12 sampling points). During each sampling, lizards behavior was sampled in a random order to account for order effects. The order was predetermined using the sample function in R (R Core Team, 2022). 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 weekdays 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 of 18 individuals) per individual in 2021 and 240 data points per individual in 2024 (5760 data points for the whole group of 24 individuals).

During each sampling event we entered the room from the same door and as quietly as possible. First, we tried to record a lizard's location from a distance (1.5 m) so as to not disturb natural behavior. If this was not possible, we used a dim white light (LED, SPYLUX® LEDVANCE 3000 K, 0.3 W, 17 lumen) and carefully moved closer to an enclosure. In case the lizard could still not be found, we opened the terrarium door and took a mirror to check behind shelters or branches. Each sampling event took between 2-4 min total to sample all lizards within the room. We detected lizards in all scans and as we approached the enclosures carefully, lizards were not disturbed during sampling.

Table 1

Individual Specific Information for the 25 Geckos that Participated in the Study

Vocal ID	Sex	Origin	2021		2024	
			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

Note. Information given are the focal 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.

Table 2

Description of the Scan Sampling Done in Both 2021 and 2024

2021	12 weeks					
Morning	8:00-11:45	12 scans	Afternoon	11:30-14:15	12 scans	= 66h / 5760 scans
2024	10 weeks					
Morning	8:00-11:45	12 scans	Afternoon	12:00-14:45	12 scans	= 55h /5184 scans

Data Collected

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 SVL), (2) within two SVL (1-2 SVL), (3) within one SVL (0-1 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 sections 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 shelter at the same time). Finally, to be able to account for behavioral changes based on temperature, our system automatically recorded the temperature inside the terraria every 15 min.

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 behavior 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.

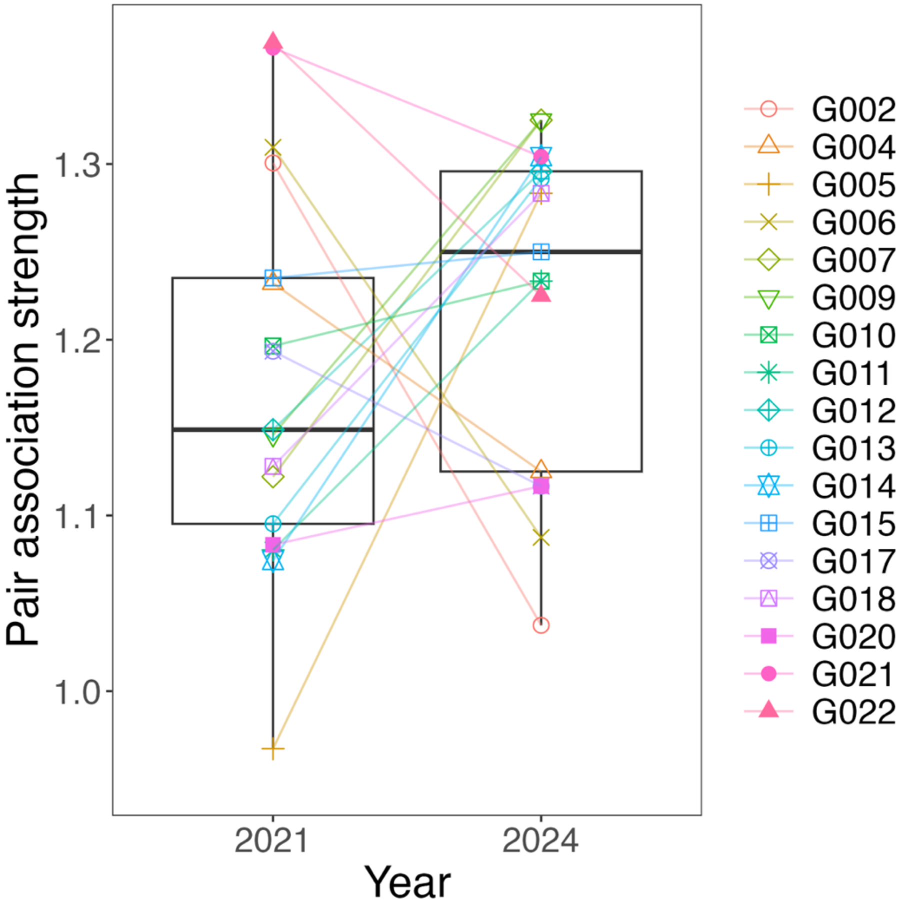
For all models, we used a generic weakly informative normal prior with a mean of 0 and a standard deviation of 1 and ran 4 chains per model of 5000 iterations each and a thinning interval of 1 (default settings). We made sure that model Rhat was 1, that the ESS was above 2000 and checked the density 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).

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, Table S1) or differed, on average across sampling years (GLMM, estimate = -0.002, CI_{low} = -0.083, CI_{up} = 0.079, BF = 0.042, Table S1). However, all geckos demonstrated a change in pair association strength from 2021 to 2024 when paired with a new individual (Figure 1).

Figure 1

Boxplots Showing the Distribution of Measures of Pair Association Strength Across Sampling Years



Note. 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 colors. Lines between points indicate the change in pair association related to a change in mating partner across sampling years.

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, Table S2). Therefore, we removed the interaction between pair association strength and sampling year 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, Table S3).

We found evidence that the probability to be found behind a shelter was influenced by an interactive effect of pair association strength and sampling year (GLMM, estimate = 0.624, CI_{low} = 0.431, CI_{up} = 0.819, BF = $8.2*10^7$, Table S4). 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, Table S5). 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).

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 (Verger et al., 2024). 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. This could show that they use some individual quality to assess compatibility even though they might not recognise the mate as an individual that they have previously mated with.

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

Even though physical closeness was not associated with movement, we found associations with hiding behavior 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 behavior. In the future, our study could be repeated within larger enclosures that offer more space and opportunity for the male and female to spend time apart to confirm the robustness of our results.

In our study, we ensured that all pairs were stable before starting behavioral observations. After moving a female into the enclosure of a male, we monitored their behavior 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 (based on aggression observed). In a few cases, we observed immediate rejection by either the male or the female (high levels of aggression). 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 success (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 behavior of these geckos already provides a firm foundation to further investigate if tokay geckos pair bonding is similar to mammals and birds.

Finally, 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 but further research on the topic is needed in reptiles (Warwick et al., 2023). Therefore, we suggest closely monitoring the behavior of newly paired individuals at the beginning to identify signs of aggression early as well as continue monitoring aggression in relation to the mating partner to recognise issues and separate individuals if needed.

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Code availability statement: The code used to analyse the data generated in this study are available on the Open Science Framework (OSF, https://doi.org/10.17605/OSF.IO/8H7WY)

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Supplementary Materials

Table S1

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)

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

Note. Both animal identity and mate identity were included as random effects. CI – confidence interval.

Table S2

Estimates and Test Statistics from the Bayesian Model Investigating the Relationship Between Movement and Physical Closeness Including the Interactions Between Closeness and Sampling Year

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

Note. Both animal identity nested in session and mate identity were included as random effects. CI – confidence interval.

Table S3

Estimates and Test Statistics from the Bayesian Model Investigating the Relationship Between Movement and Physical Closeness without the Interactions Between Closeness and Sampling Year

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

Note. Both animal identity nested in session and mate identity were included as random effects. CI – confidence interval.

Table S4

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

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

Note. Both animal identity nested in session and mate identity were included as random effects. CI – confidence interval.

Table S5

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

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

Note. Both animal identity nested in session and mate identity were included as random effects. CI – confidence interval.