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Strength and Stability Components of Pair Bonds and Their Influence on Reproductive Success in Greylag Geese

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Declaration

I hereby declare that

- I have written this thesis independently.
- I have not used any sources other than those indicated, and that all statements taken literally or in spirit from other works are identified as such.
- This thesis has neither in whole nor in substantial parts been submitted for any other examination procedure.
- Because Ukrainian and Russian are my mother tongues, I used ChatGPT to assist with correcting grammar; however, all ideas and content are entirely my own.

Mariia Klymenko

26.09.2025, Grünau im Almtal

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1. Abstract

Pair bond theory predicts that the quality of the pair bond helps to predict reproductive success, and could therefore be a target of selection on trait components that define pair bond quality. Greylag geese (*Anser anser*) provide a valuable model system of social complexity and exhibit marked variance in pair bond quality, with some pairs forming stable, affiliative long-term bonds, while others engage in divorce or maintain lower-quality affiliative interactions. This study investigated whether components of bond strength—measured through proximity, movement responsivity (leading–following behaviour), and vocal responsivity (contact calls)—were associated with reproductive success. While call responsivity was not significantly repeatable, leading–following behaviour was significantly repeatable across pairs. Pair bond duration was not related to behavioural responsivity, but leading–following behaviour increased with spatial proximity, whereas call responsivity was independent of proximity. Neither call responsivity, leading–following behaviour, nor spatial proximity predicted clutch size, hatching success, or fledging success. By contrast, reproductive output was positively associated with pair bond duration: long-term pairs laid more eggs and showed a trend toward higher hatching success. These findings suggest that short-term behavioural measures of bond strength do not directly predict reproductive outcomes, whereas the stability of the pair bond itself plays a central role, underscoring the importance of long-term studies for understanding monogamous pair bonds.

Zusammenfassung

Die Paarbindungstheorie sagt voraus, dass die Qualität der Paarbindung den Reproduktionserfolg mitbestimmt und daher ein Ziel der Selektion auf jene Merkmalskomponenten sein könnte, die die Qualität der Paarbindung definieren. Graugänse (*Anser anser*) sind ein wertvolles Modellsystem für soziale Komplexität und zeigen eine deutliche Varianz in der Qualität der Paarbindung: Einige Paare bilden stabile, affiliative Langzeitbindungen, während andere sich trennen oder niedrigqualitative affiliative Interaktionen aufrechterhalten. In dieser Studie wurde untersucht, ob Komponenten der Bindungsstärke – gemessen über Nähe, Bewegungs-Responsivität (Führungs- und Folgeverhalten) und vokale Responsivität (Kontaktlaute) – mit dem Reproduktionserfolg zusammenhängen. Während die vokale Responsivität nicht signifikant wiederholbar war, zeigte sich das Führungs- und Folgeverhalten über Paare hinweg als signifikant wiederholbar. Die Dauer der Paarbindung stand nicht im Zusammenhang mit der Verhaltensresponsivität, jedoch nahm das Führungs- und Folgeverhalten mit räumlicher Nähe zu, während die vokale Responsivität unabhängig von der Nähe blieb. Weder vokale Responsivität, Führungs- und Folgeverhalten noch räumliche Nähe sagten Gelegegröße, Schlupferfolg oder Flüggerate voraus. Dagegen war der Reproduktionserfolg positiv mit der Dauer der Paarbindung assoziiert: Langfristige Paare legten mehr Eier und zeigten einen Trend zu höherem Schlupferfolg. Diese Ergebnisse deuten darauf hin, dass kurzfristige Verhaltensmaße der Bindungsstärke den Reproduktionserfolg nicht direkt vorhersagen, während die Stabilität der Paarbindung eine zentrale Rolle spielt, was die Bedeutung langfristiger Studien für das Verständnis monogamer Paarbindungen unterstreicht.

Introduction

1.1 Social Relationships

Since the early 20th century, researchers have investigated animal social behaviour, focusing in particular on individual characteristics as well as the evolutionary and functional aspects of social relationships. Foundational works defined animal relationships as consistent and repeatable interactions characterized by their content, patterns, and quality and argued that these must be valuable to the individuals involved (Hinde, 1976; Kummer, 1978). Several studies show that ecological and social factors, as well as levels of relatedness between individuals, affect the formation and maintenance of social relationships (Parsons et al., 2003). Specifically, species with high kinship typically exhibit organizational complexity through cooperative breeding strategies that enhance indirect fitness. In contrast, species with low kinship rely on relational complexity, where reproductive success depends on competition, dominance, and strategic social alliances (Lukas & Clutton-Brock, 2018). Understanding how pair bond attributes are associated with reproductive success may shed light on selective processes that shape the psychological and/or cognitive building blocks favouring investment into social relationships.

Empirical evidence from studies on mammals and birds demonstrates that social bonds can reduce stress, enhance access to limited resources, decrease predation risk, and overall improve reproductive success (Ostner & Schülke, 2018). For example, in primates, females who form strong affiliative ties have higher infant survival rates, longer lifespans, and reduced stress (Archie et al., 2014; J. B. Silk et al., 2003, 2006, 2009). Similarly, male macaques gain offspring survival and reproductive advantages through coalition formation supported by strong bonds (Schülke et al., 2010).

These fitness outcomes also extend beyond primates. Long-term associations enhance coordination and offspring survival in cooperative non-human animals as birds (Riehl & Strong, 2018) and dolphins (Wiszniewski et al., 2009). In feral horses, social bonds among mares enhance foal birth rates and first-year survival by reducing harassment from stallions (Cameron et al., 2009). Some relationships are short, while others last longer, depending on previous experiences that ensure benefits from a particular partner. Beyond kinships, animals also form friendships, alliances and partnerships (Seyfarth & Cheney, 2012).

Mating systems represent a special form of dyadic relationship that evolved specifically to increase reproductive success. Among the different types – polygamy, monogamy, promiscuity – monogamy is most unexpected, occurring when polygamy is not feasible due to ecological conditions such as poor territories or limited food, which male cooperation between individuals necessary to protect resources, territory and offspring (Emlen & Oring, 1977a)

1.2 Monogamous Pair Bond

Monogamy is a mating system in which a male and female form a lasting relationship that increases reproductive success through cooperation and coordinated investment. It is widespread in birds (Møller, 2003; Orians, 1969) but less common in mammals, reptiles, and fishes (Kleiman, 1977; Lukas & Clutton-Brock, 2013; Whiteman & Côté, 2004). Monogamy is thought to evolve under ecological or social conditions that constrain alternative mating strategies. Limited food resources, restricted territories, or reduced access to multiple partners decrease opportunities for polygyny or promiscuity, making monogamy more advantageous (Emlen & Oring, 1977b; Kleiman, 1977; Lukas & Clutton-Brock, 2018, 2013). Female birds illustrate this ecological plasticity. In environments with scarce food and nesting opportunities,

monogamy is favoured, while in resource-rich habitats, females may engage in extra-pair copulations with already paired male (Goymann et al., 2015).

Several non-exclusive hypotheses explain the emergence of monogamy, including ecological constraints (Emlen & Oring, 1977), habitat limitation and mate availability (Kvarnemo, 2018), female intolerance of co-breeding (Lukas & Clutton-Brock, 2013), and the high demands of biparental care (Gubernick & Teferi, 2000). These perspectives highlight that there is no universal driver of monogamy; rather, monogamy arises from taxon-specific ecological and social contexts that shape reproductive strategies.

1.3 Mechanisms, Qualities, and Quality of Relationships

Ultimate explanations for monogamy are well described, yet the proximate mechanisms underlying pair bond maintenance, and the frameworks for studying them at the behavioural level, are less well understood. There remains a shortage of studies that clearly demonstrate the mechanisms that support the development and maintenance of social relationships, and how these mechanisms connect to fitness and reproductive success (Ostner & Schülke, 2018) Because not all social bonds provide the same adaptive benefits, it is important to study proximate mechanisms in relation to different bond types.

Mechanisms can be physiological, such as testosterone compatibility in greylag geese (Hirschenhauser, 2012) or oxytocin and vasopressin pathways that regulate partner preference in prairie voles (Carter & Getz, 1993; Getz et al., 1987; Young & Wang, 2004) They can also be cognitive, such as partner recognition and memory in primates and corvids (Emery et al., 2007) The challenge arises when researchers attempt to establish universal frameworks that

span taxa and reveal how dyadic relationships develop and are maintained at the individual level.

The recognition that not all relationships are equal led to the concept of **relationship quality** and **relationship qualities**, first introduced by Hinde (1976). These terms require careful distinction. According to the *Oxford English Dictionary* (OED), "quality" refers to a specific standard of excellence or a degree of an attribute, whereas "qualities" denote collections of attributes, often referring to traits or characteristics such as those measured in animal personality research (Réale et al., 2007). At the behavioural level, "qualities" can thus be understood as the components of a relationship, while "quality" refers to its overall value or grade.

(Cords and Aureli., 2000) were among the first to propose a universal framework of relationship qualities in primates, defining social relationships in terms of **value**, **compatibility**, and **security**. This framework was subsequently applied to chimpanzees (Fraser et al., 2008), ravens (Fraser & Bugnyar, 2010), macaques (Majolo et al., 2010; McFarland & Majolo, 2011), and dolphins (Themelin et al., 2020). These studies quantified relationship qualities through principal component analysis and then assessed the overall quality of dyadic interactions. Across taxa, high-quality relationships are characterized by reciprocity, stability, and reduced conflict.

J. Silk et al., 2013 extended this framework by proposing a set of measurable methods to quantify social relationships, making comparative research across species more feasible. While their approach overlaps with Cords and Aureli's dimensions of compatibility and security, the analogue of "value" proved difficult to operationalize. (Thompson, 2019) advanced the

framework further by connecting social relationships more explicitly to fitness. He identified three categories of social relationship measures: **gregariousness**, **integration**, and **bondedness**. Bondedness, in particular, is a quality of dyads characterized by strength, stability, and symmetry.

Thus, early work Cords et al., 2000; Hinde, 1976 established the conceptual basis for social relationship qualities, while subsequent studies J. Silk et al., 2013; Thompson, 2019 provided operational tools and theoretical frameworks to link relationship quality more directly to fitness outcomes.

1.4 Quality of Monogamous Relationships

Compared to group-living primates, monogamous dyads represent a unique social context where reproductive success is directly linked to the strength and stability of one primary relationship (Rasmussen, 1981). Growing evidence highlights that the robustness of these bonds has measurable consequences for breeding. Work on zebra finches shows that partners who maintain strong and stable associations prior to reproduction are more likely to form pairs, begin laying earlier, and produce larger clutches, while also facing a reduced risk of separation once breeding begins (Maldonado-Chaparro et al., 2021). In a different system, studies of wild jackdaws reveal that pair-bond strength is not only stable over time but also linked to the degree to which males respond to subtle changes in their partner's condition, indicating a role for socio-cognitive processes in maintaining cooperation (Hahn et al., 2025). These findings extend the general framework of relationship quality into the context of pair bonds, showing that even within dyads, the strength and stability of the relationship can predict reproductive outcomes.

1.5 Markers of Strength in Dyadic Relationships

Functionally, monogamy contributes to reproductive success through multiple pathways. It promotes cooperative territory defence and food provisioning (Whiteman & Côté, 2004), increases offspring survival. Exclusive characteristic of this kind of dyadic bond is to ensure biparental investment, thereby increasing reproductive succeess (Angelier & Chastel, 2009; Bart & Tornes, 1989). For example, paired Djungarian hamsters raise young more successfully than solitary females (Wynne-Edwards, 1987). Similarly, in species exhibiting extra-pair copulations, secondary females often produce fewer fledglings than primary females (Gubernick & Teferi, 2000; Webster, 1991).

Effective parental care requires coordination between the sexes, which not only improves reproductive outcomes but also reduces sexual conflict within the pair (Balshine et al., 2002; Barta et al., 2002; Harrison et al., 2009; Schell et al., 2018; Székely, 2014). However, whether parental care is a driver or a consequence of monogamy remains debated (Klug, 2018). Some evidence suggests that male guarding arose secondarily, after parental care had already appeared in basal archosaurs, implying that this behaviour became consolidated only later in birds (Burley & Johnson, 2002). In non-human mammals, however, parental care is more often considered a consequence of monogamy, emerging in contexts where males are unable to monopolize more than one female (Lukas & Clutton-Brock, 2013)

Studying monogamous relationships requires operational markers of bond strength. General principles emphasize behavioural coordination as central to social cohesion (Conradt & Roper, 2000). Behavioural coordination, the synchronized actions of individuals, is a key component of social dynamics across various species. It serves to strengthen social bonds, enhance

265 communication, and facilitate cooperative behaviours. In pair bonds, three markers are
266 particularly relevant:

267 1. **Behavioural Responsivity** – reciprocity in affiliative behaviours such as grooming,
268 preening, or other social responses.
269 2. **Vocal Responsivity** – acoustic exchanges that maintain contact and coordination,
270 particularly in dynamic environments.
271 3. **Spatial Proximity** – physical closeness that reflects the investment and attentional
272 focus of partners.

273 **Behavioural responsivity** refers to the ability of individuals to mimic or respond to the actions
274 of others, which is a fundamental aspect of behavioral synchronization. This can be seen in
275 various contexts, such as the synchronized vigilance of black-headed gulls, where individuals
276 resting in a flock coordinate their alert behaviors (Evans et al., 2018). This type of responsivity
277 is not always a deliberate act. For instance, nonconscious behavioral mimicry, like the "scratch
278 contagion" observed in Tibetan macaques, highlights a form of multilayered empathy that
279 strengthens social cohesion within a group (McDougall & Ruckstuhl, 2018; Zhang et al., 2022).
280 These coordinated movements and responses are critical for group stability and can reflect the
281 emotional and social closeness of the individuals involved.

282 **Spatial proximity,** or the physical closeness of individuals, plays a significant role in
283 influencing the likelihood and quality of behavioral synchronization. Research on fallow deer
284 has shown that behavioral synchronization is directly linked to spatial proximity, with
285 individuals in close quarters being more likely to exhibit synchronized behaviors (Hoyle et al.,
286 2021). This connection is also evident in studies of emotional proximity, which suggest that
287 closer physical and social relationships lead to higher quality and more frequent
288 synchronization. The synchronization of vigilance in black-headed gulls, for example, is

influenced by the proximity of individuals to their nearest neighbors, with closer distances increasing the likelihood of synchronized behavior (Evans et al., 2018). Thus, spatial arrangement within a group is a powerful factor that facilitates and reinforces the complex dynamics of behavioral synchronization.

Vocal responsivity is a crucial element of behavioural coordination in animal social groups, facilitating everything from parent-offspring communication to the maintenance of pair bonds. This form of communication involves a dynamic exchange of vocal signals, with individuals adjusting their own calls in response to those of others.

Vocal calls serve a vital role in maintaining group cohesion and social structure. For example, contact calls are used by many species, such as pygmy marmosets, to facilitate group movement and maintain social connections, even when individuals are not in sight (Snowdon & Cleveland, 1980). These calls are often individually distinct, allowing for the recognition of specific group members and reinforcing social bonds. The frequency and structure of these vocalizations are highly flexible and can change based on social context. Alarm calls, for instance, are a form of vocal responsivity that can communicate predator threats, with frequency and complexity varying to minimize eavesdropping risks while ensuring the message is received by kin (Magrath et al., 2007). In species like orange-fronted squirrels, individuals adjust their vocal responses to playback calls, indicating they can assess the identity and intent of other callers from a distance (Vehrencamp et al., 2003). This demonstrates a sophisticated level of vocal responsivity that underpins cooperative behaviours and collective decision-making.

In the context of pair bonds and reproduction, vocal responsivity is a cornerstone of coordinated behaviour. Male songbird song output is temporally associated with their mate's fertility, and

coordination of timing enhances reproductive success (Moller, 1991). In duetting species like siamangs and gibbons, the synchronized singing of a pair strengthens their bond and serves as a form of social advertisement (Geissmann, 1999; Geissmann & Orgeldinger, 2000). The coordination of these duets is a form of vocal responsivity that correlates with other indicators of a strong pair bond, such as grooming activity. Parent-offspring vocalizations also showcase a high degree of responsivity. Mothers in species like cattle and baboons exhibit strong vocal recognition of their offspring and respond to their calls, with the maternal response often influencing the calf's behavioural development (Padilla De La Torre et al., 2016)). Similarly, offspring vocalizations, such as begging calls in superb fairy-wrens, elicit specific parental responses, although these responses can show sex-based differences and are influenced by factors like the offspring's begging intensity (MacGregor & Cockburn, 2002). This reciprocal vocal exchange is vital for ensuring offspring survival and reflects a complex interplay between vocal communication and parent-offspring dynamics.

These measures allow researchers to quantify abstract concepts such as “bond strength” and connect them to outcomes like reproductive success, survival, and resilience to stress.

1.6 Greylag Geese (*Anser anser*)

Greylag geese have long served as a model species for studying monogamous pair bonds. In the 1950s and 1960s, Heidi Burow and Helga Fischer conducted pioneering observations on Konrad Lorenz’s colony in Seewiesen, Germany. (Nedelcu & Hirschenhauser, 2013).Their unpublished notes represent one of the earliest systematic attempts to describe pair bonds in birds. They identified key behavioural elements and examined partner interactions in contexts of affiliation, conflict, and reproduction. Central to their observations was the concept of “harmony” — consistency in partner behaviour, which appeared to predict reproductive success. Although their methodology did not meet modern scientific standards, their work

highlighted that, by the mid-20th century, researchers were already considering both behavioural and physiological bases of pair bond quality.

Contemporary research has advanced these early ideas. The concept of **hormonal compatibility** (within-pair hormonal covariance) describes synchrony between the hormonal profiles of partners. In greylag geese, testosterone and other steroid levels covary within pairs, and this hormonal synchrony is associated with cooperation, pair stability, and reproductive success (Hirschenhauser, 2012; Weiß et al., 2010). Importantly, compatibility is not a fixed property of a pair; rather, it reflects the dynamic state of the relationship. Under stress or conflict, hormonal synchrony decreases, which may predict declines in cooperation and, in extreme cases, pair dissolution (Nedelcu & Hirschenhauser, 2013).

Other physiological measures also support the link between pair bonds and fitness. Frigerio and colleagues have shown that the presence of a partner and family reduces physiological stress, increases digestive efficiency, and enhances offspring survival through coordinated parental behaviour (Szipl et al., 2019). These findings reinforce the view that pair bonds in greylag geese are more than social constructs: they are supported by physiological synchrony and confer measurable fitness benefits.

Vocalisation represents another mechanism potentially contributing to pair bond strength. Contact calls in greylag geese are thought to facilitate coordination and maintain partner proximity, especially in dynamic or challenging environments (Lesigang et al., in review). Despite their importance, systematic studies of vocal responsivity in greylag geese remain scarce, highlighting an important gap in the literature.

1.7 Aims and Predictions

The aim of this project is to assess patterns of strength and stability in pair bonds of greylag geese (*Anser anser*). Specifically, this study investigates (i) variation in within-pair responsivity (as a measure of strength), (ii) the correlation between within-pair responsivity and pair bond duration (as a measure of stability), and (iii) the influence of within-pair responsivity and pair bond duration on reproductive outcomes, including hatching and fledging success.

I predict that pair bonds will differ in responsivity, such that some pairs respond more consistently to their partner by following movements and answering contact calls. I further predict that higher bond strength — measured by following events, vocal responsivity to contact calls, and spatial proximity — will be positively associated with pair bond duration. Finally, I predict that higher within-pair responsivity will correspond to greater reproductive output, with more eggs laid, higher hatching success, and more fledged goslings. These predictions align with previous work linking behavioural coordination and pair bond dynamics to fitness outcomes (Maldonado-Chaparro et al., 2021; Rasmussen, 1981).

2. Methods

2.1 Study Site and System

I observed 21 male–female pair bonds in greylag geese (*Anser anser*) (Table S1). Same-sex pairs were not considered, as they do not contribute to reproductive success. Observations were conducted during feeding and non-feeding times at two sites. The first site was the Auingerhof (47.814028, 13.947539), where the flock typically overnighted and was fed by Konrad Lorenz Research Station (KLF) staff in the morning (0800) and afternoon (1700). The second site was Cumberland Wildpark Grünau (47.808282, 13.950712), where geese fly daily to be fed by tourists and engage in activities such as foraging, bathing, and social interactions.

Observations took place at three times of day: mornings at the KLF (0730–0900), midday at the Wildpark (1130–1400), and afternoons at the KLF (1700–1900), between September 2023 and February 2024. This schedule was designed to capture the main daily activities of geese, including feeding, preening, resting, and bathing. Each observation session lasted 10 minutes per pair bond. Observations were recorded directly in the field and video recorded. Videos were scored using *Solomon Coder by Andras Peter* (András Péter, https://solomoncoder.com).

From the recordings, I extracted three variables: (i) call responsivity, (ii) lead–follow behaviour, and (iii) spatial proximity. For each pair, data collection ranged from 250–500 minutes (approx. 25–50 data sets per individual, equivalent to 120–250 minutes). In total, 827 data sets were collected (8270 minutes). Each pair contributed on average X ± Y SE observations (range = X–Y).

2.2 Ethics Statement

This study complied with Austrian laws and local government guidelines, in accordance with the statutes of the University of Vienna on animal research. It was conducted under Animal Experiment License No. 66.006/0026-WF/V/3b/2014, issued by the Austrian Federal Ministry for Science and Research (EU Standard, equivalent to approval by an Animal Ethics Board). Observations were non-invasive, and the geese were habituated to human presence, as the flock has been monitored at the Konrad Lorenz Research Station since 1973.

2.3 Pair Bond Strength

Pair bond strength was measured using behavioural indicators of responsiveness to contact calls, following the partner, and spatial proximity. These were classified as either "behavioural states" or "behavioural events" (J. Silk et al., 2013).

2.3.1 Vocal Responsivity

Call responsivity was assessed by recording initiation and response to contact calls between partners. Four interaction types were coded:

- CC_MD: male initiates, female does not respond
- CC_MDF: male initiates, female responds
- CC_FD: female initiates, male does not respond
- CC_FDM: female initiates, male responds

The variable analysed, *call responsivity*, was the proportion of calls responded to out of the total number of contact call bouts (Table S2).

2.3.2 Movement Responsivity

Lead–follow behaviour was assessed by recording initiation of movement and partner response. Four interaction types were coded:

- F_MD: male walks away, female does not follow
- F_MDF: male walks away, female follows
- F_FD: female walks away, male does not follow
- F_FDM: female walks away, male follows

The variable analysed, *lead–follow behaviour*, was the proportion of instances in which an individual was followed by its partner, relative to the total number of times that individual initiated movement (Table S2).

2.3.3 Spatial Proximity

Spatial proximity was measured as the proportion of time a pair spent within two goose lengths of each other (Table S2).

2.4 Statistical Analyses

All analyses were conducted in R version 4.4.1 (R: The R Project for Statistical Computing, n.d.). Linear and generalized linear (mixed) models (LMMs, GLMMs) were calculated using the package **lme4** version 1.1-35.5 (Bates et al., 2015). Residual diagnostics for mixed models were assessed using **DHARMa** version 0.4.6 (Hartig, 2024). Results were visualised using **ggeffects** (Lüdecke, 2018) and **ggplot2** (Wickham, 2016)

451 *2.4.1 Within-Pair Responsivity: Differences Between Pairs*

452 To determine whether affiliative behaviours (call responsivity, lead–follow behaviour) were
453 repeatable and differed among pairs, I calculated adjusted repeatability (R) for all 21 pairs
454 using the package **rptR** (version 0.0.22; Stoffel et al., 2017). Pair ID was included as a random
455 effect and grouping variable, with fixed effects "call responsivity" and "movement
456 responsivity". Significance of R was tested with likelihood ratio tests, and 95% confidence
457 intervals were obtained using 1000 parametric bootstrap iterations (Nakagawa & Schielzeth,
458 2010)

459

460 *2.4.2 Within-Pair Responsivity: Association With Pair Bond Duration*

461 The association between call responsivity, lead–follow behaviour, and pair bond duration was
462 assessed using two GLMs: a binomial distribution for lead–follow behaviour and a
463 quasibinomial distribution for call responsivity.

464

465 *2.4.3 Within-Pair Responsivity: Association With Spatial Proximity*

466 To test associations between call responsivity, lead–follow behaviour, and spatial proximity, I
467 used two GLMs: quasibinomial for call responsivity and binomial for lead–follow behaviour.

468

469 *2.4.4 Within-Pair Responsivity: Clutch Size, Hatching, and Fledging Success*

470 The effect of pair bond strength on reproductive output was tested with LMMs and GLMMs.
471 LMMs assessed the relationship between call responsivity and number of eggs, as well as the
472 effect of combined affiliative behaviours on clutch size. GLMMs tested effects of call
473 responsivity and lead–follow behaviour on numbers of hatched and fledged goslings. Pair ID
474 was included as a random effect in all models.

475

3. Results

3.1 Within-Pair Responsivity: Differences Between Pairs

Call responsivity was not significantly repeatable (R = 0.01 ± Y, $P = 0.292$; Figure 1, Table 1). In contrast, lead–follow behaviour was significantly repeatable across pairs (R = 0.07, $P < 0.001$; Figure 1, Table 1).

3.2 Within-Pair Responsivity: Association With Pair Bond Duration

There was no significant correlation between pair bond duration and the proportion of call responsivity (estimate = –0.0089 ± Y, $P = 0.633$; Table 2a) or lead–follow behaviour (estimate = –0.0145 ± Y, $P = 0.559$; Table 2b).

3.3 Within-Pair Responsivity: Association With Spatial Proximity

Spatial proximity had a significant effect on lead–follow behaviour (estimate = 0.0028, $P = 3.49 \times 10^{-9}$; Table 2b, Figure 2). As proximity increased, the proportion of lead–follow behaviour also increased. By contrast, there was no significant association between spatial proximity and call responsivity (estimate = –0.00036, $P = 0.42$; Table 2a).

3.4 Within-Pair Responsivity: Clutch Size, Hatching, and Fledging Success

Within-pair call responsivity had no significant effect on clutch size (estimate = 0.612, $P = 0.282$; Table 3a), hatching success (estimate = 0.321, $P = 0.260$; Table 3b), or fledging success (estimate = –0.041, $P = 0.978$; Table 3c). Lead–follow behaviour also showed no significant effect on the number of eggs (estimate = –0.124, $P = 0.829$; Table 3a), hatched goslings (estimate = –0.246, $P = 0.354$; Table 3b), or fledged goslings (estimate = –1.138, $P = 0.368$; Table 3c). Similarly, spatial proximity had no significant effect on clutch size (estimate =

500 0.215, P = 0.699; Table 4a), hatching success (estimate = 0.020, P = 0.943; Table 4b), or
501 fledging success (estimate = –0.403, P = 0.748; Table 4c).
502
503 By contrast, pair bond duration was positively associated with reproductive output. The number
504 of eggs was significantly correlated with pair bond duration (estimate = 1.240, P = 0.041; Table
505 7, Figure S1), and there was a trend toward a positive association between pair bond duration
506 and the number of hatched goslings (estimate = 0.461, P = 0.123; Table 11, Figure S2).
507
508

4. Discussion

4.1 Summary of Main Findings

This study examined behavioural components of pair bond strength in greylag geese, focusing on vocal responsivity, movement responsivity, and spatial proximity. The aim was to test whether these behaviours varied across pairs and predicted reproductive success or pair bond duration.

Results showed that movement responsivity, but not vocal responsivity, was significantly repeatable across pairs, providing partial support for the hypothesis that behavioural responsivity can be pair-specific. Contrary to expectations, neither vocal nor movement responsivity was significantly associated with pair bond duration. However, movement responsivity was strongly correlated with spatial proximity, suggesting that physical closeness facilitates or reflects behavioural coordination. None of the behavioural components directly predicted reproductive success. By contrast, pair bond duration showed a positive correlation with clutch size, suggesting a possible indirect link between long-term stability and reproductive investment.

4.2 Interpretation and Theoretical Context

The absence of a direct link between behavioural responsivity and reproductive success may reflect the **food-supplemented, low-risk conditions** of the study population. Geese were free-ranging but received ad libitum food and experienced reduced predation pressure due to human presence. Under such benign conditions, selective pressures for tight behavioural coordination may be relaxed, enabling even moderately coordinated pairs to reproduce successfully.

Another explanation lies in behavioural compensation. In many monogamous species, one partner may increase investment when the other is less responsive, thereby maintaining pair function (Balshine et al., 2002). Such compensation could mask correlations between within-pair responsivity and reproductive outcomes. In long-lived species such as greylag geese, pair success may depend more on pre-existing compatibility than on short-term behavioural coordination (Kotrschal et al., 2010; Nedelcu & Hirschenhauser, 2013).

The results also suggest that movement responsivity may be a more reliable behavioural marker of pair coordination than vocal responsivity. Movement-based behaviours directly influence proximity and synchrony, whereas vocal signals may be more context-dependent (e.g., feeding vs. affiliative calls) and therefore less consistent. The low repeatability of vocal responsivity could reflect variability in call function or individual personality differences, underscoring the need for finer classification of call types in future studies.

4.3 Methodological and Contextual Limitations

Several limitations constrain the interpretation of these findings. First, data were collected during a single non-breeding season, restricting assessment of temporal stability—a core dimension of pair bond quality in long-term monogamous systems. Without multi-seasonal data, it remains unclear whether observed coordination reflects consistent traits or context-specific states. Second, individual-level factors such as age, reproductive experience, physiological condition, or health status were not controlled for. These variables may influence both coordination and reproductive outcomes, especially in a long-lived species. Third, behavioural measures—particularly vocal responsivity—may have been confounded by context. Contact calls can serve multiple functions (feeding, distress, affiliation), and their role in pair cohesion could not be systematically distinguished. Fourth, the **food-supplemented**

study setting provided ecological validity but may have reduced the need for strong coordination. In harsher conditions, tighter synchrony may be critical for survival and reproduction. Similarly, health-related stressors, including parasite infections and disease outbreaks, likely contributed to gosling mortality independent of pair behaviour. Finally, unusual climatic conditions during the breeding seasons studied (Ebensperger et al., 2014) resulted in exceptionally low gosling survival across the population, further limiting the ability to detect behavioural predictors of reproductive success. Together, these limitations suggest that the observed absence of behavioural effects on reproductive outcomes may reflect short study duration, benign ecological conditions, and high background mortality.

4.4 Comparison to Other Studies

These findings differ from research on other monogamous species. In zebra finches, behavioural coordination and personality matching predict reproductive outcomes and lower divorce rates (Adkins-Regan & Tomaszycki, 2007; Maldonado-Chaparro et al., 2021) In great tits, exploratory behaviour matching predicts chick condition and fledging success (Both et al., 2005), while in barn owls, hormonal synchrony predicts fledging numbers (Béziers et al., 2019)

Such differences may reflect species-specific ecology. Greylag geese form lifelong pair bonds, potentially relying less on short-term behavioural coordination once bonds are established. Compatibility may be based on intrinsic factors—morphological, hormonal, or cognitive—rather than behavioural synchrony that develops over time. Coordination in geese may also serve indirect functions, such as stress reduction (Scheiber et al., 2009), social support, or group stability, rather than directly enhancing reproductive success. These comparisons highlight that while behavioural coordination is widely recognized as a component of pair bond quality, its expression and functional relevance are strongly species- and context-dependent.

4.5 Future Directions

Future studies should adopt a multi-seasonal approach to assess both strength and stability of pair bonds. Longitudinal data spanning pair formation, breeding, and gosling-rearing phases are needed to test whether coordination is a persistent trait or context-dependent state. Integrating hormonal measures (e.g., corticosterone, testosterone) and personality profiling would provide a more mechanistic understanding of pair compatibility. Further, communicative behaviours—particularly vocalisations—should be classified into functional categories (affiliative, feeding, distress) to better capture their relevance to pair bonding. Advances in acoustic analysis will aid in refining these classifications. Given the role of disease in gosling mortality, health monitoring should be incorporated into long-term studies. A standardised parasite management protocol could reduce uncontrolled mortality and improve interpretation of behavioural effects on reproductive outcomes. Comparative analyses across Anatidae and other monogamous taxa would also help distinguish taxon-specific dynamics from general principles of pair bond quality.

4.6 Conclusion

This study contributes to our understanding of behavioural coordination in monogamous pair bonds by quantifying pair bond strength in greylag geese. Movement responsivity was repeatable across pairs and strongly associated with proximity, while vocal responsivity showed high variability and was not associated with pair bond duration or reproductive success parameters. None of the pair bond strength measures predicted reproductive outcomes, although longer pair bond duration was correlated with larger clutch size. These findings suggest that behavioural coordination may not directly determine reproductive outcomes in **food-supplemented, resource-rich environments**. Instead, coordination may contribute to long-term pair maintenance in subtler ways. This highlights the importance of distinguishing

608 between bond strength and bond stability, and the need for long-term, multimodal research to
609 clarify the mechanisms supporting long-term pair bonds in socially complex species.
610
611

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6. Figures and Tables

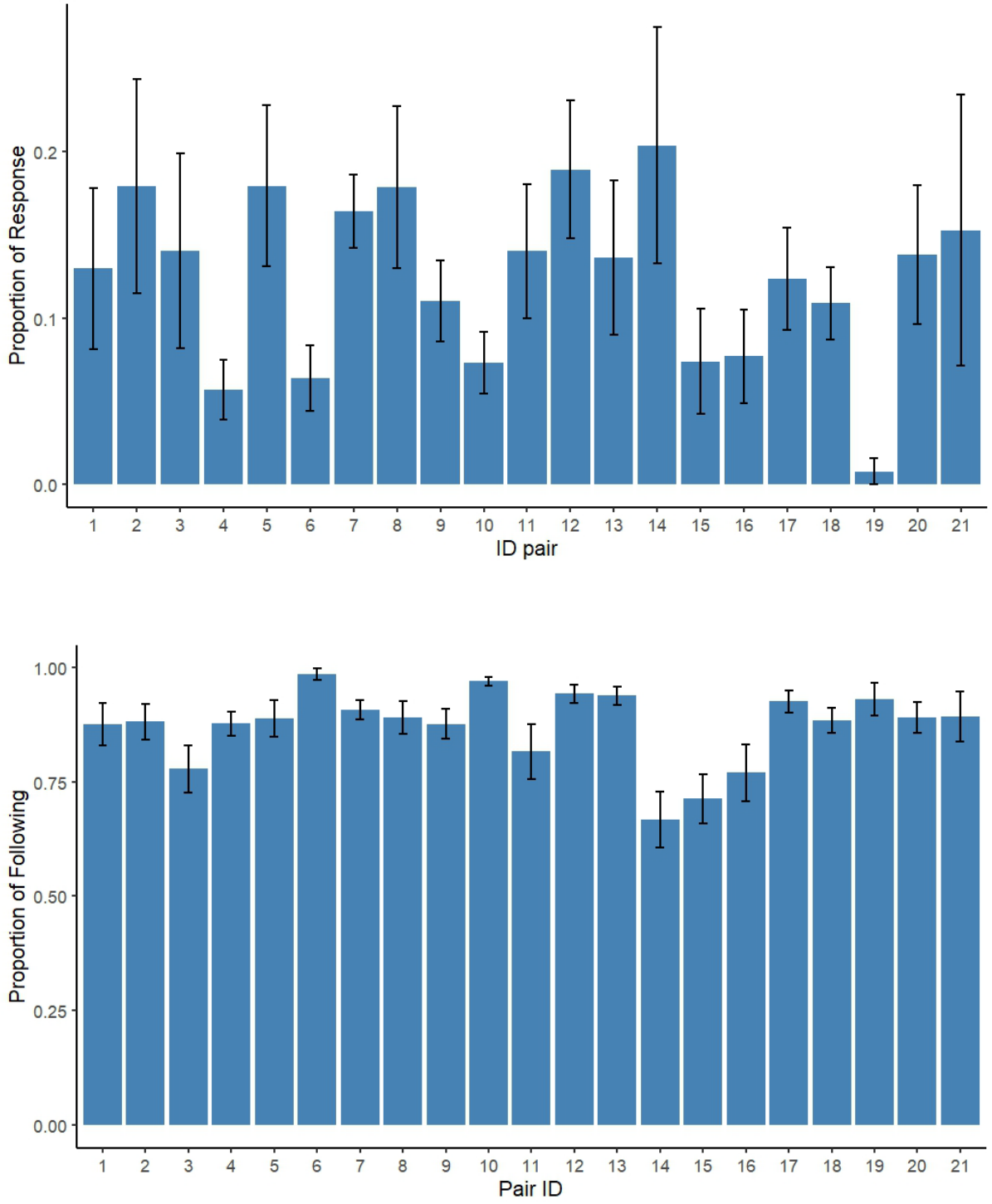

Figure 1. Adjusted repeatability (R) for (a) within-pair call responsivity and (b) lead–follow behaviour across 21 pair-bonded greylag geese (*Anser anser*). Call responsivity was defined as

867 the proportion of contact calls initiated by one partner that were answered by the other partner.
868 Lead–follow behaviour was defined as the proportion of movement events (one partner
869 walking away) that elicited a following response from the other partner. Data represent mean
870 ± SE for each pair across all observed pairs. Repeatability estimates were calculated using
871 mixed-effects models with pair ID as a random effect. Sample size: $N = 21$ pairs, with 827 total
872 observation sessions (8270 minutes of data).
873

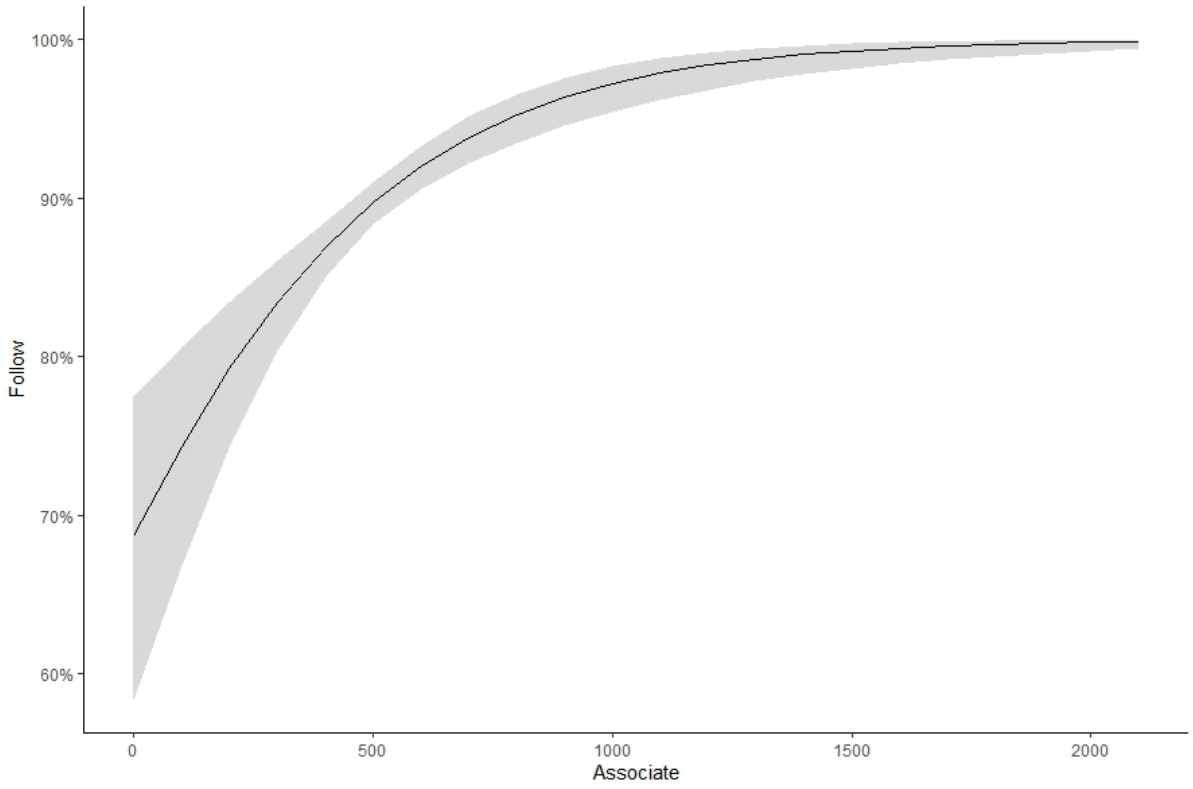

Figure 2. Association between spatial proximity and the proportion of lead–follow behaviour in 21 pair-bonded greylag geese (*Anser anser*). Spatial proximity was measured as the proportion of time a pair spent within two goose lengths of one another. Lead–follow behaviour was measured as the proportion of movement events in which one partner-initiated walking away and the other partner followed. The solid regression line represents the fitted relationship from a generalized linear model (binomial distribution), and the grey shading indicates the 95% confidence interval. Each point represents a pair-level mean across all observations. Statistical output for this model is provided in Table 2b. Sample size: $N = 21$ pairs, 827 total observation sessions.

Table 1. Adjusted repeatability (R) of within-pair call responsivity and lead–follow behaviour in greylag geese (*Anser anser*). Call responsivity was defined as the proportion of contact calls initiated by one partner that were answered by the other partner. Lead–follow behaviour was defined as the proportion of movement events in which one partner initiated walking away and the other partner followed. R values were estimated using mixed-effects models with pair ID as a random effect. SE = standard error of repeatability; CI = 95% confidence interval; LRT_P = *P*-value from likelihood ratio tests. Bold values indicate statistical significance ($P < 0.05$). Sample size: $N = 21$ pairs, 827 observation sessions (8270 minutes of data).

Behaviour	R	SE	2.5% CI	97.5% CI	LRT_P
Call responsivity	0.0132	0.0152	0	0.0519	0.292
Lead-follow behaviour	0.0694	0.0303	0.0162	0.134	**< 0.001**

Table 2. Generalized linear models (GLMs) testing the effects of spatial proximity and pair bond duration on (a) call responsivity and (b) lead–follow behaviour in greylag geese (*Anser anser*). Estimates are shown with standard error (SE), *t*-values, and *P*-values. Bold values indicate statistical significance ($P < 0.05$). Sample size: $N = 21$ pairs.

	Estimate	**SE**	**t-value**	**P**
a) Call responsivity				
Intercept	-1.48	0.25	-5.876	**< 0.001**
Proximity	< -0.001	< 0.001	-0.808	0.420
Pair bond duration	< -0.001	0.02	-0.478	0.633
b) Lead-follow behaviour				
Intercept	0.82	0.23	3.483	**< 0.001**
Proximity	0.31	< 0.001	5.907	**< 0.001**
Pair bond duration	-0.01	0.02	-0.585	0.559

Table 3. Effects of within-pair call responsivity and lead–follow behaviour on (a) clutch size (LMM), (b) number of hatched goslings (GLMM), and (c) number of fledged goslings (GLMM, Poisson distribution) in greylag geese (*Anser anser*). Pair ID was included as a random effect. SE = standard error; *Df* = degrees of freedom; *t/z* = test statistic. Bold values indicate statistical significance ($P < 0.05$). Sample size: $N = 21$ pairs.

a) Clutch size					
	Estimate	**SE**	**Df**	**t-value**	**P**
Intercept	4.37	0.55	16.17	7.965	**< 0.001**
Responsivity	0.61	0.55	18.43	1.109	0.282
Lead-follow behaviour	-0.12	0.56	15.18	-0.220	0.829
Pair bond duration	1.24	0.56	16.63	2.216	**0.041**
Year	-0.42	0.42	62.63	-1.022	0.311
b) Hatched goslings					
	Estimate	**SE**		**z-value**	**P**
Intercept	0.11	0.28		0.400	0.689
Responsivity	0.32	0.28		1.126	0.260
Lead-follow behaviour	-0.25	0.27		-0.927	0.354
Pair bond duration	0.39	0.35		1.111	0.267
Year	-0.06	0.30		-0.206	0.837
c) Fledged goslings					
	Estimate	**SE**		**z-value**	**P**
Intercept	-6.45	3.02		-2.135	0.033
Responsivity	-0.04	1.49		-0.028	0.978
Lead-follow behaviour	-1.14	1.26		-0.901	0.368
Pair bond duration	0.18	1.24		0.147	0.883
Year	-0.88	0.54		-1.630	0.103

910 **Table 4.** Effects of average proximity (time spent within two goose lengths) on (a) clutch size
911 (LMM), (b) number of hatched goslings (GLMM, Poisson distribution), and (c) number of
912 fledged goslings (GLMM, Poisson distribution) in greylag geese (*Anser anser*). Estimates are
913 shown with standard error (SE), *t/z*-values, and *P*-values. Bold values indicate statistical
914 significance ($P < 0.05$). Sample size: $N = 21$ pairs.

a) Clutch size					
	Estimate	**SE**	**Df**	**t-value**	**P**
Intercept	4.35	0.55	16.90	7.971	**< 0.001**
Proximity	0.21	0.55	17.14	0.393	0.699
Pair bond duration	1.22	0.55	17.37	2.200	**0.041**
Year	-0.47	0.41	63.42	-1.139	0.259
b) Hatched goslings					
	Estimate	**SE**		**z-value**	**P**
Intercept	-0.36	0.33		-1.091	0.275
Proximity	0.02	0.29		0.071	0.943
Pair bond duration	0.46	0.30		1.542	0.123
Year	-0.03	0.15		-0.182	0.856
c) Fledged goslings					
	Estimate	**SE**		**z-value**	**P**
Intercept	-7.16	2.99		-2.394	0.017
Proximity	-0.40	1.25		-0.322	0.748
Pair bond duration	0.16	1.25		0.130	0.897
Year	-0.88	0.55		-1.611	0.107

915

Supplementary Materials

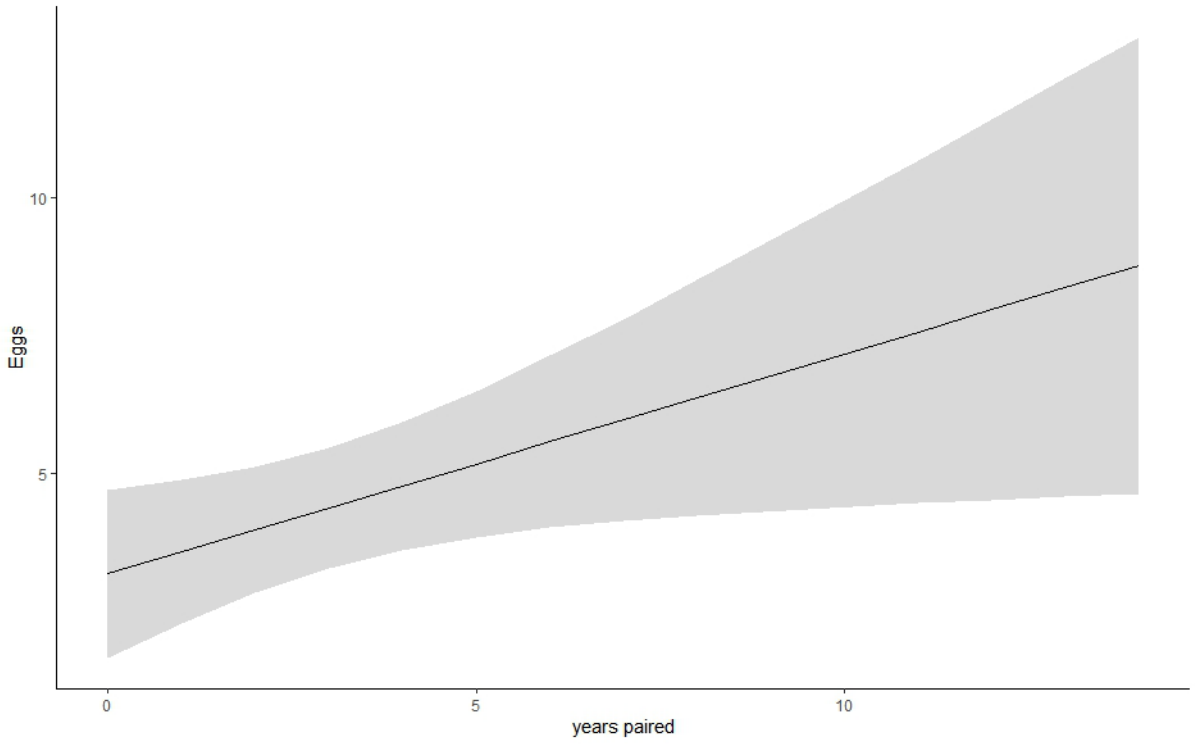

Figure S1. Relationship between pair bond duration (years paired) and clutch size (number of eggs) in greylag geese (*Anser anser*). The solid line represents the fitted relationship from a linear mixed model (LMM), and the grey shading indicates the 95% confidence interval. Each point represents the mean clutch size per pair. Pair ID was included as a random effect. Statistical output for this model is provided in Table 3. Sample size: $N = 21$ pairs.

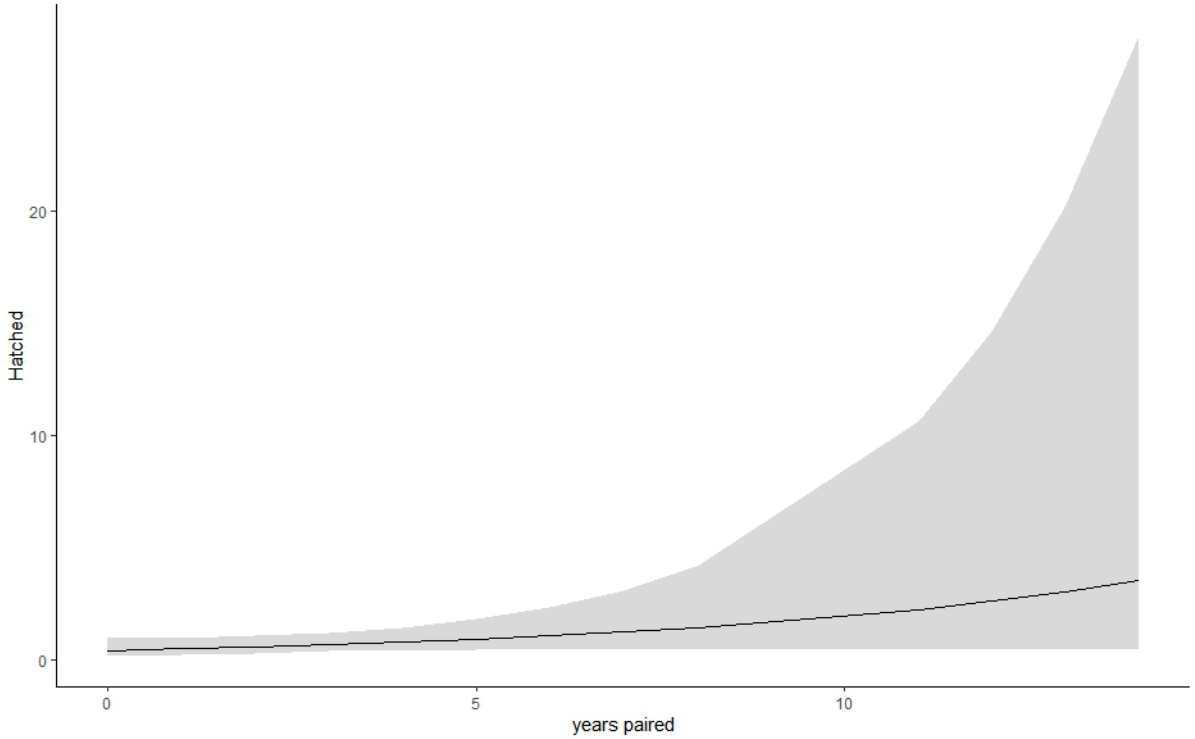

Figure S2. Relationship between pair bond duration (years paired) and the number of hatched goslings in greylag geese (*Anser anser*). The solid line represents the fitted relationship from a generalized linear mixed model (GLMM), and the grey shading indicates the 95% confidence interval. Each point represents the mean number of hatched goslings per pair. Pair ID was included as a random effect. Statistical output for this model is provided in Table 4. Sample size: $N = 21$ pairs.

930 **Table S1.** Summary of the 21 observed pair-bonded greylag geese (*Anser anser*), including
931 goose name, pair ID, hatch year, sex, and duration of pair bonding (years).
932

Goose Name	**Pair ID**	**Hatch Year**	**Sex**	**Duration of bonding (years)**
Erdbeere	1	2017	m	1
Lagertha	1	2018	f	1
Dimitri	2	2018	m	1
Ginny	2	2006	f	1
Oberlix	3	2020	m	1
Krümmel	3	2020	f	1
Pasha	4	2021	m	0.5
Bolzano	4	2022	f	0.5
Lumpy	5	2017	m	0.5
Trevor	5	2014	f	0.5
Jafar	6	2017	m	0.5
Ornella	6	2019	f	0.5
Besenstiel	7	2017	m	2
Olga	7	2019	f	2
Sherlock	8	2016	m	3
Lauri	8	2018	f	3
Babaco	9	2015	m	6
Dorothea	9	2015	f	6
Demant	10	2015	m	6
Lauffuß	10	2014	f	6
Jurek	11	2014	m	7
Batate	11	2015	f	7
Belmont	12	2007	m	3
Longshanks	12	2007	f	3
Bayou	13	2007	m	5
Luna	13	2008	f	5
Paso	14	2011	m	2
Kendo	14	2012	f	2
Kolibri	15	2011	m	3
Lotta	15	2014	f	3
Bernard	16	2008	m	13
Lukka	16	2008	f	13
Bruce Springsteen	17	2010	m	3
Lando	17	2009	f	3
Balantine	18	2009	m	4
Leia	18	2009	f	4
Lausbursch	19	2019	m	0.5
Frodo	19	2021	f	0.5
Kiki	20	2020	m	1
Ericsson	20	2020	f	1
Luzifer	21	2019	m	1
Sturmwind	21	2014	f	1

933 **Table S2.** Ethogram of behavioural variables used to assess pair bond strength in greylag geese
934 (*Anser anser*), including spatial proximity, vocal responsivity, and movement responsivity.
935

Assoc_1	distance between partners 1 length of goose
Assoc_2	distance between partners 2 length of goose
CC_MDF	male is calling initiator; female responds
CC_MD	male is calling initiator; female does not respond
CC_FDM	female is calling initiator; male responds
CC_FD	female is calling initiator; male does not respond
F_MDF	male is movement initiator; female follows
F_MD	male is movement initiator; female does not follow
F_FDM	female is movement initiator; male follows
F_FD	female is movement initiator; male does not follow

936